

Avian speciation and biodiversity in South-east Sulawesi, Indonesia: drivers of diversification

by

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B.A. (Mod.), Zoology, 2013

Volume I

A thesis submitted in partial fulfilment of
the requirements for the degree of
Doctor of Philosophy



School of Natural Sciences (Zoology)

Trinity College Dublin

The University of Dublin

2019



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Summary

Global biodiversity is poorly understood, despite its importance for humanity. As biodiversity loss reaches critical levels, greater knowledge of its distribution is needed to concentrate conservation efforts. Biodiversity can be measured at several levels, with the species typically the unit used in conservation planning. As resources for conservation are limited, a good knowledge of species diversity and distribution is needed for informed decision making. Attempts to set accurate conservation priorities face a number of prominent challenges; 1. species distributions are often poorly known, particularly in the tropics where the rate of biodiversity loss is highest, 2. the number of currently described species is known to be a huge underestimate, with many cryptic species awaiting formal description, and 3. much remains unknown about the drivers of speciation, particularly what adaptations are associated with population divergence in the early stages of the process. In this thesis I explore each of these main topics in a study system in South-east Sulawesi, in the biodiversity hotspot of the Wallacea region. I focus on the avifauna of the region, contributing to characterising the community composition of unstudied islands, assess the species status of island populations which have diverged from the mainland and provide insight into how adaptations to island life may drive population divergence.

In Chapters 2 and 3 we filled in some of the gaps in the knowledge of the avifaunal distribution in South-east Sulawesi on the previously unsurveyed islands of Kabaena, Muna and Wawonii, identifying potentially important populations, particularly for the Endangered Milky Stork *Mycteria cinerea*. Chapters 4 and 5 evaluated the diversification of the ‘great speciator’ taxa of South-east Sulawesi, assessing divergence in mitochondrial DNA, morphology and song in *Todiramphus* kingfishers and *Zosterops* white-eyes, lineages renowned for their wide range and propensity for speciation. We propose two new white-eye species, an isolated population descended from the widespread island coloniser the Lemon-bellied White-eye *Zosterops chloris*, the ‘Wakatobi White-eye’, and a single island endemic the ‘Wangi-wangi White-eye’. The ‘Wangi-wangi White-eye’ is a particularly intriguing new species, as its closest relatives are found >3000 km away in the Solomon Islands. Chapters 4 and 5 also discover other populations for further taxonomic refinement, the Wakatobi Islands Collared Kingfisher *Todiramphus chloris* population and Runduma Island Lemon-bellied White-eye populations may represent endemic subspecies for South-east Sulawesi.

Chapters 4-7 investigated different morphological adaptations that are associated with island colonisation and the early stages of speciation. Chapter 5 suggested that a reduced

dispersal ability, in comparison to source populations, may be a feature of populations of widespread island colonisers which become isolated. In Chapter 4 we discussed how potential differences in habitat, and associated increases in interspecific competition, may have driven a niche shift in Collared Kingfishers on the Wakatobi Islands. These ideas were investigated further in Chapters 6 and 7 with an assessment of the morphological niche hypervolume and population density of target species. Chapter 6 outlined how Lemon-bellied White-eyes had a larger morphological niche volume and greater population density in allopatry from the Pale-bellied White-eye *Zosterops consobrinorum*, on both a small island and in urban areas. These Lemon-bellied White-eye populations may have been experiencing density compensation due to greater access to resources in a species depauperate environment. Reduced interspecific competition, and greater intraspecific competition in high density populations, likely led to the increase in niche volume seen in the Lemon-bellied White-eye populations. This chapter highlights the potential for urban areas to act as ecological islands for island colonising edge species in the Indo-Pacific. Local endemic species are likely to lose out in human altered landscapes dominated by edge species. Chapter 7 looked at some of the effects of island colonisation on sexual dimorphism. Populations of Olive-backed Sunbirds *Cinnyris jugularis* on the small oceanic Wakatobi Islands showed greater sexual dimorphism and higher population density than those on the mainland and continental islands. However, this was not associated with an increase in morphological niche volume, in either sex, in the absence of mainland competitors, as is typically assumed to be the case. There was no difference in the niche volume of males from Wakatobi and mainland populations, but females from the Wakatobi Islands had a smaller niche volume than those from the mainland. Potentially, because females experience greater intraspecific competition in the high density populations of the Wakatobi Islands, their niche volume has contracted to reduce intersexual competition. Intersexual competition of this nature is likely an important factor shaping the evolution of island radiations of sexually dimorphic species.

This thesis illustrates how studying the populations of Indo-Pacific island colonisers, particularly the 'great speciator' lineages, provides the opportunity to contribute both taxonomic revision and insight into the early stages of speciation. Their rapid speed of evolutionary change, ability to colonise islands and the frequency with which they are found in secondary sympatry makes 'great speciators' ideal groups in which to study speciation. This work is given impetus by the looming biodiversity crisis that threatens not just Southeast Asia, but the whole world. Much biodiversity, and the evolutionary lessons it can teach us, faces extinction before being formally recognised.

Acknowledgements

My PhD has been an amazing journey which I have enjoyed from start to finish. This would not have been possible without my supervisors Nicola Marples and Dave Kelly. I owe them massive thanks for their support and advice at every stage and for giving me such freedom in my research. More than anything they introduced me to the wonderful world of birds! It's fundamentally all about the birds. We have made a great team. A big thanks also to my collaborators Kangkuso Analuddin and Adi Karya for their help and advice, particularly when working in the field in Indonesia.

The Department of Zoology has been a great environment in which to do a PhD, it never really felt like work. Ruth Kelly and Andrew Jackson must be given great credit for going above and beyond to contribute their knowledge to the community. Anna Csergő and the rest of the Biogeography Discussion Group provided stimulating discussion and the opportunity to collaborate on some cool ideas. Many a good vent was had with Maureen Williams since we started together in 2014. Sure we got there. The PhD certainly would not have been the same without Conor Owens, Thomas Guillerme and Luca Coscieme always being there to make sure my PhD never got in the way of my education.

Of course none of this would have been possible without money and licences! I would like to thank Kementerian Riset Teknologi Dan Pendidikan Tinggi (RISTEKDIKTI) for providing the necessary permits and approvals for this study, permit numbers: 0143/SIP/FRP/SM/VII/2010, 278/SIP/FRP/SM/VII/2012, 279/SIP/FRP/SM/VIII/2012, 174/SIP/FRP/E5/Dit.KI/V/2016, 159/SIP/FRP/E5/Fit.KIVII/2017 and 160/SIP/FRP/E5/Fit.KIVII/2017. I would also like to thank the Irish Research Council for funding my PhD, and Operation Wallacea and all their staff (in particular Tim Coles) for providing me with logistical and financial support in Indonesia.

I have been blessed with having brilliant co-workers throughout my PhD data collection. Huge thanks must go to the teams who put in the hard yards with me in the field, particularly Síofra Sealy, Adi Karya, Nur Fajrhi, Alex Delamer and Sulaiman La Ode. Their tireless efforts (such endless planter) are a credit to their endurance and psychological robustness. Huge credit must also go to Naomi Lawless for being effortlessly methodical in her stint with us in the lab. I would be remiss if I failed to give a shout out to my seabird brethren and all round academic muse Andrew Power, many a scheme was hatched over a warm can of cider while minding terns.

Finally a special thanks to my family for their unwavering support in everything. The industry of the O’Connell and Kenny clans has always inspired me, and put the labours of a PhD in perspective. My PhD is the culmination of my dad’s endless hard graft (‘tipping away’ as he calls it). My mam has the unenviable distinction of reading every piece of work I’ve ever produced. She has spotted a million typos and is now probably one of the foremost experts in the avifauna of South-east Sulawesi!

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1. General Introduction

1.1. Biodiversity monitoring and assessment

Biodiversity loss is one of the foremost challenges facing the planet today (Cardinale *et al.* 2012). This impending disaster places emphasis on the need for biodiversity monitoring, to understand the distribution of biodiversity and how this is changing (Pereira and Cooper 2006). Biodiversity can be measured at several levels (Proença *et al.* 2017), with species typically the primary unit used to assess and study biodiversity (Hillebrand *et al.* 2018). An accurate assessment of species diversity and distribution, and the conservation status of these species, is essential for setting conservation priorities (Isaac *et al.* 2004; Costello *et al.* 2015; Isaac and Pearse 2018; IUCN 2018) and identifying biodiversity hotspots (Myers *et al.* 2000; Mittermeier *et al.* 2011). While species, and to a lesser extent subspecies, are often used to set conservation priorities (Ando *et al.* 1998; Isaac *et al.* 2004; Zink 2004; Phillimore and Owens 2006; Zink 2016), current estimates of species diversity are known to be huge underestimates (May 2010; Mora *et al.* 2011; Costello *et al.* 2013). Efforts to catalogue this unrecognised biodiversity are given impetus by the fact that many species face extinction before being recognised (Pimm *et al.* 2014; Costello 2015). However, there is not universal agreement on what constitutes a species and how it should be delimited (de Queiroz 2007).

A range of species concepts have been developed by biologists seeking to understand this fundamental unit of classification; the biological, ecological, phylogenetic and phenetic species concepts among others, summarised in de Queiroz (2007). A unified or general lineage species concept has gained prominence in recent years (de Queiroz 2007; Fišer *et al.* 2018), particularly among avian taxonomists (Tobias *et al.* 2010; Barrowclough *et al.* 2016). This concept requires only that a population be an independently evolving lineage to be considered a separate species (de Queiroz 2007). By applying this criterion, Barrowclough *et al.* (2016) concluded that the number of bird species has been underestimated by at least a factor of two. Modern molecular tools have led to a huge increase in the number of such cryptic species being recognised (Beheregaray and Caccione 2007). Cryptic species have typically been unrecognised as they are phenotypically similar to species already recognised by taxonomic authorities (Bickford *et al.*, 2007). A large number of cryptic species have been recognised from a diversity of taxa in recent years (Mayer and Helversen 2001; Hebert *et al.* 2004a; Ibáñez *et al.* 2006; Fouquet *et al.* 2007; Kerr *et al.* 2007; Pfenninger and Schwenk 2007; Siler *et al.* 2011; Demos *et al.* 2014). While molecular methods have allowed cryptic populations to be uncovered, they

remain under-represented in biodiversity research (Bickford *et al.* 2007; Fišer *et al.* 2018) and the point at which species limits should be set remains controversial (Hebert *et al.* 2004b; Brower 2006; Carstens *et al.* 2013). A combined approach, utilising multiple lines of evidence, is recommended for species delimitation, and is typically required in avian taxonomy (Padiál *et al.* 2010; Tobias *et al.* 2010; del Hoyo *et al.* 2018d). In addition to providing the opportunity for taxonomic reassessment, speciation research allows us to gain insight into what constitutes a species and the evolutionary processes that promote and maintain diversity (Scheffer *et al.* 2006; Dennis and Hellberg 2010; Pedersen *et al.* 2018).

1.2. Drivers of diversification

Studying species traits gives great insight into where biodiversity is concentrated (Kluge and Kessler 2011) and how traits experience selection during the speciation process (Hoskin and Higgie 2010). Species will generally have a range of conditions which they can tolerate (Williams 1966; Logan *et al.* 2014; Nicolaus and Edelaar 2018). Adapting to different habitats within this range of conditions can have a significant impact on a species' traits (Ghosh-Harihar and Price 2014; Alberti *et al.* 2017b). If adaptive trait divergence is strong enough, it may also contribute to reproductive isolation between populations of a species in different habitats, a process known as Isolation By Adaptation (Nosil *et al.* 2009; Orsini *et al.* 2013). However reproductive isolation seldom occurs without an ecological barrier between populations, such as open water between islands or lowlands between mountains (Whittaker and Fernández-Palacios 2007; Caplat *et al.* 2016). Water barriers provide a stringent filter so that only species with strong dispersal abilities are successful island colonists, and the individuals that succeed in dispersing across the water barrier are typically stronger dispersers than an average individual in the source population (MacArthur and Wilson 1967; Mayr and Diamond 2001; Vasudev *et al.* 2015). Uncommon long-distance dispersal events (i.e. dispersal facilitated by a storm blowing sufficient colonist to an island) often lead to speciation and endemism in island clades, as the colonising population may not have sufficient dispersal ability to maintain gene flow with the source population (Matzke 2014).

In addition to being affected by their abiotic environment and resource availability, species traits are also affected by interspecific interactions (Lawrence *et al.* 2012). These interactions can be competitive, cooperative or predatory (Benítez-López *et al.* 2014; Walsh *et al.* 2016; Barker *et al.* 2017) and may affect a species' ability to access resources. Darwin (1859) proposed interspecific competition as a primary driver of diversification. Where species with very similar ecological niche requirements cannot co-exist, the weaker competitor will be

excluded (Hardin 1960; Pigot and Tobias 2013; Price *et al.* 2014). As direct competition may result in exclusion of the weaker competitor, selection would be expected to favour adaptations to minimise niche overlap between interspecific competitors and reduce direct competition in sympatry (Gause 1934; MacArthur and Levins 1967). These interactions are likely to be strongest between closely related species (McCormack *et al.* 2010; Reifová *et al.* 2011; Sottas *et al.* 2018), as the principle of phylogenetic niche conservatism means they are likely to have similar niches (Lee-Yaw and Irwin 2015). Phenotypic divergence of sympatric populations due to interspecific competition is known as ecological character displacement (Brown and Wilson 1956; Schluter and McPhail 1992; Stuart and Losos 2013). The reverse of character displacement is character release (Grant 1972; Arthur 1982; Dayan and Simberloff 2005). If a competitor is absent from an ecosystem, the remaining species may be able to expand their niche, to take advantage of the vacant niche space (Boag and Grant 1984; Bolnick *et al.* 2010).

Competition happens not only between species, but within them (Doebeli 2011; Meiri *et al.* 2014). Intraspecific competition has been shown to be at its strongest in high-density populations, typically in species-depauperate islands (Robinson-Wolrath and Owens 2003; Pafilis *et al.* 2009). This has been associated with increased body size, likely a result of larger individuals having greater success in intraspecific agonistic encounters (Robinson-Wolrath and Owens 2003). Intraspecific competition has also been shown to select for a wider ecological niche in a population (Svärdson 1949; Roughgarden 1974; Svanbäck and Bolnick 2007). Several studies have shown that populations with wider overall ecological niches are not made up of generalist individuals, all exploiting the same wide niche, but a diversity of individual specialists (Bolnick and Doebeli 2003; Sargeant 2007; Sheppard *et al.* 2018). Such diversification is driven by selection in high density populations favouring the exploitation of novel resources that are not being utilised by intraspecific rivals (Svanbäck and Bolnick 2005; Svanbäck and Bolnick 2007). In sexually dimorphic species, greater intraspecific competition can take the form of strong intersexual competition (Selander 1966). This promotes selection for sexual dimorphism between males and females in body size or feeding morphology, facilitating resource partitioning between the sexes (Slatkin 1984; Shine 1989; Bolnick and Doebeli 2003; Temeles *et al.* 2010) and increasing the overall niche space occupied by a species (Butler *et al.* 2007).

1.3. Speciation and biodiversity research in the Indo-Pacific

Islands have long been of great importance to research into evolution and speciation (Darwin and Wallace 1858; Darwin 1859). They are discrete geographical units that may contain isolated populations, the key component of allopatric speciation, which is the most common mode of speciation (Phillimore *et al.* 2008a). The Indo-Pacific, in particular, has been central to the development of many fundamental ideas underpinning speciation and island biogeographical research, due to the number and diversity of islands that span the region (Mayr 1942; Wilson 1961; Diamond 1974; Diamond *et al.* 1976). Modern molecular methods have allowed many Indo-Pacific radiations to be investigated, uncovering much cryptic diversity (Lohman *et al.* 2010; Andersen *et al.* 2015a), providing an insight into the effects of island colonisation (Clegg and Phillimore 2010; Leisler and Winkler 2015) and allowing the patterns of island colonisation to be determined (Cibois *et al.* 2011; Cibois *et al.* 2014).

The 'great speciator' lineages of the Indo-Pacific, taxa renowned for their large geographic ranges and rapid diversifications, have proved particularly important study species (Diamond *et al.* 1976). Mayr and Diamond (2001) developed the 'great speciator' concept for their study system in Northern Melanesia. It describes a group of birds with high inter-island geographic variation, including diverse taxa found across many islands (e.g. Louisiade White-eye *Zosterops griseotinctus*, Moluccan Dwarf Kingfisher *Ceyx lepidus*, Australian Golden Whistler *Pachycephala pectoralis* and Collared Kingfisher *Todiramphus chloris*). Their rapid speed of evolutionary change and ability to colonise islands have made them an ideal group in which to study evolutionary change. Research into 'great speciator' lineages has given much insight into the mode and tempo of speciation (Moyle *et al.* 2009; Andersen *et al.* 2015b) and shown these lineages to be made up of multiple independent species (Andersen *et al.* 2013; Andersen *et al.* 2014). 'Great speciators' have also provided the opportunity to study what causes lineages which spread so readily to then go on to form isolated endemic species, and why their dispersal ability does not prevent the populations differentiating (Jønsson *et al.* 2014; Pedersen *et al.* 2018). This research has begun to outline the morphological adaptations that are associated with this process (Irestedt *et al.* 2013; Pedersen *et al.* 2018). The frequency with which 'great speciators' are found in secondary sympatry with close relatives allows investigation of the effect of species interaction on diversification. Such closely related species typically have to segregate by habitat choice (Diamond and Marshall 1977; Andersen *et al.* 2013; Sottas *et al.* 2018) or partition ecological niche (Gill 1971; Grant and Grant 2006; Wijesundara and Freed 2018) in order to avoid direct competition (Hardin 1960).

1.4. Avian diversity in Sulawesi

“We now come to the Island of Celebes, in many respects the most remarkable and interesting in the whole region, or perhaps on the globe, since no other island seems to present so many curious problems for solution.”

Wallace (1876)

In the heart of the Indo-Pacific, Sulawesi (Celebes) has been of great interest to naturalists, since the pioneering work of Alfred Russel Wallace (Wallace 1860; Wallace 1869). Due to its unique biogeographic position at the intersection between Asian and Austral flora and fauna (Esselstyn *et al.* 2010) and its extended period of geological isolation from continental landmasses (Watling 1983), Sulawesi has particularly high endemism (Michaux 2010). The unique faunal composition of this biogeographical region makes it one of the world’s top 25 biodiversity hotspots (Myers *et al.* 2000). It also remains relatively poorly studied (Cannon *et al.* 2007) and several novel species have been found on Sulawesi in recent years (Rasmussen 1999; Indrawan and Rasmussen 2008; Esselstyn *et al.* 2012; Harris *et al.* 2014).

The south-eastern peninsula of Sulawesi provides an excellent study system to test the effects of island life on isolated populations (Figure 1.1). There are continental islands (Buton, Muna, Kabaena and Wawonii) which were connected to Sulawesi at the time of the last glacial maximum, around 20,000 years ago (Voris 2000) and oceanic islands (the Wakatobi Islands and Runduma Island) which have never been connected to the Sulawesi mainland (Milsom and Ali 1999; Carstensen *et al.* 2012). The region has been fruitful for recent speciation research. While the Wakatobi Islands are only separated from Buton by 27 km, they are home to six endemic bird subspecies (Kelly and Marples 2010; Collar and Marsden 2014) and a proposed new species (Kelly *et al.* 2014). Kabaena Island, only 16 km from the mainland, is also home to an endemic subspecies of Red-backed Thrush *Geokichla erythronota kabaena* (Robinson-Dean *et al.* 2002). It is likely that there remains much uncharted biodiversity in the region, as the avifaunas of the islands are almost unknown, with only Buton Island receiving thorough scientific surveys (Catterall 1996; Martin *et al.* 2012; Martin *et al.* 2015; Martin *et al.* 2017). In addition the island populations in the region have not been investigated with modern taxonomic methods (though see, Kelly 2014; Kelly *et al.* 2014). South-east Sulawesi is home to a number of island bird lineages known for their tendency to diversify, including the ‘great speciator’ lineages *Todiramphus* and *Zosterops* (including a potentially unrecognised single island endemic, the

'Wangi-wangi White-eye' (Eaton *et al.* 2016)). The need for urgent action to document and conserve the biodiversity of South-east Sulawesi is given impetus by the widespread degradation and homogenisation of habitats in the region (Kelly and Marples 2010; Martin *et al.* 2012; Martin *et al.* 2019).

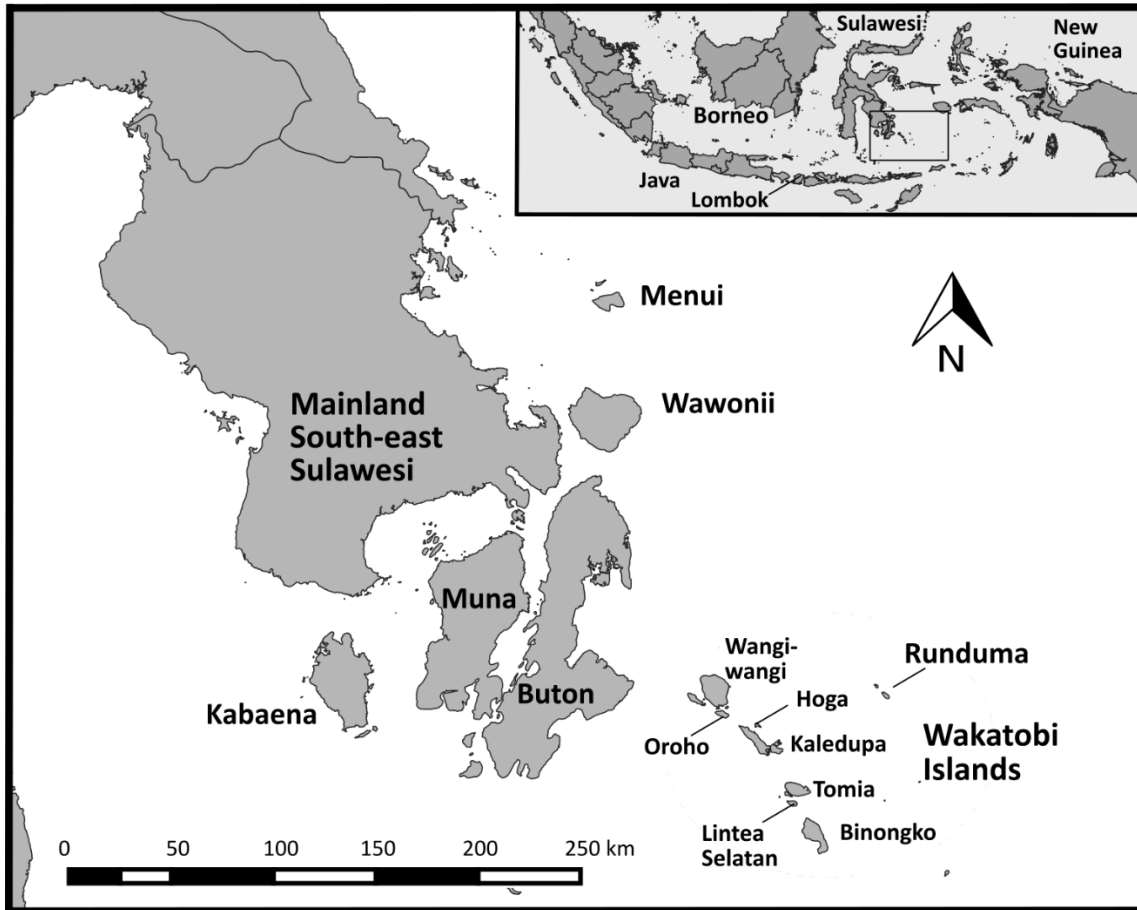


Figure 1.1: The islands of South-east Sulawesi. The main panel shows the core study area of this thesis. The inset panel shows the wider region.

1.5. Thesis structure

In this thesis, I explore speciation and biodiversity in the South-east Sulawesi region, with a particular focus on the 'great speciator' lineages *Todiramphus* and *Zosterops*. I investigate biodiversity, and the processes that maintain and promote it, in three broad ways:

- 1) **Avian community composition:** a species list was produced for the first time for the islands of Kabaena, Muna and Wawonii (Chapters 2 and 3), with an assessment of the abundance and conservation status of the populations monitored. This allowed us to

place our subsequent results in the context of the avian community present in our study sites.

- 2) **Patterns of species diversification:** the diversification and speciation of the ‘great speciator’ taxa of South-east Sulawesi, *Todiramphus* and *Zosterops*, was investigated using multiple measures to draw taxonomic divisions and examine the early stages of speciation (Chapters 4 and 5). The patterns of diversification were interpreted to explore the processes that drive speciation.
- 3) **Island effects on niche and abundance:** the morphological niche and abundance of island colonising taxa was investigated (Chapters 6 and 7) on both geographical and ecological islands. An assessment was made of how the observed patterns conformed to the expectations for island colonising populations, and the relationship between population abundance and morphological niche was explored.

1.5.1 Chapter 2 - The avifauna of Kabaena Island, South-east Sulawesi, Indonesia

While the avifauna of the Wakatobi Islands have received some attention (Hartert 1903; Kelly and Marples 2010) and Buton Island has been well surveyed (van Bemmelen and Voous 1951; Schoorl 1987; Catterall 1996; Martin *et al.* 2012; Martin *et al.* 2015; Martin *et al.* 2017), the avifauna of Kabaena Island was virtually unknown in the literature. This chapter outlines the bird community of Kabaena, finding 89 species, four of which are of conservation concern.

1.5.2 Chapter 3 - The avifauna of Muna and Wawonii Island, with additional records from mainland South-east Sulawesi, Indonesia

Much like Kabaena Island, Wawonii Island has been almost completely unknown to the scientific literature. Muna Island has also received little biodiversity monitoring and has been heavily developed since it was last assessed (van Bemmelen and Voous 1951). Mainland South-east Sulawesi is known to be home to some areas of high biodiversity (Wardill *et al.* 1998), but much of the peninsula remains unknown, with little site specific information apart from a few scattered records of individual species (Kelly *et al.* 2010; Trochet *et al.* 2014). This chapter outlines the bird community of sites on these islands, providing the first scientific assessment of the avifauna of Wawonii. It provides much needed information on the avifauna of Muna Island and the south-east peninsula of Sulawesi, finding 121 species in total, five of which are of conservation concern.

1.5.3 Chapter 4 - Diversification of a 'great speciator' in the Wallacea region: differing responses of closely related resident and migratory kingfisher species (Aves: Alcedinidae: *Todiramphus*)

The Collared Kingfisher species complex is the most widespread of the 'great speciator' lineages of the Indo-Pacific. As a result of this rapid diversification and excellent colonising ability *Todiramphus* species are often found in secondary sympatry. In South-east Sulawesi, Indonesia, two *Todiramphus* species are present, the breeding resident Collared Kingfisher *Todiramphus chloris* and the over-wintering migrant Sacred Kingfisher *Todiramphus sanctus* (Figure 1.2). We investigated the effect of isolation on these closely related species by comparing two populations: one on the mainland and the other on the small, oceanic Wakatobi Islands. We found that populations of Collared Kingfisher on the Wakatobi had diverged from those on mainland Sulawesi, differing both in morphology and mitochondrial DNA. In contrast there was no divergence between the corresponding Sacred Kingfisher populations in either morphology or mitochondrial DNA. We propose that a difference in habitat occupied by Collared Kingfisher populations between the mainland and continental islands versus oceanic islands, has caused this divergence. Mainland Collared Kingfishers are predominately found inland, while Wakatobi Collared Kingfishers are also found in coastal habitats. The larger body size of Wakatobi Collared Kingfisher populations may be a result of niche partitioning with predominantly coastal Sacred Kingfisher populations. Sacred Kingfishers show consistent habitat choice throughout South-east Sulawesi, and their migratory lifestyle means they are less likely to experience selection for adaptations to local conditions on the Wakatobi Islands than resident Collared Kingfishers.



Figure 1.2: photos of the *Todiramphus* species studied. Sacred Kingfisher *Todiramphus sanctus* (right panel) and Collared Kingfisher *Todiramphus chloris* (left panel). Photo credits Darren O'Connell and Nicola Marples.

1.5.4 Chapter 5 - A sympatric pair of undescribed white-eye species with very different origins

White-eyes are amongst the fastest evolving vertebrate groups. The *Zosterops* genus contains both widespread 'supertramp' species and a high proportion of single island endemics (van Balen 2018a). Therefore they exemplify the paradox of the 'great speciators'; what causes lineages which spread so readily, to then go on to form isolated endemic species and why does their dispersal ability not prevent the populations differentiating (Diamond *et al.* 1976)? We investigated the evolutionary history of white-eye species in South-east Sulawesi (Figure 1.4), using mitochondrial DNA, morphometric, song and plumage analyses, to draw species limits and assess which techniques offer best resolution. Our investigation revealed the 'Wangi-wangi White-eye' is indeed a novel *Zosterops* species, >3000km from its closest relative. Additionally, we demonstrated unanticipated biodiversity in the alleged 'supertramp' Lemon-bellied White-eye *Zosterops chloris* and propose the Wakatobi Islands subspecies (*Z. c. flavissimus*) deserves promotion to full species status, the 'Wakatobi White-eye'. We also provide the first assessment of the Pale-bellied White-eye *Zosterops consobrinorum*. By integrating multiple measures we confirmed its current taxonomy, showing it to be monotypic. We consider the different populations of white-eyes assessed in light of the taxon cycle concept, and provide evidence for reduced dispersal ability in the isolated *Z. c. flavissimus* population in comparison to mainland Lemon-bellied populations, and greater dispersal ability in a Lemon-bellied White-eye population that recently colonised an isolated oceanic island. These results indicate the

possibility that rapid shifts in dispersal ability may explain the paradox of ‘great speciator’ lineages.



Figure 1.3: photos of the *Zosterops* species studied. The right column shows the Pale-bellied White-eye *Zosterops consobrinorum* (top right) and ‘Wangi-wangi White-eye’ *Zos. sp. nov.* (bottom right). The left column shows the Lemon-bellied White-eye *Zosterops chloris*, with the *Z. c. intermedius* subspecies (Muna Island, top left) and *Z. c. flavissimus* subspecies (Wakatobi Islands, bottom left). Photo credits Nicola Marples and David Kelly.

1.5.5 Chapter 6 - Island-like processes in urban populations of a ‘great speciator’

While Chapter 5 outlined the taxonomic divisions in the Lemon-bellied White-eye lineage across South-east Sulawesi, there are more subtle patterns of differentiation within these taxonomic units. Kelly (2014) found evidence of ecological character displacement in the Wangi-wangi population of *Z. c. flavissimus* in the presence of a congeneric competitor, the ‘Wangi-wangi White-eye’. The Wangi-wangi population had a shorter bill length in comparison to a population

of *Z. c. flavissimus* on Oroho Island, which did not experience the same competitive pressure. In this chapter we investigated whether there was evidence of similar competitively mediated selection in populations of Lemon-bellied White-eyes, when in sympatry or allopatry with another congeneric competitor, the Pale-bellied White-eye. Lemon-bellied White-eyes are the sole white-eye species on small islands and in urban areas. They are replaced by Pale-bellied White-eyes inland on larger islands. The two species were found in sympatry in a thin coastal strip on large islands. We used n -dimensional hypervolumes, incorporating multiple traits, to represent morphological niche. Lemon-bellied White-eyes had a larger morphological niche hypervolume and denser populations when in allopatry, whether on a small island or in urban areas. Pale-bellied White-eyes were unaffected by the presence or absence of Lemon-bellied White-eyes suggesting that they are likely the dominant competitor. This chapter documents a potential case of character release in Lemon-bellied White-eyes in the absence of a congeneric competitor, and illustrates island-like processes in species-depauperate urbanised areas.

1.5.6 Chapter 7 - Female birds crowded out by males on small islands: niche contraction in dense populations of Olive-backed Sunbirds is asymmetric.

In Chapter 5 we illustrated that the Wakatobi Islands population of Lemon-bellied White-eyes (*Z. c. flavissimus*) likely deserves recognition as a separate species. The next most common small passerine species on the Wakatobi Islands is the Olive-backed Sunbird *Cinnyris jugularis*. Kelly (2014) investigated the Wakatobi Olive-backed Sunbird subspecies *C. j. infrenatus* and found that it had only diverged sufficiently from the mainland Sulawesi subspecies *C. j. plateni* to be considered an 'incipient species'. It may simply be that the Olive-backed Sunbird has had less time to diverge on the Wakatobi Islands, or is a species that is less prone to diverge in isolation. However Bolnick and Doebeli (2003) proposed that the same selection pressures that can lead to speciation, can alternatively lead to greater sexual dimorphism in dimorphic species like the Olive-backed Sunbird. Change in the level of sexual dimorphism in a species is a common feature of island radiations. This is often interpreted as ecological release from interspecific competitors absent from small islands, coupled with an increase in the level of intraspecific competition in denser island populations. Therefore to provide greater insight into the diversification of the Olive-backed Sunbird populations on the Wakatobi Islands, we investigated whether they showed greater sexual dimorphism than mainland populations. We found that Olive-backed Sunbirds on the Wakatobi Islands showed greater sexual dimorphism than those on the mainland and continental islands, as males and females overlapped less in morphological niche. Further investigation showed that this increase in sexual dimorphism was associated with a decrease in morphological niche volume for Wakatobi Islands females in comparison to the

mainland, but no change for males between populations. We found no evidence of increased niche volume in the absence of interspecific competitors. Wakatobi populations of Olive-backed Sunbirds were significantly denser than mainland populations, suggesting that intraspecific competition in denser island populations may be playing a role in increased sexual dimorphism, and that the smaller sex (females) may have contracted niche to avoid intersexual competition with the larger sex (males).



Figure 1.4: photos of the Olive-backed Sunbird *Cinnyris jugularis*. The right column is the Wakatobi Islands subspecies *C. j. infrenatus*, showing a male (top right) and female (bottom right). The left column is the mainland Sulawesi subspecies *C. j. plateni*, showing a male (top left) and female (bottom left). Photo credits David Kelly, Nicola Marples and Seán Kelly.

1.5.7 Chapter 8 - Discussion

In the final chapter of my thesis I draw general conclusions, discuss the importance of studying speciation and the key role the island radiations of the Indo-Pacific play in this, and outline future avenues of research.

1.6. Additional Work

In addition to the chapters enclosed in this thesis, my PhD provided me the opportunity to contribute to a number of other research projects. Published work from these contributions are listed below:

1.6.1 Biodiversity of South-east Sulawesi

I provided data and feedback on drafts for these collaborative papers led by Dr Tom Martin of Operation Wallacea.

Martin, T.E., **O’Connell, D.P.**, Kelly, D.J., Karya, A., Analuddin, K. and Nicola Marples (2018) Range extension for Dwarf Sparrowhawk (*Accipiter nanus*) in South-east Sulawesi – is it really restricted to upland forests? *BirdingASIA*. **29**: 103-104. Available at: <https://bit.ly/2KZhh89>

Martin, T.E., Monkhouse, J., **O’Connell, D.P.**, Analuddin, K., Karya, A., Priston, N.E.C., Palmer, C.A., Harrison, B., Baddams, J., Mustari, A.H., Wheeler, P.M. and Tosh, D.G. (2018) Distribution and status of threatened and endemic marsupials on the offshore islands of south-east Sulawesi, Indonesia. *Australian Mammalogy*, **41** (1): 76-81. doi: 10.1071/AM17052.

1.6.2 Seabird ecology

I led the data collection, analysis and writing of two papers addressing aspects of the ecology, and conservation management, of a seabird species of conservation concern.

O’Connell, D.P., Power, A., Keogh, N.T., McGuirk, J., Macey, C. and Newton, S.F. (2015) Egg fostering in Little Terns (*Sternula albifrons*) in response to nest abandonment after a depredation event. *Irish Birds*, **10** (2): 159 – 162. Available at: <https://goo.gl/qzd1SP>.

O’Connell, D.P., Power, A., Doyle, S. and Newton, S.F. (2014) Nest movement by Little Terns (*Sternula albifrons*) and Ringed Plovers (*Charadrius hiaticula*) in response to inundation by high tides. *Irish Birds*, **10** (1): 19 – 22. Available at: <https://goo.gl/gC9FY1>.

2. The avifauna of Kabaena Island, South-east Sulawesi, Indonesia

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Author contributions: DOC, DJK, NMM, KA, AB and AK conceived this study. DOC, DJK, NMM, SS and AK carried out field work. SS and FOM searched the literature for historical records. DOC and SS led the writing. All authors contributed to revising and improving the manuscript.

Status: This manuscript has been published in Forktail (2017) 33: 40-45.

Available at <https://bit.ly/2Aw1A8c>

2.1. Abstract

Kabaena is a satellite island of mainland Sulawesi, located off the south-east peninsula. Despite the relatively extensive surveys on the nearby larger islands of Buton and Muna, Kabaena has remained ornithologically neglected. Researchers visited the island several times between 1999 and 2016 to collect data for avian biogeographic research. Data collection between 1999 and 2003 focused mainly on mist-netting small passerines. The 2016 expedition focused on transect surveys, allowing for a wider assessment of the island's avifauna. During these visits all bird species encountered were recorded, providing the first scientific assessment of the avifauna of Kabaena. In total 89 species were recorded, of which 27 are regional endemics, three are classified as Near Threatened and one as Endangered.

2.2. Introduction

Since the pioneering work of Alfred Russel Wallace, Wallacea has been of great interest to naturalists (Wallace 1860; Wallace 1869). The unique faunal composition of this biogeographical region makes it one of the world's top 25 biodiversity hotspots (Myers *et al.* 2000). Sulawesi, the largest island in Wallacea, is an important centre of endemism in the region (Michaux 2010). However, it possesses a relatively depauperate avifauna compared to some smaller Indonesian islands such as Java, but boasts a high degree of endemism (BirdLife International 2016a) due to an extended period of geological isolation from continental landmasses (Watling 1983). The island's east and south-east peninsulas, including their satellite islands, have received little attention from ornithologists relative to the north, south and central provinces. Extensive ornithological surveying has yet to be carried out in much of South-east Sulawesi (White and Bruce 1986; Rheindt *et al.* 2014).

Kabaena is the third-largest satellite island (873 km²) of South-east Sulawesi and lies 18 km south of the south-east peninsula (Figure 2.1). The island is rugged, with a central mountainous region of limestone and igneous material with a maximum altitude of 1,570 m. Although accounts from the nearby islands of Buton (Butung) and Muna have been published from the colonial period to the present (Hartert 1903; van Bemmelen and Voous 1951; Schoorl 1987; Catterall 1996; Martin *et al.* 2012), none of these surveys included Kabaena. This is surprising, given its proximity, and may be a result of logistical constraints. Currently the primary ornithological information on Kabaena comes from White and Bruce (1986) who noted that Kabaena is '[almost] ornithologically unknown'. In their species accounts, White and Bruce (1986) mentioned only four species 'known to occur' on Kabaena: Jerdon's Baza *Aviceda jerdoni*, Grey-rumped Treeswift *Hemiprocne longipennis*, Sulawesi Cicadabird *Coracina morio* and Black-naped Oriole *Oriolus chinensis*. Coates and Bishop (1997) repeated the same four in their accounts, although neither of these authors revealed the source(s) of these data. Three of these species have been recorded on Kabaena in the modern era, the only exception being the Near Threatened Jerdon's Baza, although Catterall (1996) recorded it on Buton. Aside from this, very little ornithological information is available for Kabaena and the only other published information on the avifauna of the island is the discovery of a new endemic subspecies of Red-backed Thrush *Zoothera erythronota kabaena* (Robinson-Dean *et al.* 2002).

The islands of Kabaena, Muna and Buton are presently separated from each other and the mainland by shallow seas, but historically these islands have been linked during earlier glacial periods (Millsom and Ali 1999; Carstensen *et al.* 2012). As a result, the islands would be

expected to have comparable avifauna, however some variation in Kabaena's avifauna may be expected due to Kabaena's different geology. The underlying geology of the island is an unusual combination of pompango schist and ultramafic rocks, whereas the larger islands of Muna, Buton and the extreme southern tip of Sulawesi's south-east peninsula are mostly comprised of sedimentary rock (Hall and Wilson 2000). This difference in the underlying geology of Kabaena, in comparison to neighbouring islands, might be expected to lead to significantly different flora on this island (Hall and Wilson 2000). However extensive floral surveys have not been undertaken to confirm this, though two new plant species have been described for Kabaena suggesting that the flora of the island does show at least some distinctiveness (Keim 2009; Low 2013). In contrast to Kabaena, Muna has a maximum altitude of only 250 m, whilst the highest part of Buton, the largest of the three islands, attains 1,100 m. It is possible that this geological difference has caused significant differences in the flora and fauna of Kabaena in comparison to its neighbours. Kabaena, Buton and Muna have a tropical climate with temperatures ranging from 22-32°C; there is a dry season between June and September and a rainy season between December and March (Whitten *et al.* 1987). The mountainous centre and less accessible valleys of Kabaena hold areas where relatively undisturbed forest persists (Gillespie *et al.* 2005; Tweedley *et al.* 2013). However much of the lowlands has been deforested and the remaining vegetation is characterised by open forest, savannah woodlands and grasslands occurring on exposed ridges (Gillespie *et al.* 2005).

The main purpose of the field expeditions to Kabaena between 1999 and 2016 was to gather data for biogeographical research being carried out by DOC, DJK, NMM, KA, AB and AK. However all avian species encountered were recorded in order to better understand the island's avian community structure. This paper provides the first scientific assessment of the avifauna of Kabaena and details a number of geographical range extensions, which were recorded during this fieldwork.

2.3. Methods

Records of Kabaena's avifauna were primarily collected during line transect surveys in June 2016. Although the primary purpose of the 1 km long transects was to gather behavioural data from a guild of small passerines (Nectariniidae, Dicaeidae and Zosteropidae), all bird species seen or heard were recorded. Data were collected by DOC, AK and SS between 06h00-08h30 and 15h15-17h30 each day. Observations were made using 8 × 42 binoculars. During the 2016 field season, 110.4 hours of transect surveying was carried out covering 35 routes, each

surveyed in the morning and evening. Informal observations were also recorded whenever sightings were made e.g. during exploration of new sites and when undertaking floral surveys.

The areas surveyed were in the vicinity of the villages of Enano (10 transect routes), Tangkeno (11 transect routes) and Sikeli (14 transect routes) (Figure 2.1). Enano (5.263°S 121.969°E) was an inland lowland site, where transect altitudes varied between 85 and 170 m, with the habitats surveyed comprising scrub, mixed farmland, mixed plantation and forest edge. Tangkeno (5.279°S 121.923°E) was an inland upland site, where transect altitudes varied between 430 m and 710 m, with the habitats comprising secondary forest, scrub and mixed plantation. Sikeli (5.263°S 121.796°E) was a coastal lowland site, where the transect altitude varied between sea level and 50 m, with habitats comprising coconut plantation, cashew plantation, mangrove and scrub. There was much more evidence of intensified mono-cropping around the more heavily populated village of Sikeli than at the other two sites.

Further records were obtained from mist-netting data and informal sight records made during the previous explorations undertaken in late August and September 1999, 2001 and 2003; these were added to the information obtained in 2016. Researchers also visited Kabaena during 2000 to obtain further information on the possible new subspecies of Red-backed Thrush *Zoothera erythronota* first found in 1999, but unfortunately we cannot trace records of other species that may have been recorded during visits to Kabaena by Robinson-Dean and Catterall in 2000. During survey work in 2000, focused on finding sites suitable for trapping Red-backed Thrush specimens, 10 days were spent in the Tangkeno area and habitats up to 1,400 m were explored (Robinson-Dean *et al.* 2002). The mist-netting activity was part of avian biogeographic research focused on small passerines and during this field work specimens of Red-backed Thrush were obtained which resulted in the description and procurement of type specimens of the endemic *kabaena* subspecies (Robinson-Dean *et al.* 2002). Mist-nets were placed in habitat types suited to the capture of small passerines, such as abandoned farmland, forest edge and mangrove habitats. The nets were regularly opened between 06h00–10h00 and were checked every 15 minutes; some additional roost catches were made at dusk between 17h30–18h00. Approximately 127 hours of mist-netting were carried out between 1999 and 2003. The 2016 transect surveys were carried out in the vicinity of the same three villages (Enano, Tangkeno and Sikeli) as the earlier mist-netting field work.

Species identification was confirmed using Coates and Bishop (1997) and Eaton *et al.* (2016), as well as consulting relevant literature (e.g. White and Bruce (1986)). Sulawesi endemics

were designated following Coates and Bishop (1997) and were classified as those found only on mainland Sulawesi and its satellite islands, including Buton, Muna and the Talaud, Sangihe, Togian, Banggai, Sula and Wakatobi (formerly Tukangbesi) island groups. All taxonomy followed (del Hoya *et al.* 2016). The abundance estimates for each species were based on frequency of sightings, following Martin *et al.* (2012). The designated categories were: abundant (usually recorded several times each day in suitable habitat); common (usually recorded at least once per day); fairly common (typically recorded at least once per week); locally common (usually recorded daily, but restricted to specific habitats); uncommon (recorded less than five or six times in a season); and rare (known only from one or two records).

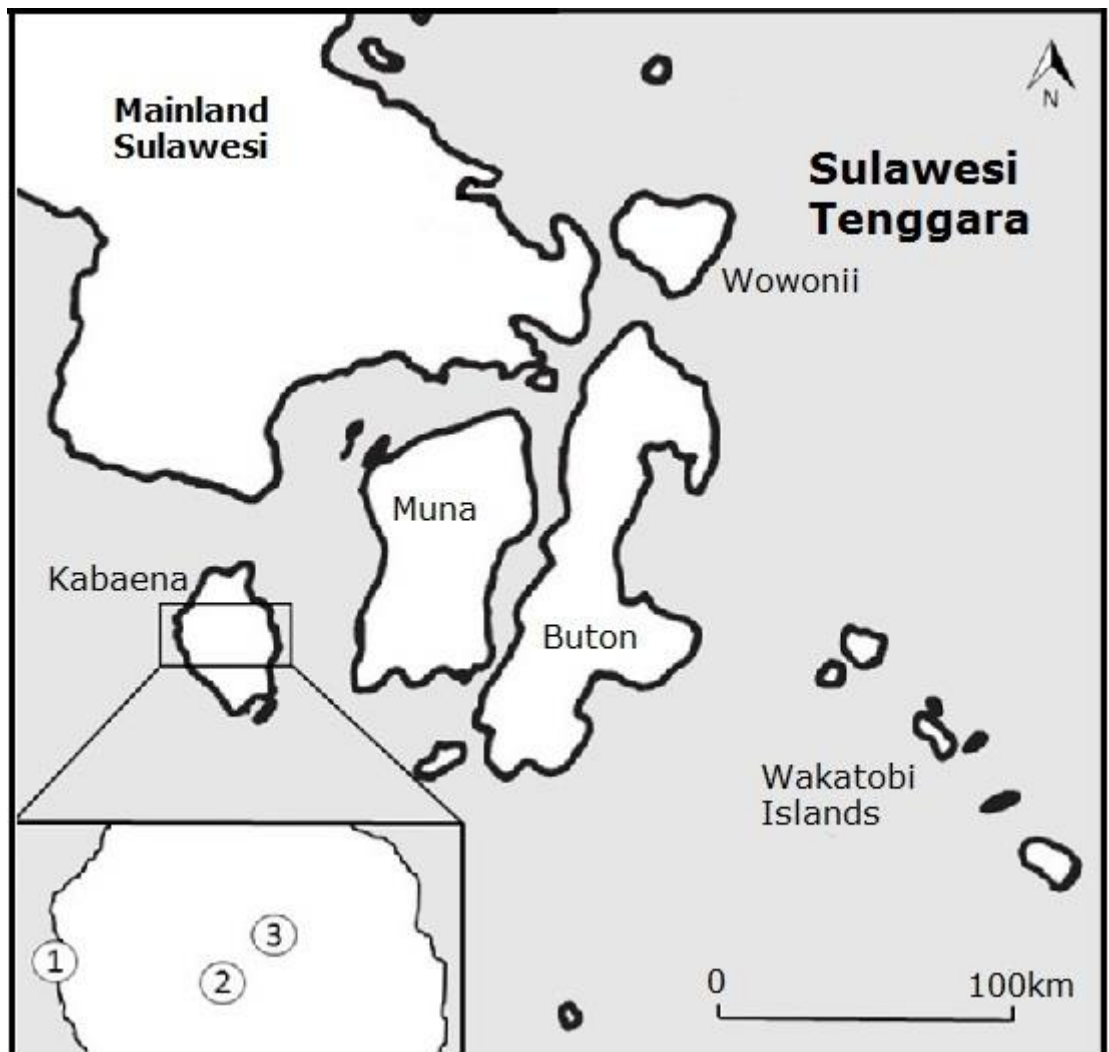


Figure 2.1: Map of South-east Sulawesi (Sulawesi Tenggara) showing the three survey sites on Kabaena Island in the inset panel; ① Sikeli, ② Tangkeno, ③ Enano.

2.4. Results

In total 89 bird species were recorded on Kabaena Island between 1999 and 2016, all but four of which were new records for the island (Table 2.1). Of the total, 27 species (30.3%) are endemic to Sulawesi, three species are defined as Near Threatened and one as Endangered (BirdLife International 2016b). No species were observed outside their usually reported altitudinal range, all range extensions detailed are geographic in nature.

The following annotated list provides details of species listed as Near Threatened or Endangered and Sulawesi endemic species occurring on Kabaena. Sulawesi endemics are marked with an *.

Ashy Woodpecker *Mulleripicus fulvus* *

Present on mainland Sulawesi and some satellite islands, including Muna and Buton (Winkler and Christie 2016). Observed to be locally common in secondary forest and forest edge habitats.

Black-billed Kingfisher *Pelargopsi melanorhyncha* *

Widespread on mainland Sulawesi and its offshore islands, including Muna and Buton (Woodall and Kirwan 2017). A single individual was seen in 2016 perched along the coast in coconut plantation near Sikeli, making occasional plunge dives for food.

Yellow-billed Malkoha *Phaenicophaeus calyrorhynchus* *

Widespread on mainland Sulawesi and also present on Buton (Payne 2016b). An uncommon species on Kabaena, it was recorded in forest edge habitats.

Bay Coucal *Centropus celebensis* *

Present on mainland Sulawesi and some satellite islands, including Muna and Buton (Payne 2016a). A rarely recorded species during the study, its distinctive call was heard from areas of relatively pristine forest.

Ornate Lorikeet *Trichoglossus ornatus* *

Present on mainland Sulawesi and some satellite islands, including Muna and Buton (Collar 2016b). Recorded once during the 2001 expedition.

Golden-mantled Racquet-tail *Prioniturus platurus* *

Widespread on mainland Sulawesi, also occurs on several satellite islands including Muna and

Buton (Collar 2016a). An uncommon species on Kabaena, observed flying overhead in small groups.

Sulawesi Hanging-parrot *Loriculus stigmatus* *

Widespread on mainland Sulawesi, also occurs on Muna, Buton and the Togian islands (Collar 2016d). Regularly recorded, it was an abundant species on the island, occurring in most habitats.

Pygmy Hanging-parrot *Loriculus exilis* * NT

Fragmented distribution on mainland Sulawesi (Collar and Kirwan 2016) and also recorded on Buton (Catterall 1996; Martin *et al.* 2012). Uncommon on Kabaena, recorded in forest edge habitats. Much rarer than the similar Sulawesi Hanging-parrot.

Sulawesi Masked-owl *Tyto rosenbergii* *

Present on mainland Sulawesi and Buton (Bruce and Marks 2016). A pair of birds feeding a chick on the crossbar of a soccer goal frame near Rahadopi village (5.279°S 121.882°E) was seen by NMM and DJK in 1999.

Sulawesi Scops-owl *Otus manadensis* *

Present on mainland Sulawesi and some satellite islands, including Muna and Buton (Holt *et al.* 2017). Locally common, heard calling at night in secondary forest areas.

Sulawesi Nightjar *Caprimulgus celebensis* *

Patchily distributed in northern and central Sulawesi, also Taliabu and Buton islands (Cleere 2017). Recorded once during the 2003 expedition.

White-faced Cuckoo-dove *Turacoena manadensis* *

Present on mainland Sulawesi and some satellite islands including Muna and Buton, east to the Sula islands (Baptista *et al.* 2016). An uncommon species on Kabaena, usually identified by call in forest edge habitats.

White-bellied Imperial-pigeon *Ducula forsteni* *

Widespread and fairly common on Sulawesi and several satellite islands including Togian, Banggai and Sula islands (Baptista *et al.* 2017), also recorded from Buton (Catterall 1996; Martin *et al.* 2012). A rare species on Kabaena, only identified by calls from relatively untouched forested areas.

Sulawesi Serpent-eagle *Spilornis rufipectus* *

Present on mainland Sulawesi and some satellite islands including Muna and Buton, east to the Sula islands (Clark and Kirwan 2016b). Infrequently observed on Kabaena; single birds were seen flying over open habitat.

Spot-tailed Goshawk *Accipiter trinotatus* *

Present on mainland Sulawesi, Muna and Buton (Clark *et al.* 2016). Rarely recorded calling from thick secondary forest re-growth in 2016. Two individuals were mist-netted near to Tangkeno in September 2001.

Sulawesi Hawk-eagle *Nisaetus lanceolatus* *

Found on mainland Sulawesi and some satellite islands including Muna and Buton, east to the Sula islands (Clark and Kirwan 2016a). Rarely observed.

Milky Stork *Mycteria cinerea* EN

This Endangered species (BirdLife International 2016b) has a fragmented distribution in Cambodia, Malaysia, Sumatra, Java and South and South-east Sulawesi (Elliott *et al.* 2016). Up to 21 individuals, including one immature reported on three dates in November 1996 from south-east Buton (Catterall 1996). It was recorded once on Kabaena, a pair seen at a nest close to Sikeli in early September 1999, although further evidence of breeding (incubation or feeding) was not confirmed.

Ivory-backed Woodswallow *Artamus monachus* *

Found on mainland Sulawesi and some satellite islands including Buton, east to the Sula islands (Rowley *et al.* 2016). Locally common in mixed farmland habitats in the vicinity of Enano, seen singly and in pairs, occasionally in groups with the White-breasted Woodswallow *Artamus leucorhynchus*.

Pied Cuckooshrike *Coracina bicolor* * NT

Recorded on mainland Sulawesi and several satellite islands, including Kabaena, Buton and Muna, according to (Taylor 2016a). The report of the species's occurrence on Kabaena in Taylor (2016a) is a mystery, we are unable to find any prior record from the island (see White and Bruce (1986)). Neither Taylor (2005) nor Eaton *et al.* (2016) show Kabaena as part of the species range. Generally uncommon to rare on Sulawesi, and range apparently fragmented—it is absent from large parts of central and eastern regions, locally common in the north and

uncommon on Buton (Taylor 2016a). It was recorded on Kabaena only once (in a coconut plantation) during the 2016 surveys.

White-rumped Cuckooshrike *Coracina leucopygia* *

Present on mainland Sulawesi and some satellite islands, including Muna and Buton (Taylor 2016b). Uncommon on Kabaena, observed in overgrown farmland singly and in pairs.

Sulawesi Cicadabird *Coracina morio* *

Present on mainland Sulawesi and some satellite islands, including Muna and Buton (Taylor 2017). Found at all three sites on Kabaena and was common in coastal farmland areas.

Sulawesi Myna *Basilornis celebensis* *

Present on mainland Sulawesi and some satellite islands, including Muna and Buton (Craig and Feare 2016b). Rarely observed; seen singly and as a group of three in 2016 on the edge of Enano village.

Grosbeak Starling *Scissirostrum dubium* *

Present on mainland Sulawesi and some satellite islands including Buton (Craig and Feare 2016a). Locally common, observed in groups of up to seven individuals, although no breeding colonies were located.

Red-backed Thrush *Zoothera erythronota* * NT

Kabaena is home to the subspecies *Z. e. kabaena* of the Sulawesi endemic Red-backed Thrush (Robinson-Dean *et al.* 2002), a species known from the Sulawesi mainland and Buton (Collar 2016c). A secretive and probably under-recorded species on Kabaena, largely found in forest habitats, it was first recorded in 1999. A small number of birds were mist-netted in forest and forest edge habitat in 1999, 2000 and 2001 as part of the research into the Kabaena Red-backed Thrush's taxonomy (Robinson-Dean *et al.* 2002). Recorded once during the 2016 field season in forest edge habitat.

Pale-bellied White-eye *Zosterops consobrinorum* *

Present on the south-eastern peninsular arm of Sulawesi and Buton (van Balen 2016). Found to be widespread and common in inland areas of Kabaena, in mixed farmland and forest edge habitats. Replaced by the Lemon-bellied White-eye *Zosterops chloris* in coastal areas. Observed regularly in pairs and small groups.

Sulawesi Babbler *Trichastoma celebense* *

Widely distributed on mainland Sulawesi and also recorded on Buton (Collar and Robson 2016). Found to be abundant in most habitats. Several individuals were often heard calling at all three sites.

Yellow-sided Flowerpecker *Dicaeum aureolimbatum* *

Widespread on mainland Sulawesi and its offshore islands, including Muna and Buton (Cheke and Mann 2017b). Abundant at all sites on Kabaena in most habitats.

Grey-sided Flowerpecker *Dicaeum celebicum* *

Widespread on mainland Sulawesi and its offshore islands, including Muna and Buton (Cheke and Mann 2017a). Common at all sites on Kabaena in most habitats.

2.5. Discussion

Despite the Sulawesi region being a hotspot of endemism (Myers *et al.* 2000), knowledge of the avifauna of the area is fragmentary. This study has shed new light on the avian community of one of the more neglected satellite islands of Sulawesi and is the first scientific assessment of the avifauna of Kabaena, during which 89 species were recorded. Many of these records for Kabaena are unsurprising as the species are already well known on the neighbouring islands, Buton and Muna and the south-east peninsula, all of which lie close by, allowing free dispersal between them.

The check-list provided in the Appendix is not representative of the complete avian community present on Kabaena. Our surveys were not designed specifically for recording avian biodiversity, but to maximise behavioural observations of Nectariniidae, Dicaeidae and Zosteropidae as part of research into biogeographic patterns in South-east Sulawesi. This determined the location and timing of surveys, as well as the habitat types covered. As a result, marine species, nocturnal species, and those restricted to primary forest habitat may have been overlooked. In order to assess the migratory species that utilise Kabaena, surveys at several different times of the year would be required.

While surveys have been carried out on Kabaena for a variety of taxa, such as fish (Tweedley *et al.* 2013), reptiles and amphibians (Gillespie *et al.* 2005; Hayden *et al.* 2008), mammals (Froehlich *et al.* 2003) and plants (Keim 2009; Low 2013), there is undoubtedly further

biodiversity to be uncovered. This paper makes an initial assessment of the little known biodiversity of Kabaena's avian community. The island is experiencing continued habitat loss and degradation, lending urgency to the need for more rigorous biodiversity surveying. It is hoped that this paper will draw attention to the neglected fauna of this island.

Table 2.1: Species recorded on Kabaena in the years 1999, 2001, 2003 and 2016. Records which represent a range extension, by being the first record of that species for Kabaena, are indicated by a dagger (†) beside the species name. Sulawesi endemics are indicated by *. Abundance estimates are given for records made during the 2016 field season: A = abundant; C = common; F = fairly common; L = locally common; U = uncommon; R = rare. (M) = seasonal migrant. Species recorded in 1999, 2001 and 2003 are marked ✓ as no abundance estimates are available. Conservation status NT = Near Threatened, EN = Endangered (BirdLife International 2016b).

Species	1999	2001	2003	2016
Asian Blue Quail <i>Synoicus chinensis</i> †		✓	✓	
Barred Buttonquail <i>Turnix suscitator</i> †				R
Red-backed Buttonquail <i>Turnix maculosa</i> †				R
Ashy Woodpecker <i>Mulleripicus fulvus</i> * †				L
Common Kingfisher <i>Alcedo atthis</i> †		✓	✓	R
Blue-eared Kingfisher <i>Alcedo meninting</i> †		✓		
Black-billed Kingfisher <i>Pelargopsis melanorhyncha</i> * †				R
Ruddy Kingfisher <i>Halcyon coromanda</i> †		✓		
Collared Kingfisher <i>Todiramphus chloris</i> †	✓	✓	✓	C
Sacred Kingfisher <i>Todiramphus sanctus</i> (M) †				L
Rainbow Bee-eater <i>Merops ornatus</i> †				C
Plaintive Cuckoo <i>Cacomantis merulinus</i> †		✓	✓	U
Brush Cuckoo <i>Cacomantis variolosus</i> †			✓	U
Moluccan Drongo-cuckoo <i>Surniculus musschenbroeki</i> †				U
Little Bronze-cuckoo <i>Chrysococcyx minutillus</i> †				R
Eastern Koel <i>Eudynamys orientalis</i> †	✓			
Yellow-billed Malkoha <i>Phaenicophaeus calyorrhynchus</i> * †				U
Lesser Coucal <i>Centropus bengalensis</i> †				L
Bay Coucal <i>Centropus celebensis</i> * †		✓		U
Ornate Lorikeet <i>Trichoglossus ornatus</i> * †		✓		
Golden-mantled Racquet-tail <i>Prioniturus platurus</i> * †		✓		U
Blue-backed Parrot <i>Tanygnathus sumatranus</i> †				R

Species	1999	2001	2003	2016
Sulawesi Hanging-parrot <i>Loriculus stigmatus</i> * †				A
Pygmy Hanging-parrot <i>Loriculus exilis</i> * NT †				U
Glossy Swiftlet <i>Collocalia esculenta</i> †	✓	✓	✓	C
Moluccan Swiftlet <i>Aerodramus infuscata</i> †				R
Uniform Swiftlet <i>Aerodramus vanikorensis</i> †				U
Asian Palm-swift <i>Cypsiurus balasiensis</i> †				R
Grey-rumped Treeswift <i>Hemiprocne longipennis</i>				C
Sulawesi Masked-owl <i>Tyto rosenbergii</i> * †	✓			
Sulawesi Scops-owl <i>Otus manadensis</i> * †	✓			L
Great Eared-nightjar <i>Lyncornis macrotis</i> †				U
Savanna Nightjar <i>Caprimulgus affinis</i> †	✓			L
Sulawesi Nightjar <i>Caprimulgus celebensis</i> * †			✓	
Rock Pigeon <i>Columba livia</i> †			✓	L
Eastern Spotted Dove <i>Spilopelia chinensis</i> †			✓	U
Slender-billed Cuckoo-dove <i>Macropygia amboinensis</i> †			✓	U
White-faced Cuckoo-dove <i>Turacoena manadensis</i> * †			✓	L
Grey-capped Emerald Dove <i>Chalcophaps indica</i> †		✓	✓	U
Pink-necked Green-pigeon <i>Treron vernans</i> †				U
Grey-cheeked Green-pigeon <i>Treron griseicauda</i> †			✓	U
Black-naped Fruit-dove <i>Ptilinopus melanospila</i> †	✓		✓	C
White-bellied Imperial-pigeon <i>Ducula forsteni</i> * †			✓	U
Green Imperial-pigeon <i>Ducula aenea</i> †			✓	U
Pied Imperial-pigeon <i>Ducula bicolor</i> †				R
Barred Rail <i>Hypotaenidia torquatus</i> †				R
Whimbrel <i>Numenius phaeopus</i> (M) †				R
Common Sandpiper <i>Actitis hypoleucos</i> †	✓			
Brahminy Kite <i>Haliastur indus</i> †				U
White-bellied Sea-eagle <i>Haliaeetus leucogaster</i> †				U
Sulawesi Serpent-eagle <i>Spilornis rufipectus</i> * †				U
Spot-tailed Goshawk <i>Accipiter trinotatus</i> * †		✓		R
Sulawesi Hawk-eagle <i>Nisaetus lanceolatus</i> * †				U

Species	1999	2001	2003	2016
Spotted Kestrel <i>Falco moluccensis</i> †				R
Great-billed Heron <i>Ardea sumatrana</i> †				R
Purple Heron <i>Ardea purpurea</i> †				U
Green-backed Heron <i>Butorides striatus</i> †				U
Milky Stork <i>Mycteria cinerea</i> EN †	✓			
Golden-bellied Gerygone <i>Gerygone sulphurea</i> †	✓		✓	C
Slender-billed Crow <i>Corvus enca</i> †				L
White-breasted Woodswallow <i>Artamus leucoryn</i> †				F
Ivory-backed Woodswallow <i>Artamus monachus</i> * †				U
Black-naped Oriole <i>Oriolus chinensis</i>			✓	C
Pied Cuckooshrike <i>Coracina bicolor</i> * NT †				R
White-rumped Cuckooshrike <i>Coracina leucopygia</i> * †				U
Sulawesi Cicadabird <i>Coracina morio</i> *				F
White-shouldered Triller <i>Lalage sueurii</i> †	✓		✓	C
Hair-crested Drongo <i>Dicrurus hottentottus</i> †	✓	✓		F
Black-naped Monarch <i>Hypothymis azurea</i> †	✓		✓	C
Red-backed Thrush <i>Zoothera erythronota</i> * NT	✓	✓	✓	R
Citrine Canary Flycatcher <i>Culicicapa helianthea</i> †	✓	✓	✓	
Pied Bushchat <i>Saxicola caprata</i> †	✓	✓	✓	L
Short-tailed Starling <i>Aplonis minor</i> †				R
Sulawesi Myna <i>Basilornis celebensis</i> * †				U
Grosbeak Starling <i>Scissirostrum dubium</i> * †			✓	U
House Swallow <i>Hirundo javanica</i> †				C
Lemon-bellied White-eye <i>Zosterops chloris</i> †	✓		✓	A
Pale-bellied White-eye <i>Zosterops consobrinorum</i> * †	✓	✓	✓	C
Sulawesi Babbler <i>Trichastoma celebense</i> * †	✓	✓	✓	A
Yellow-sided Flowerpecker <i>Dicaeum aureolimbatum</i> * †	✓	✓	✓	A
Grey-sided Flowerpecker <i>Dicaeum celebicum</i> * †	✓		✓	C
Brown-throated Sunbird <i>Anthreptes malacensis</i> †	✓	✓	✓	A
Black Sunbird <i>Leptocoma aspasia</i> †				A
Olive-backed Sunbird <i>Nectarinia jugularis</i> †	✓	✓	✓	A

Species	1999	2001	2003	2016
Crimson Sunbird <i>Aethopyga siparaja</i> †	✓			U
Eurasian Tree Sparrow <i>Passer montanus</i> †	✓	✓	✓	A
Black-faced Munia <i>Lonchura molucca</i> †	✓	✓	✓	C
Scaly-breasted Munia <i>Lonchura punctulate</i> †				U
Chestnut Munia <i>Lonchura atricapilla</i> †	✓	✓		U

3. The avifauna of Muna and Wawonii Island, with additional records from mainland South-east Sulawesi, Indonesia

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Author contributions: DOC, DJK, NMM, KA and AK conceived this study. DOC, DJK, NMM, AON, RG and AK carried out field work. FOM searched the literature for historical records. DOC led the writing. All authors contributed to revising and improving the manuscript.

Status: This manuscript was submitted to Forktail on 29 November 2017 and is in review.

3.1. Abstract

Despite being an important centre of endemism, the south-east peninsula of Sulawesi, and its satellite islands, have remained ornithologically neglected. While relatively extensive surveys have been carried out on Buton Island (the largest satellite of South-east Sulawesi) the avifauna of much of the rest of the region is poorly understood. Surveyors visited the islands of Muna, Wawonii and Lasada village on mainland Sulawesi in summer 2017 to collect data for avian biogeographic research. The 2017 expedition combined transect surveys and mist netting, allowing for a wide assessment of the avifauna at these sites. During these visits all bird species encountered were recorded, providing the first scientific assessment of the avifauna of Wawonii and providing much needed information on the avifauna of Muna Island and the south-east peninsula of Sulawesi. In total 121 species were recorded, of which 33 are regional endemics, two are classified as Near Threatened, two as Vulnerable and one as Endangered.

3.2. Introduction

The biodiversity hotspot of Wallacea, Indonesia, is notable for its high endemism and its mixed fauna of both Asian and Australasian origin (Whitten *et al.* 2002; Myers 2003). Sulawesi is the largest island in Wallacea. Despite possessing a relatively depauperate avifauna compared to some smaller Indonesian islands, such as Java, Sulawesi boasts a high degree of endemism (Michaux 2010; BirdLife International 2016a). This is due to an extended period of geological isolation from continental landmasses (Watling 1983). Sulawesi has a tropical climate with mean daily temperatures ranging from 22-32°C; there is a dry season between June and September and a rainy season between December and March (Whitten *et al.* 2002). Sulawesi's east and south-east peninsulas, including their satellite islands, have received little attention from ornithologists in comparison to the north, south and central provinces. Indeed, detailed ornithological surveying has yet to be carried out in much of South-east Sulawesi (White and Bruce 1986; Rheindt *et al.* 2014).

The majority of information on the avifauna of South-east Sulawesi, comes from its largest (c. 5,600 km²) satellite, Buton Island, which lies south-east of mainland Sulawesi (Figure 3.1). Accounts from Buton (frequently identified as Butung) have been published from the colonial period to the present (Hartert 1903; van Bemmelen and Voous 1951; Schoorl 1987; Catterall 1996; Martin *et al.* 2012). However, neither the islands of Muna and Wawonii, nor the mainland of South-east Sulawesi, have received the same attention. Currently the primary ornithological information on the region comes from White and Bruce (1986), with some additional records being found in Coates and Bishop (1997). The islands of Muna and Wawonii are presently separated from each other and mainland Sulawesi by shallow seas, but historically these islands have been linked during earlier glacial periods (Carstensen *et al.* 2012). As a result, the islands would be expected to have comparable avifauna, but unlike neighbouring Buton (Catterall 1996), they have not been thoroughly surveyed and may host important populations. The nearby island of Kabaena (lying to the west of Buton), has only recently received the attention of ornithologists, revealing the presence of a new subspecies of Red-backed Thrush *Zoothera erythronota kabaena* (Robinson-Dean *et al.* 2002) and showing the island to be home to at least 89 species of birds (O'Connell *et al.* 2017). It is very likely that further populations await discovery in the South-east Sulawesi region.

Muna, the second-largest of South-east Sulawesi's offshore islands (c. 2,890 km²) lies just west of Buton and south of mainland Sulawesi. It is largely comprised of a low-lying (mostly <100 m) limestone plateau, reaching a maximum elevation of 400 m (Milsom and Ali 1999). This

relatively flat, easily accessible terrain has led to Muna being almost entirely deforested and mostly covered with plantations, arable farmland and scrubland, with only very small pockets of forest remaining (Gillespie *et al.* 2005). The avifauna of Muna has received some attention in the past (van Bemmelen and Voous 1951), but this information is long out of date, due to the extensive forest clearance the island has undergone since then.

Wawonii (c. 650 km²) lies north of Buton and east of mainland Sulawesi. Substantial tracts of forest persist throughout much of the island's interior (Farida and Dahrudin 2008) which are predicted to possess species of high conservation value (Cannon *et al.* 2007). However, its ecology remains largely unexplored. The local people practice shifting agriculture (Farida and Dahrudin 2008); when a field is no longer productive for staple crops it is planted with coconuts. This practice has resulted in the more populated coastal parts of the island forming an almost unbroken ring of coconut plantation around the forested interior.

While the avifauna of peninsular South-east Sulawesi is addressed by White and Bruce (1986), the distributions given are broad, often covering the whole peninsula or the entirety of Sulawesi. It is difficult to find detailed checklists for particular areas, or habitats, save a few locations (Wardill *et al.* 1998; Wardill 2003). This means there is little information available on where biodiversity is concentrated on the south-eastern peninsula.

The main purpose of the field expeditions to Muna, Wawonii and mainland Sulawesi in 2017 was to gather data for biogeographical research being carried out by DOC, DJK, NMM, KA, and AK. All avian species encountered were recorded in order to better understand the region's avian community structure. This paper provides the first scientific assessment of the avifauna of Wawonii and provides valuable information on the avifauna in the neglected areas of Muna and the south-east peninsula of Sulawesi.

3.3. Methods

The areas surveyed were in the vicinity of the villages of Kamama Mekar in the south-east of Muna Island (5.307°S 122.640°E), Dimba in the north-east of Wawonii Island (4.042°S, 123.229°E) and Lasada on the south-east peninsula of Sulawesi (3.708°S 121.864°E), to the north-west of Kendari city, the capital of South-east Sulawesi (Figure 3.1). Kamama Mekar is an inland lowland site, with habitats comprising scrub and low mixed farmland. High density plantation agriculture was largely absent from the area. Forest was also largely absent apart from a few small patches, mostly along ridge lines. Survey altitudes varied between 15 m and

65 m above sea level. Dimba is a coastal lowland site, with habitats dominated by intensive coconut plantation, with some areas of rice paddy and coastal scrub. Large tracts of forest were visible further inland but were largely inaccessible. Survey altitudes varied between 3 m and 110 m. Lasada is an inland lowland site, dominated by a huge rice paddy c. 6.75 km² (Daft Logic 2018a). The rice paddy was fringed by patches of mixed farmland, open grassland, some teak and conifer plantation and patches of scrub. Small areas of forest survived on the hills around the rice paddy. Survey altitudes varied between 120 m and 160 m.

Records of the avifauna of the study sites were collected during line transect surveys and mist netting in July and August 2017. Although the primary purpose of the 1 km long transects was to gather behavioural data from a guild of small passerines (Nectariniidae, Dicaeidae and Zosteropidae), all bird species seen or heard were recorded. Data were collected between 06h00-08h30 and 15h15-17h30 each day. Observations were made using 8 × 42 binoculars. During the 2017 field season, 31 hours of transect surveying was carried out covering 21 routes (five in Kamama Mekar, six in Dimba and 10 in Lasada), each surveyed in the morning and evening.

Further records were obtained from mist-netting. Mist-nets were placed in habitat types suited to the capture of small passerines, such as abandoned farmland, forest edge and mangrove habitats. The nets were opened between 05h30–10h00 and were checked every 15 minutes. During the 2017 field season, 74 hours of mist netting was carried out covering 24 netting sites (five in Kamama Mekar, nine in Dimba and 10 in Lasada). Opportunistic observations were also added to formal surveys e.g. during exploration of new sites and when undertaking floral surveys.

Species identification was confirmed using Coates and Bishop (1997) and Eaton *et al.* (2016), as well as consulting relevant literature (e.g. White and Bruce (1986)). Sulawesi endemics were classified as those found only on mainland Sulawesi and its satellite islands, including Buton, Muna, Wawonii and the Talaud, Sangihe, Togian, Banggai, Sula and Wakatobi (formerly Tukangbesi) island groups, following the geographic boundaries to the Sulawesi biogeographic region used by Coates and Bishop (1997). All taxonomy followed del Hoya *et al.* (2018). The abundance estimates for each species were based on frequency of sightings, following Martin *et al.* (2012). The designated categories were: abundant (usually recorded several times each day in suitable habitat); common (usually recorded at least once per day); fairly common (typically recorded at least once per week); locally common (usually recorded daily, but

restricted to specific habitats); uncommon (recorded less than five or six times in a season); and rare (known only from one or two records).

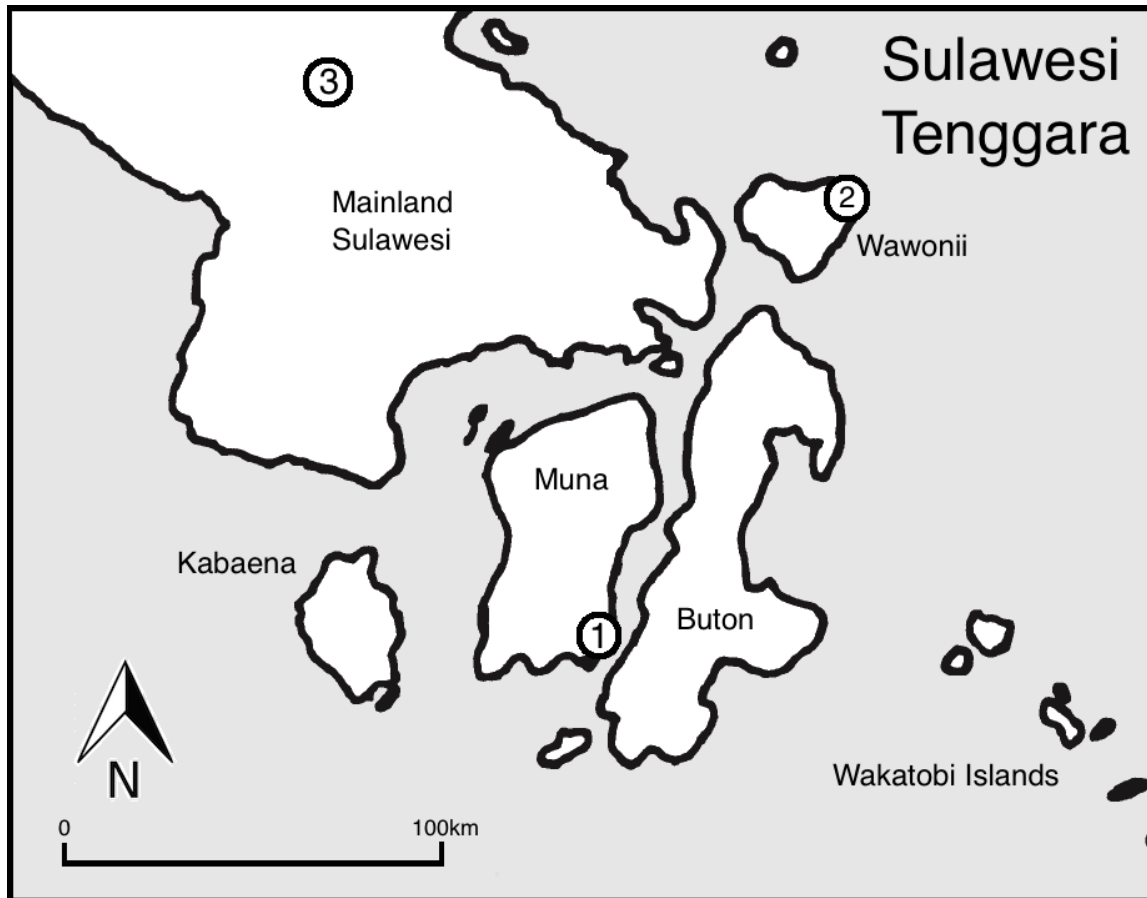


Figure 3.1: Map of South-east Sulawesi (Sulawesi Tenggara) showing the three survey sites: ① Kamama Mekar (Muna Island), ② Dimba (Wawonii Island), ③ Lasada (mainland Sulawesi).

3.4. Results

A total of 121 species were recorded; 60 on Muna, 71 on Wawonii and 101 in Lasada (Table 3.1 and Table 3.2). Of particular note was the number of records of Sulawesi endemic species making up 27.3% of the total species recorded. No species were observed outside their usually reported altitudinal range, all range extensions detailed are geographic in nature.

Table 3.1: Total numbers of species, Sulawesi Endemics, Near Threatened (NT), Vulnerable (VU) and Endangered (EN) species recorded at Kamama Mekar (Muna), Dimba (Wawonii) and Lasada (Sulawesi) on the 2017 expedition.

	Species	Sulawesi Endemics	NT	VU	EN
Muna	60	18	0	0	0
Wawonii	71	18	2	1	0
Lasada	101	24	2	2	1
Expedition total	121	33	2	2	1

The following annotated list provides details of species listed as Near Threatened, Vulnerable or Endangered as well as Sulawesi endemic species and other notable range records. Sulawesi endemic species are marked with an asterisk (*).

Sunda Teal *Anas gibberifrons* NT

Has a wide range across Sumatra, Borneo, Java and Sulawesi (Carboneras *et al.* 2018). Uncommon in coastal areas of Dimba and locally common in the rice paddy near Lasada.

Ashy Woodpecker *Mulleripicus fulvus* *

Recorded as present on mainland Sulawesi and some satellite islands, including Buton, Muna and Kabaena (O'Connell *et al.* 2017; Winkler and Christie 2018). Observed to be common in plantation and forest edge habitats near Dimba and Lasada.

Knobbed Hornbill *Rhyticeros cassidix* * VU

Recorded as present on mainland Sulawesi, Muna and Buton (Kemp and Boesman 2018). Rare, a single pair seen regularly by the edge of a remaining forest patch near Lasada.

Purple-winged Roller *Coracias temminckii* *

Widespread on mainland Sulawesi and its offshore islands, including Muna and Buton (Fry and Kirwan 2018). Uncommon around Kamama Mekar and Dimba, recorded in thicker scrub or village edges. Seen in groups of up to four individuals near Kamama Mekar.

Black-billed Kingfisher *Pelargopsis melanorhyncha* *

Widespread on mainland Sulawesi and its offshore islands, including Muna, Buton and Kabaena (O'Connell *et al.* 2017; Woodall and Kirwan 2018a). A single individual was seen near Dimba in coastal mangrove.

Yellow-billed Malkoha *Rhamphococcyx calyborhynchus* *

Widespread on mainland Sulawesi and also present on Buton and Kabaena (Payne 2018b). Found in forest edge and thicker scrub, uncommon around Kamama Mekar, common around Lasada, with groups of 6-8 being seen following troops of Booted Macaques (*Macaca ochreata*).

Bay Coucal *Centropus celebensis* *

Recorded as present on mainland Sulawesi and some satellite islands, including Muna, Buton and Kabaena (O'Connell *et al.* 2017; Payne 2018a). Found to be locally common around Kamama Mekar and Lasada, its distinctive call was heard from the remaining forest patches.

Ornate Lorikeet *Trichoglossus ornatus* *

Recorded as present on mainland Sulawesi and some satellite islands, including Muna, Buton and Kabaena (O'Connell *et al.* 2017; Collar and Boesman 2018b). Uncommon in coconut plantation near Dimba.

Golden-mantled Racquet-tail *Prioniturus platurus* *

Widespread on mainland Sulawesi, also occurs on several satellite islands including Muna, Buton and Kabaena (O'Connell *et al.* 2017; Collar and Boesman 2018a). Uncommon around Dimba and fairly common around Lasada, observed flying overhead in small groups along forest edge.

Sulawesi Hanging-parrot *Loriculus stigmatus* *

Widespread on mainland Sulawesi, also occurs on Muna, Buton, Kabaena and the Togian islands (O'Connell *et al.* 2017; Collar and Boesman 2018c). Common around Dimba and Lasada, occurring in most habitats. Single individual seen near Kamama Mekar.

Pygmy Hanging-parrot *Loriculus exilis* * NT

Fragmented distribution on mainland Sulawesi (Collar *et al.* 2018) and also recorded on Buton and Kabaena (Catterall 1996; Martin *et al.* 2012; O'Connell *et al.* 2017). Much rarer than the similar Sulawesi Hanging Parrot, a single individual seen at both Dimba and Lasada.

Sulawesi Masked-owl *Tyto rosenbergii* *

Recorded as present on mainland Sulawesi, Buton and Kabaena (O'Connell *et al.* 2017; Bruce and Marks 2018). Rare, a single individual heard near Lasada calling from forest.

Sulawesi Scops-owl *Otus manadensis* *

Recorded as present on mainland Sulawesi and some satellite islands, including Muna, Buton and Kabaena (Holt *et al.* 2017; O'Connell *et al.* 2017). Fairly common around Dimba and Lasada, heard calling at night in secondary forest areas.

Sulawesi Nightjar *Caprimulgus celebensis* *

Patchily distributed in northern and central Sulawesi, also Taliabu, Buton and Kabaena islands (Cleere 2017; O'Connell *et al.* 2017). Rare, heard once near to Lasada.

White-faced Cuckoo-dove *Turacoena manadensis* *

Recorded as present on mainland Sulawesi and some satellite islands including Muna, Buton and Kabaena, east to the Sula islands (O'Connell *et al.* 2017; Baptista *et al.* 2018b). Common around Kamama Mekar and fairly common around Dimba, found in forest edge, plantation and thicker scrub.

White-bellied Imperial-pigeon *Ducula forsteni* *

Widespread and fairly common on Sulawesi and several satellite islands including Togian, Banggai and Sula islands (Baptista *et al.* 2017), also recorded from Buton and Kabaena (Catterall 1996; Martin *et al.* 2012; O'Connell *et al.* 2017). Rare, heard once calling from a forest fragment at Kamama Mekar.

White Imperial-pigeon *Ducula luctuosa* *

Widespread and generally uncommon on Sulawesi and several satellite islands including Buton, Muna, Togian, Banggai and Sula islands (Baptista *et al.* 2018a). Uncommon near Kamama Mekar (~6 seen feeding in a mixed flock with other doves on a large fruiting tree) and fairly common near Dimba (seen along the forest edge).

Isabelline Bush-hen *Amaurornis isabellina* *

Definitely known only from the northern peninsula of Sulawesi and from the south of the south-eastern peninsula (Taylor 2018a). This species is data deficient. It was locally common near Lasada in the area of the rice paddy.

Sulawesi Serpent-eagle *Spilornis rufipectus* *

Recorded as present on mainland Sulawesi and some satellite islands including Muna, Buton and Kabaena, east to the Sula islands (O'Connell *et al.* 2017; Clark and Kirwan 2018c). The most regularly encountered raptor, seen flying over open areas, fairly common around Kamama Mekar and Dimba, common around Lasada.

Spot-tailed Goshawk *Accipiter trinotatus* *

Recorded as present on mainland Sulawesi, Muna, Buton and Kabaena (O'Connell *et al.* 2017; Clark *et al.* 2018). Locally common around Lasada, heard calling from forest edge.

Sulawesi Goshawk *Accipiter griseiceps* *

Recorded as present on mainland Sulawesi, Muna and Buton (Clark and Kirwan 2018a). Rare, observed once near Kamama Mekar and Dimba along forest edge.

Sulawesi Hawk-eagle *Nisaetus lanceolatus* *

Recorded as present on mainland Sulawesi and some satellite islands including Muna, Buton and Kabaena, east to the Sula islands (O'Connell *et al.* 2017; Clark and Kirwan 2018b). Uncommonly heard and seen along the rice paddy near Lasada

Milky Stork *Mycteria cinerea* EN

This Endangered species (BirdLife International 2018c) has a fragmented distribution in Cambodia, Malaysia, Sumatra, Java and south and South-east Sulawesi (Elliott *et al.* 2018a). A breeding population is present in Rawa Aopa Watumohai National Park, South-east Sulawesi (Wardill *et al.* 1998). Up to 21 individuals, including one immature, reported on three dates in November 1996 from south-east Buton (Catterall 1996). A single pair was recorded on Kabaena in 1999 (O'Connell *et al.* 2017). A flock of 12-15 individuals was seen in the rice paddy near Lasada on several occasions.

Asian Woollyneck *Ciconia episcopus* VU

Has a wide range throughout South-east Asia (Elliott *et al.* 2018b). Locally common in rice paddy fields near Dimba and Lasada.

Sulawesi Pitta *Erythropitta celebensis* *

Found throughout mainland Sulawesi and some satellite islands including Buton and Togian (del Hoyo *et al.* 2018c). A member of the Red-bellied Pitta species complex (Irestedt *et al.* 2013). Rare near Kamama Mekar, heard once calling along the forest edge.

Piping Crow *Corvus typicus* *

Recorded as present in south, central and south-eastern mainland Sulawesi and some satellite islands, including Muna and Buton (Madge 2018). Fairly common around Kamama Mekar, seen along forest edge.

Ivory-backed Woodswallow *Artamus monachus* *

Recorded as present on mainland Sulawesi and some satellite islands including Buton and Kabaena, east to the Sula islands (Rowley *et al.* 2017). Uncommon in Lasada, seen in small groups both in and near the village

White-rumped Cuckoo-shrike *Coracina leucopygia* *

Recorded as present on mainland Sulawesi and some satellite islands, including Muna, Buton and Kabaena (Taylor 2018c). Found on overgrown farmland at each site; uncommon around Kamama Mekar, fairly common around Dimba and rare around Lasada.

Sulawesi Cicadabird *Edolisoma morio* *

Recorded as present on mainland Sulawesi and some satellite islands, including Muna, Buton and Kabaena (Taylor 2018b). Found in forest edge and plantation, rare around Dimba and fairly common around Lasada.

Pale-blue Monarch *Hypothymis puella* *

Recorded as present on mainland Sulawesi and some satellite islands including Muna, Buton and Kabaena, east to the Sula islands (del Hoyo *et al.* 2018a). Recently split from the Black-naped Monarch *Hypothymis azurea* based on molecular evidence (Fabre *et al.* 2012). Found in mixed farmland and forest edge habitats, individuals and pairs commonly recorded at all three sites.

Southern White-necked Myna *Streptocitta albicollis* *

Recorded as present on southern and south-east peninsula of Sulawesi and some satellite islands, including Muna and Buton (Craig *et al.* 2018). Seen in farmland areas, fairly common around Kamama Mekar, being seen in groups of 3-4, rare around Lasada (seen once).

Grosbeak Starling *Scissirostrum dubium* *

Recorded as present on mainland Sulawesi and some satellite islands including Buton and Kabaena (O'Connell *et al.* 2017; Craig and Feare 2018). Rare, one flock of 6-7 birds were seen in flight near Lasada.

Pale-bellied White-eye *Zosterops consobrinorum* *

Recorded as present on the south-eastern peninsular arm of Sulawesi, Buton and Kabaena (O'Connell *et al.* 2017; van Balen 2018c). Found in mixed farmland and forest edge habitats, abundant around Kamama Mekar and common around Lasada. Observed regularly in pairs and small groups.

Sulawesi Babbler *Trichastoma celebense* *

Widely distributed on mainland Sulawesi and also recorded on Buton and Kabaena (O'Connell *et al.* 2017; Collar and Robson 2018). Found in most habitats. Abundant around Kamama Mekar and Lasada, locally common (in thicker plantation) around Dimba. Several individuals were often heard calling at all three sites.

Sooty-headed Bulbul *Pycnonotus aurigaster*

An introduced species to Sulawesi, thought to have originated from Javan cagebirds which escaped in South Sulawesi (Coates and Bishop 1997). The Javan population itself may be an introduction from the species' native range on mainland south-east Asia (Fishpool and Tobias 2018). It is now widespread in South, North and East Sulawesi (Coates and Bishop 1997; Fitzsimons *et al.* 2011; Rheindt *et al.* 2014). The Sooty-headed Bulbul has previously been noted in Kendari city South-east Sulawesi (Trochet *et al.* 2014). It was abundant in the farmland around Lasada. These records extend the known range of this species and suggest it is likely widespread in all anthropogenically altered habitats on mainland South-east Sulawesi.

Yellow-sided Flowerpecker *Dicaeum aureolimbatum* *

Recorded as widespread on mainland Sulawesi and its offshore islands, including Muna, Buton and Kabaena (O'Connell *et al.* 2017; Cheke and Mann 2017b). Found in farmland and scrub, fairly common around Kamama Mekar, uncommon around Dimba and common around Lasada

Grey-sided Flowerpecker *Dicaeum celebicum* *

Recorded as widespread on mainland Sulawesi and its offshore islands, including Muna, Buton and Kabaena (O'Connell *et al.* 2017; Cheke and Mann 2018d). Found in farmland and scrub, common around Kamama Mekar and Lasada, fairly common around Dimba.

3.5. Discussion

Despite the Sulawesi region being a hotspot of endemism (Myers *et al.* 2000), knowledge of the avifauna of the area is fragmentary. This study has shed new light on the avifaunal community of some of the lesser known parts of Sulawesi and is the first scientific assessment of the avifauna of Wawonii Island. Many of our expedition's records were unsurprising as the species recorded at our three sites were already well known on the neighbouring island of Buton. However these results highlight the presence of potentially important populations of Vulnerable and Endangered species such as the Knobbed Hornbill, Asian Woollyneck and Milky Stork. The paddy field areas to the north-west of Kendari city, on the south-east peninsula of Sulawesi, may be an important refuge for these species and deserve consideration within any regional conservation plans.

The check-list recorded (Table 3.2), adds a large number of new records but is unlikely to be an exhaustive record of the avian community present at the expedition sites. Our surveys were not designed to record general avian biodiversity, but to maximise behavioural observations of Nectariniidae, Dicaeidae and Zosteropidae and mist netting of small passerines and kingfishers, as part of research into biogeographic patterns in South-east Sulawesi. This determined the location and timing of surveys, as well as the habitat types covered. As a result, marine species, nocturnal species, and those restricted to primary forest habitat may have been under-recorded or overlooked entirely. Furthermore, in order to assess the migratory species that utilise this region, surveys at several different times of the year would be required. Despite such caveats, our data make an important contribution to filling knowledge gaps about the biodiversity of Sulawesi.

The records of Milky Stork, and other species of conservation concern, from the southeastern peninsula of Sulawesi highlight the potential conservation value of this relatively unknown peninsula. Outside of Rawa Aopa Watumohai National Park (Wardill *et al.* 1998), very little is known about the avifauna of this biodiverse peninsula outside of a handful of other records (see, Trochet *et al.* 2014). Further biodiversity monitoring may prove fruitful in uncovering populations of conservation significance on this peninsula. Additionally the biodiversity of Muna was not as degraded as had been feared, despite the intensive agricultural development on that island. Some forest species such as the Sulawesi Pitta survived in strips of forest along exposed ridges. Our survey even recorded 26 species which had not been previously noted for Muna (van Bemmelen and Voous 1951; White and Bruce 1986). However all habitats observed on Muna were highly degraded, so it is unlikely that the section of the island that was surveyed is home to any populations of conservation significance.

In particular, it is hoped that this paper will draw attention to the neglected fauna of Wawonii. The forested core of Wawonii may be of high conservation value (Cannon *et al.* 2007) and the island has been shown to be important for other threatened taxa (Farida and Dahrudin 2008). Nearby Buton Island is home to some of the most biodiverse remaining lowland forest in Sulawesi, but is experiencing serious deforestation (Howard and Gillespie 2007; Martin *et al.* 2012; Martin *et al.* 2019). Much like Buton, Wawonii is experiencing continued habitat loss and degradation, lending urgency to the need for more rigorous surveying and protection of its almost uncharted biodiversity.

Table 3.2: All species recorded in Kamama Mekar (Muna Island), Dimba (Wawonii Island) and Lasada (mainland Sulawesi) in 2017. Sulawesi endemics are indicated by an asterisk (*). Records which are new additions to the avifauna of Wawonii, Muna or the south-eastern peninsula of Sulawesi are indicated by a dagger (†) by the abundance estimate for that population, showing that the indicated population represented a range extension for that species. New additions are those that have not previously been recorded for those sites by White and Bruce (1986), Coates and Bishops (1997) or elsewhere in the primary literature. Seasonal migrants are marked by (M). Conservation status NT = Near Threatened, VU = Vulnerable, EN = Endangered (BirdLife International 2018c). Abundance estimates are given for species recorded: A = abundant; C = common; F = fairly common; L = locally common; U = uncommon; R = rare.

Species	Muna	Wawonii	Lasada
Sunda Teal <i>Anas gibberifrons</i> NT		U†	L
Pacific Black Duck <i>Anas superciliosa</i>			L
Wandering Whistling-duck <i>Dendrocygna arcuata</i>			L
Asian Blue Quail <i>Synoicus chinensis</i>			U
Barred Buttonquail <i>Turnix suscitator</i>		F†	C
Red-backed Buttonquail <i>Turnix maculosus</i>			R
Ashy Woodpecker <i>Mulleripicus fulvus</i> *		C†	C
Knobbed Hornbill <i>Rhyticeros cassidix</i> * VU			R
Purple-winged Roller <i>Coracias temminckii</i> *	U	U†	
Oriental Dollarbird <i>Eurystomus orientalis</i>		R†	
Common Kingfisher <i>Alcedo atthis</i>	R	F†	R
Blue-eared Kingfisher <i>Alcedo meninting</i>	R†	F†	R
Black-billed Kingfisher <i>Pelargopsis melanorhyncha</i> *		R†	
Ruddy Kingfisher <i>Halcyon coromanda</i>		R†	
Collared Kingfisher <i>Todiramphus chloris</i>	A	C†	A
Sacred Kingfisher <i>Todiramphus sanctus</i> (M)	R†	F†	L
Rainbow Bee-eater <i>Merops ornatus</i>	A†	L†	A
Plaintive Cuckoo <i>Cacomantis merulinus</i>	C†	F†	C
Brush Cuckoo <i>Cacomantis variolosus</i>	U†		F
Moluccan Drongo-cuckoo <i>Surniculus musschenbroeki</i>	U†	U†	C
Little Bronze-cuckoo <i>Chalcites minutillus</i>	C†	U†	C
Eastern Koel <i>Eudynamys orientalis</i>		L†	
Yellow-billed Malkoha <i>Rhamphococcyx calyorhynchus</i> *	U†		C
Lesser Coucal <i>Centropus bengalensis</i>	C	L†	C

Species	Muna	Wawonii	Lasada
Bay Coucal <i>Centropus celebensis</i> *	L		L
Ornate Lorikeet <i>Trichoglossus ornatus</i> *		U†	
Golden-mantled Racquet-tail <i>Prioniturus platurus</i> *		U†	F
Blue-backed Parrot <i>Tanygnathus sumatranus</i>		F†	F
Sulawesi Hanging-parrot <i>Loriculus stigmatus</i> *	R	C†	C
Pygmy Hanging-parrot <i>Loriculus exilis</i> * NT		R†	R
Glossy Swiftlet <i>Collocalia esculenta</i>	A†	F†	C
Moluccan Swiftlet <i>Aerodramus infuscatus</i>			A
Uniform Swiftlet <i>Aerodramus vanikorensis</i>			F
Asian Palm-swift <i>Cypsiurus balasiensis</i>		R†	U
Grey-rumped Treeswift <i>Hemiprocne longipennis</i>	R	L†	F
Sulawesi Masked-owl <i>Tyto rosenbergii</i> *			R
Sulawesi Scops-owl <i>Otus manadensis</i> *		F†	F
Great Eared-nightjar <i>Lyncornis macrotis</i>		U†	U
Sulawesi Nightjar <i>Caprimulgus celebensis</i> *			R†
Eastern Spotted Dove <i>Spilopelia chinensis</i>	F	C†	C
Slender-billed Cuckoo-dove <i>Macropygia amboinensis</i>	C	U†	U
White-faced Cuckoo-dove <i>Turacoena manadensis</i> *	C	F†	
Grey-capped Emerald Dove <i>Chalcophaps indica</i>	F	F†	R
Pink-necked Green-pigeon <i>Treron vernans</i>	R†		
Grey-cheeked Green-pigeon <i>Treron griseicauda</i>		R†	R
Black-naped Fruit-dove <i>Ptilinopus melanospila</i>	C	F†	F
White-bellied Imperial-pigeon <i>Ducula forsteni</i> *	R†		
Green Imperial-pigeon <i>Ducula aenea</i>	R	L†	L
White Imperial-pigeon <i>Ducula luctuosa</i> *	U	F†	
Barred Rail <i>Hypotaenidia torquata</i>			R
Buff-banded Rail <i>Hypotaenidia philippensis</i>		R†	L
White-browed Crake <i>Amaurornis cinerea</i>			R
Isabelline Bush-hen <i>Amaurornis isabellina</i> *			L
White-breasted Waterhen <i>Amaurornis phoenicurus</i>			F
Dusky Moorhen <i>Gallinula tenebrosa</i>			L

Species	Muna	Wawonii	Lasada
Common Sandpiper <i>Actitis hypoleucos</i>			R
Black-winged Stilt <i>Himantopus himantopus</i>		L†	
Comb-crested Jacana <i>Irediparra gallinacea</i>			L
Australian Pratincole <i>Stiltia isabella</i>		R†	
Osprey <i>Pandion haliaetus</i>		F†	
Black Kite <i>Milvus migrans</i>			C
Black-shouldered Kite <i>Elanus axillaris</i>			F
Brahminy Kite <i>Haliastur indus</i>	R	C†	C
White-bellied Sea-eagle <i>Haliaeetus leucogaster</i>	U	F†	U
Sulawesi Serpent-eagle <i>Spilornis rufipectus</i> *	F	F†	C
Spotted Harrier <i>Circus assimilis</i>			F
Spot-tailed Goshawk <i>Accipiter trinotatus</i> *			L
Sulawesi Goshawk <i>Accipiter griseiceps</i> *	R	R†	
Sulawesi Hawk-eagle <i>Nisaetus lanceolatus</i> *			U
Spotted Kestrel <i>Falco moluccensis</i>	U		
Oriental Hobby <i>Falco severus</i>			U
Brown Booby <i>Sula leucogaster</i>		R†	
Little Pied Cormorant <i>Microcarbo melanoleucos</i>		L†	
Little Egret <i>Egretta garzetta</i>		U†	L
Intermediate Egret <i>Ardea intermedia</i>		U†	L
Great White Egret <i>Ardea alba</i>		F†	L
Cattle Egret <i>Bubulcus ibis</i>			A
Great-billed Heron <i>Ardea sumatrana</i>	R		U
Purple Heron <i>Ardea purpurea</i>	R†	C†	L
Green-backed Heron <i>Butorides striata</i>	C	A†	
Javan Pond-heron <i>Ardeola speciosa</i>			L
Glossy Ibis <i>Plegadis falcinellus</i>			L
Cinnamon Bittern <i>Ixobrychus cinnamomeus</i>			L
Black Bittern <i>Ixobrychus flavicollis</i>			R
Yellow Bittern <i>Ixobrychus sinensis</i>			U
Milky Stork <i>Mycteria cinerea</i> EN			U

Species	Muna	Wawonii	Lasada
Asian Woollyneck <i>Ciconia episcopus</i> VU		L†	L
Sulawesi Pitta <i>Erythropitta celebensis</i> *	R†		
Golden-bellied Gerygone <i>Gerygone sulphurea</i>	U†	F†	C
Slender-billed Crow <i>Corvus enca</i>	C†	C†	C
Piping Crow <i>Corvus typicus</i> *	F		
White-breasted Woodswallow <i>Artamus leucorhyn</i>	C	C†	C
Ivory-backed Woodswallow <i>Artamus monachus</i> *			U
Black-naped Oriole <i>Oriolus chinensis</i>	A	C†	C
White-rumped Cuckooshrike <i>Coracina leucopygia</i> *	U	F†	R
Sulawesi Cicadabird <i>Edolisoma morio</i> *		R†	F
White-shouldered Triller <i>Lalage sueurii</i>	C†		R
Hair-crested Drongo <i>Dicrurus hottentottus</i>	C	C†	A
Pale-blue Monarch <i>Hypothymis puella</i> *	A†	C†	C
Grey-streaked Flycatcher <i>Muscicapa griseisticta</i> (M)			R
Pied Bushchat <i>Saxicola caprata</i>	C†		L
Short-tailed Starling <i>Aplonis minor</i>	L	L†	R†
Southern White-necked Myna <i>Streptocitta albicollis</i> *	F		R
Grosbeak Starling <i>Scissirostrum dubium</i> *			R
House Swallow <i>Hirundo javanica</i>	F	F†	C
Zitting Cisticola <i>Cisticola juncidis</i>	R		L
Golden-headed Cisticola <i>Cisticola exilis</i>			R
Lemon-bellied White-eye <i>Zosterops chloris</i>	A	L†	U
Pale-bellied White-eye <i>Zosterops consobrinorum</i> *	A†		C
Sulawesi Babbler <i>Trichastoma celebense</i> *	A†	L†	A
Sooty-headed Bulbul <i>Pycnonotus aurigaster</i>			A
Yellow-sided Flowerpecker <i>Dicaeum aureolimbatum</i> *	F	U†	C
Grey-sided Flowerpecker <i>Dicaeum celebicum</i> *	C	F†	C
Brown-throated Sunbird <i>Anthreptes malacensis</i>	A†	A†	A
Black Sunbird <i>Leptocoma aspasia</i>	C	A†	A
Olive-backed Sunbird <i>Cinnyris jugularis</i>	C†	L†	L
Crimson Sunbird <i>Aethopyga siparaja</i>	U†		U

Species	Muna	Wawonii	Lasada
Eurasian Tree Sparrow <i>Passer montanus</i>	L†	L†	L
Black-faced Munia <i>Lonchura molucca</i>	C†	R†	U
Scaly-breasted Munia <i>Lonchura punctulata</i>	R†	U†	C
Chestnut Munia <i>Lonchura atricapilla</i>			C

4. Diversification of a 'great speciator' in the Wallacea region: differing responses of closely related resident and migratory kingfisher species (Aves: Alcedinidae: *Todiramphus*)

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Author contributions: DOC, DJK, NMM, KA and AK conceived this study. DOC, DJK, NMM and AK carried out field work. DOC and NL carried out the lab work. DOC conducted the analyses and led the writing. All authors contributed to revising and improving the manuscript.

Status: This manuscript has been published in Ibis. Paper early view available online from 07 November 2018. doi: 10.1111/ibi.12688

4.1. Abstract

The Collared Kingfisher species complex is the most widespread of the ‘great speciator’ lineages of the Indo-Pacific. They have shown a remarkable ability to spread and diversify. As a result of this rapid diversification *Todiramphus* species are often found in secondary sympatry. In South-east Sulawesi, Indonesia, two *Todiramphus* species are present, the breeding resident Collared Kingfisher *Todiramphus chloris* and the over-wintering migratory Sacred Kingfisher *Todiramphus sanctus*. We investigated the effect of isolation on these closely related species by comparing their populations on mainland Sulawesi and its larger continental islands, with populations on the small, oceanic Wakatobi Islands. Within our wider analysis we provide further support for the distinctiveness of the Sulawesi Collared Kingfisher population, perhaps isolated by the deep water barrier of Wallace’s Line. Within Sulawesi we found that populations of Collared Kingfisher on the Wakatobi had diverged from those on mainland Sulawesi, differing both in morphology and mitochondrial DNA. In contrast there was no divergence between Sacred Kingfisher populations in either morphology or mitochondrial DNA. We propose that a difference in habitat occupied by Collared Kingfisher populations between the mainland and continental islands versus oceanic islands, has caused this divergence. Mainland Collared Kingfishers are predominately found inland, while Wakatobi Collared Kingfishers are also found in coastal habitats. The larger body size of Wakatobi Collared Kingfisher populations may be a result of increased competition with predominantly coastal Sacred Kingfisher populations. The uniform nature of Sacred Kingfisher populations in this region likely reflects their consistent habitat choice (coastal mangrove) and their migratory nature. The demands of their breeding range are likely to have an even stronger selective influence than their Sulawesi wintering range, limiting their scope for divergence. These results provide insight into the adaptability of the widespread *Todiramphus* lineage and provide evidence of the need for further taxonomic revision of Collared Kingfisher populations.

4.2. Introduction

Island bird populations have historically been of great importance in the study of evolution and biogeography (Darwin 1859; Wallace 1869). They provide discrete units which allow us insight into how species adapt and change in relative isolation (MacArthur and Wilson 1967; Whittaker and Fernández-Palacios 2007). Modern molecular tools have provided new avenues for this research, allowing for both greater insight into the evolutionary history of the taxa (Jetz *et al.* 2012) and the discovery of previously unrecognised ‘cryptic’ species (Bickford *et al.* 2007). The Indo-Pacific is of particular importance to this area of research. This region has great potential for cryptic diversity (Lohman *et al.* 2010) and its many islands make it perfect for studying the tempo and mode of speciation in birds. The Indo-Pacific is home to a number of groups of birds known as ‘great speciators’ (Diamond *et al.* 1976), taxa renowned for their large geographic ranges and rapid diversifications (Mayr and Diamond 2001).

Mayr and Diamond (2001) developed the ‘great speciator’ concept for their study system in Northern Melanesia. It describes a group of birds with high inter-island geographic variation, including diverse taxa found across many islands (e.g. Louisiade White-eye *Zosterops griseotinctus*, Moluccan Dwarf Kingfisher *Ceyx lepidus*, Australian Golden Whistler *Pachycephala pectoralis* and Slender-billed Cicadabird *Edolisoma tenuirostre*). Because of their wide ranges and multiple distinct populations, the ‘great speciators’ have provided ideal study systems for developing many key concepts in evolutionary biology (Mayr 1942; Diamond 1974; Diamond *et al.* 1976). In recent years modern molecular methods have allowed researchers to begin to uncover the intricate evolutionary histories of the ‘great speciators’, showing them to be complexes of closely related species (Irestedt *et al.* 2013; Andersen *et al.* 2013; Andersen *et al.* 2014; Pedersen *et al.* 2018).

The Collared Kingfisher *Todiramphus chloris* species complex is one of the most widespread of the ‘great speciator’ lineages of the Indo-Pacific covering over 16,000 km from the Red Sea to Polynesia (Woodall 2001; Andersen *et al.* 2015b). This species complex shows great diversification across its wide range, encompassing the Collared Kingfisher (14 subspecies) and five species recently taxonomically split from the Collared Kingfisher in the IOC World Bird List (v. 8.1), based on work by Andersen *et al.* (2015b): the Torresian Kingfisher *Todiramphus sordidus* (three subspecies), Islet Kingfisher *Todiramphus colonus* (monotypic), Mariana Kingfisher *Todiramphus albicilla* (three subspecies), Melanesian Kingfisher *Todiramphus tristrami* (seven subspecies) and Pacific Kingfisher *Todiramphus sacer* (22 subspecies) (Gill and Donsker 2018). This level of diversification is particularly remarkable given that the Collared

Kingfisher species complex started diversifying within the last 0.57-0.85 Ma (Andersen *et al.* 2015b), making it one of the fastest diversifying lineages of birds (Moyle *et al.* 2009; Jetz *et al.* 2012). The colonisation of oceanic islands is thought to have played a major part in the extraordinary diversification of the Collared Kingfisher species complex. The rapid diversification seen in this group occurred when colonising the oceanic islands of Wallacea, the Philippines and the Pacific (Andersen *et al.* 2018).

This ability to colonise islands has led to multiple instances of secondary sympatry, where two or more recently diverged *Todiramphus* species are found on the same island (Woodall 2001). Such closely related species have similar ecological requirements so they might be expected to compete strongly for resources (MacArthur and Levins 1967; Martin and Martin 2001; Lovette and Hochachka 2006). However, multiple colonisations of island archipelagos have occurred in many taxa, with very different outcomes, depending on the traits of those taxa. For example, while multiple colonisations of Pacific reed-warblers (*Acrocephalus*) occurred in three archipelagos, species from different lineages do not co-occur on any island (Cibois *et al.* 2011). Reed-warblers live in high density populations of territorial pairs and trios, potentially saturating available habitat and preventing the establishment of new immigrants (Craig 1992; Graves 1992; Thibault and Cibois 2006). In contrast, two species of white-eye (*Zosteropidae*) co-exist on several Mariana Islands (Slikas *et al.* 2000), likely aided by the social flocking behaviour of white-eyes (van Balen 2008). The phenomenon of multiple colonisations of island archipelagos is perhaps best studied in the Indian Ocean archipelago, a diverse collection of islands, in both island area and ecology (Whittaker and Fernández-Palacios 2007). White-eyes and sunbirds (*Nectarinia*) show a complex pattern of island occupancy in the Indian Ocean archipelago. Most islands are home to only one species from each genus and competition with congeneric species limits the further diversification of colonists (Warren *et al.* 2003; Warren *et al.* 2006). There are only a few exceptions. White-eye species live in sympatry on only three Indian Ocean islands, segregating altitudinally (Warren *et al.* 2006). Sunbirds are also only found in sympatry on three islands, partitioning by morphological niche (Bijnens *et al.* 1987). Sunbirds are even excluded from La Réunion and Mauritius by the endemic white-eyes (Reunion Olive White-eye *Zosterops olivaceus* and Mauritius Olive White-eye *Zosterops chloronothos* respectively), which have abnormally long bills for white-eyes and fill the sunbird niche (Gill 1971; Cheke 1987). Clearly interactions with taxonomically and ecologically similar species, as well as island characteristics, are important for the spread of island colonising species (Franzén *et al.* 2012).

Todiramphus populations in secondary sympatry have been shown to exhibit separation by habitat preference, which allow these closely related species to partition niches and maintain reproductive isolation (Fry 1980; Woodall 2001). The Collared Kingfisher complex shows great adaptability in its habitat preferences in different parts of its range (Woodall 2018a), facilitating this partitioning. Human modification of the environment can also alter the dynamic of this habitat partitioning. Ward (1968) noted that one result of increasing urbanisation in Singapore was that the Collared Kingfisher replaced the White-breasted Kingfisher *Halcyon smyrnensis* as the most common garden kingfisher. The Collared Kingfisher species complex is found in sympatry with multiple local endemic congeneric taxa throughout its range, including; the Beach Kingfisher *Todiramphus saurophagus* (north and east New Guinea and surrounding islands), Vanuatu Kingfisher *Todiramphus farquhari* (central Pacific), Talaud Kingfisher *Todiramphus enigma* (Talaud Island), Rusty-capped Kingfisher *Todiramphus pelewensis* (Palau Island) and Ultramarine Kingfisher *Todiramphus leucopygius* (Solomon Islands) (Woodall 2001). The Collared Kingfisher species complex is also found in sympatry with the migratory Sacred Kingfisher *Todiramphus sanctus*. Its migratory nature makes the Sacred Kingfisher unique amongst *Todiramphus* kingfishers. This highly vagile lifestyle may be a vestige of the remarkable dispersal ability that allowed *Todiramphus* kingfishers to diversify across the Pacific (Mayr and Diamond 2001). The Sacred Kingfisher has a wide range from Western Australia to New Caledonia (Woodall and Kirwan 2018b).

While molecular work has begun uncovering the evolutionary history of the ‘great speciator’ radiations (Moyle *et al.* 2009; Andersen *et al.* 2013), more focus on the morphological adaptations of these birds is needed for a greater understanding of the ecological requirements of island colonisation (though see Irestedt *et al.* (2013)). This is also the case for the Collared Kingfisher species complex. While Andersen *et al.* (2015b) significantly revised the taxonomy of this remarkable diversification, the morphological and ecological adaptations that led to the isolation of the different populations remain to be studied. While morphology and phylogenetics have co-varied in many taxa (Jablonski and Finarelli 2009; McKay *et al.* 2010; Dong *et al.* 2015; Liu *et al.* 2016) there are multiple examples of differing morphological and phylogenetic patterns, particularly in recently diverged island fauna (Cibois *et al.* 2007; Phillimore *et al.* 2008b; Saitoh *et al.* 2012).

The south-eastern peninsula of Sulawesi provides an excellent study system to test the effect of isolation on species (Figure 4.1). It includes continental islands (Buton, Muna and Kabaena) which were connected to Sulawesi at the time of the last glacial maximum, around

20,000 years ago (Voris 2000) and also oceanic islands (the Wakatobi Islands) which have never been connected to Sulawesi mainland (Carstensen *et al.* 2012). While the Wakatobi Islands are only separated from Buton by 27 km they are home to six unique bird subspecies (Kelly and Marples 2010; Collar and Marsden 2014) and a proposed new species of flowerpecker (Kelly *et al.* 2014). However, the Wakatobi's kingfisher populations have not been investigated since early taxonomic assessments of the region (Hartert 1903). Both the Collared Kingfisher and Sacred Kingfisher are present in South-east Sulawesi, allowing the effect of isolation to be tested on closely related *Todiramphus* kingfishers, one resident and one migratory.

This study aims to; 1) assess the genetic structure of *Todiramphus* populations in South-east Sulawesi using mitochondrial molecular markers, with the prediction that the Wakatobi Collared Kingfisher population may have diverged from the mainland population, 2) assess whether the morphology of the populations mirrors the genetic structure, and interpret the ecological relevance of any morphological divergence seen and 3) assess whether the resident Collared Kingfisher shows greater evidence of local adaptation to the Wakatobi Islands than the migratory Sacred Kingfisher.

4.3. Methods

4.3.1. Study site and sampling

Sampling was carried out throughout South-east Sulawesi (Figure 4.1), on research expeditions undertaken between 1999 and 2017 in the months of June-September by DJK, NMM, KA, DOC and AK. *Todiramphus* species were sampled on 12 islands throughout the region. For additional details on sampling locations see supplementary material (Table S4.1). Collared Kingfishers and Sacred Kingfishers were caught on both the Wakatobi Islands and 'mainland' islands (mainland Sulawesi and the large continental islands of Buton, Muna and Kabaena). Only Sacred Kingfishers were caught on the isolated island of Menui (Figure 4.1), so no assessment of Collared Kingfishers could be made there. Mist-nets were used to trap birds for sampling. Care was taken with the identification and aging of these similar species. Collared Kingfisher have a 'clean white collar and underparts' (MacKinnon and Phillipps 1993) with 'white (not buff) lores' (Higgins 1999). Juvenile Collared Kingfishers were distinguished by 'forehead and secondary upperwing-coverts finely scaled buff' (Higgins 1999). Sacred Kingfishers are 'smaller than Collared Kingfisher, duller greenish blue with buffy wash to underparts and lores' (MacKinnon and Phillipps 1993). Juvenile Sacred Kingfishers were distinguished by 'feathers of forehead and secondary coverts of upperwing fringed buff' (Coates and Bishop 1997; Higgins 1999). Woodall

(2001) and Eaton *et al.* (2016) provided additional reference information for identification and aging. The morphological measurements; wing (maximum chord), bill, and skull lengths and mass (Redfern and Clark 2001) were taken. All measurements were taken by a single recorder (NMM). Only adult birds were included in this analysis. Collared Kingfishers and Sacred Kingfishers are morphologically monomorphic (Rogers *et al.* 1986; Higgins 1999), so sampled individuals were not separated according to sex in the morphological analyses. Approximately 5-10 contour feathers were plucked from the flank of each bird and stored in sealed paper envelopes. Contour feathers were sampled to minimise the risk of injury to the birds and avoid disruption to flight ability and plumage-based visual signals (McDonald and Griffith 2011). Mist-netting was carried out in a variety of habitats used by *Todiramphus* species including plantation, forest edge, farmland and mangroves.

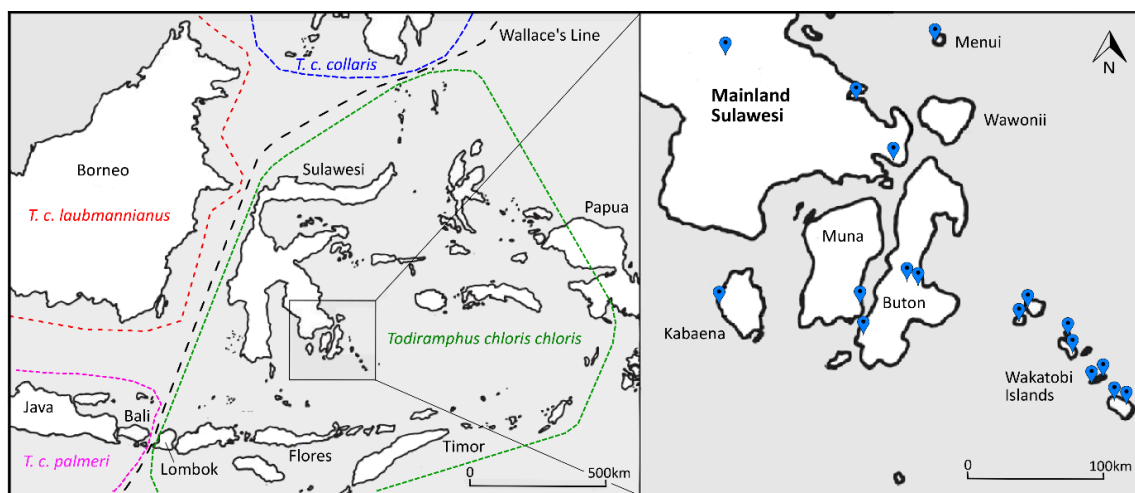



Figure 4.1: Map showing the Sulawesi region of Indonesia (left panel) and the study region of South-east Sulawesi (right panel). Current Collared Kingfisher subspecies divisions (Woodall 2018a) shown by dotted lines, with Wallace's line shown by a dashed line (left panel). Locations where *Todiramphus* kingfishers were sampled for this study marked by .

4.3.2. DNA sequencing

DNA was extracted from feathers using a Qiagen DNeasy Blood and Tissue Kit (Qiagen, California, USA), following Kelly *et al.* (2014). We sequenced three mitochondrial genes; the entire second and third subunits of mitochondrial nicotinamide adenine dinucleotide dehydrogenase (ND2 and ND3, respectively) and a 626bp region of the cytochrome c oxidase subunit 1 (COI) gene. We used established primers LTyr, COI908aH2 (Elbourne 2011) and COIHT (Tavares and Baker 2008) for COI, and L10755 for ND3 (Chesser 1999) respectively. Several novel primers were developed for use with ND2 and ND3 (supplementary material, Table S4.2), primarily to facilitate the sequencing of ND2 in two halves. The polymerase chain reaction (PCR)

procedure was adapted from Kelly *et al.* (2014). All PCR amplifications were performed in 20 μ l reactions, consisting of 8.1 μ l double-distilled H₂O, 0.4 μ l 10 mM deoxynucleoside triphosphates (dNTPs), 2 μ l 10x PCR reaction buffer, 2.4 μ l 25 mM MgCl₂, 1 μ l 10 μ M forward primer, 1 μ l 10 μ M reverse primer, 0.1 μ l Taq polymerase (New England Biolabs) and 5 μ l template DNA. Annealing temperature was 55 °C for ND2, 50 °C for ND3 and 57 °C for COI. All reactions were amplified under the following thermal cycler conditions: 4 min at 94 °C followed by 45 cycles of 1 min at 94 °C, 1.5 min at the gene specific annealing temperature and 1.5 min at 72 °C, finishing with 5 min at 72 °C. Amplified PCR products were screened on 2% agarose gels stained with Gel Red. Sanger sequencing was carried out in both directions by GATC Biotech (Cologne, Germany) using an ABI 3730xl DNA analyser system. All sequences were submitted to GenBank (Benson *et al.* 2013). The sequences produced for this study were given the accession numbers MG845604-MG845682 (Supplementary material, Table S4.1).

4.3.3. Taxon sampling

In addition to our focal study populations in South-east Sulawesi, sequence information for *Todiramphus* species and other comparison groups were sourced from GenBank (Benson *et al.* 2013) to facilitate robust phylogenetic analyses (Table S4.1). ND2 and ND3 sequences were concatenated and analysed separately to COI sequences, due to a much larger sample of *Todiramphus* ND2 and ND3 genes available on GenBank (Andersen *et al.* 2015b). Our ND2/ND3 analysis considered 83 *Todiramphus* samples (29 produced by this study, 54 by Andersen *et al.* (2015b)), including all available Sacred Kingfisher ($N = 39$) and Beach Kingfisher ($N = 4$) samples. For the Collared Kingfisher species complex we focused on its central Indo-Pacific range, clade H in Andersen *et al.* (2015b) and adjacent populations, including all samples of the Collared Kingfisher ($N = 30$), Torresian Kingfisher ($N = 5$) and Islet Kingfisher ($N = 5$). All *Todiramphus* GenBank COI sequences of at least the same length as those produced by this study were used in our analysis. Our analysis incorporated 29 *Todiramphus* COI sequences (21 produced by this study, with another 8 sourced from GenBank), including the Collared Kingfisher ($N = 12$), Sacred Kingfisher ($N = 14$), Forest Kingfisher *Todiramphus macleayii* ($N = 2$) and Mangareva Kingfisher *Todiramphus gambieri* ($N = 1$). *Halcyon* whole mitogenome sequences (Accession No.: NC_028177, NC_024198 and KY940559) provided outgroups for both ND2/ND3 and COI analysis, with the addition of *Syma* (ND2/ND3), *Actenoides* and *Dacelo* (COI) samples to represent closer relatives to *Todiramphus*.

4.3.4. Phylogenetic and genetic analyses

Sequences were assembled by producing a contig from a forward and a reverse sequence read then aligned using ClustalW multiple alignment in BioEdit v7.2.5 (Hall 1999). The ND2 and ND3 genes were concatenated using MESQUITE v3.40 (Maddison and Maddison 2018). Only one representative of each haplotype for ND2/ND3 and COI was included in each model, a full list of the samples and their haplotypes is provided (Table S4.1). Using Bayesian information criterion (BIC) (Jhvueng *et al.* 2014), implemented in the 'Find best DNA model' tool in MEGA v.7.0 (Kumar *et al.* 2016) the optimal nucleotide substitution models for concatenated ND2/3 and COI were selected. This tool tests iterations of 24 different substitution models (covering all model types possible in MEGA and MrBayes) and provides BIC, Akaike information criterion corrected (AIC_c), and Maximum Likelihood (lnL) scores of the model 'goodness of fit'. A General Time Reversible (GTR) model was selected for concatenated ND2/ND3 and a Hasegawa-Kishino-Yano (HKY) model for COI, both with five gamma categories (5 Γ). Maximum likelihood analysis was carried out in MEGA v.7.0 using these model types and run for 1000 bootstrap replicates. Genes were partitioned by codon position, to allow for different substitution rates between codons (Shapiro *et al.* 2006). Concatenated ND2/3 was partitioned globally across the two genes following Andersen *et al.* (2013) and Andersen *et al.* (2015b).

Bayesian phylogenetic inference of haplotypes was carried out using MrBayes v.3.2.6 (Ronquist and Huelsenbeck 2003) using the same models and partition strategy as above. We used two independent Markov chain Monte Carlo (MCMC) runs, with four chains per run. Convergence was assessed using TRACER v.1.6 (Rambaut *et al.* 2014), with convergence in runs accepted when the average standard deviation in split frequencies (ASDSF) reached 0.01 (Ronquist *et al.* 2012) and the effective sample size (ESS) of model parameters exceeded 200 (Drummond *et al.* 2006). The GTR + 5 Γ model of concatenated ND2/3 reached ASDSF 0.01 and an ESS of >200 for all model parameters after five million generations. The HKY + 5 Γ model for COI reached ASDSF 0.01 and an ESS of >200 for all model parameters after 3.5 million generations. Both models were sampled every 1,000 generations, with a burnin of 25%. Phylogenetic tree topology was taken from the Bayesian phylogenetic inference and produced in FigTree v.1.4.2 (Rambaut 2016), with annotations added in INKSCAPE v.0.48.5 (Team Inkscape 2018).

A TCS haplotype network of *Todiramphus* concatenated ND2/3 was constructed using POPART (Leigh and Bryant 2015). A TCS network is constructed using an agglomerative approach

where clusters are progressively combined with one or more connecting edges (Clement *et al.* 2002).

Pairwise comparisons were carried out in MEGA v.7.0 to calculate mean uncorrected proportional genetic distances (p-distances) within and between sampled populations for both longer 'barcoding' genes; ND2 and COI (where available). The distances between Collared Kingfisher populations were then compared to interspecific distances for *Todiramphus* species.

4.3.5. Morphological analyses

All morphological statistical analyses were carried out in R Software v.3.4.2 (R Core Team 2017). Two types of morphological analyses were carried out. Discriminant Function Analysis (DFA), conducted with package 'MASS' (Ripley *et al.* 2016), was used to investigate how well the morphological data supported the groupings provided by our molecular phylogenies. All available morphological measurements were used in the DFA.

Principal Component Analysis (PCA) was also carried out to investigate which traits showed the greatest morphological variability. As the morphological variables were on different scales, all were re-scaled for inclusion in the PCA using the scale function in R, such that their means were = 0 and their variances were = 1 (Thomas *et al.* 2017). To test whether the different populations of kingfishers in South-east Sulawesi (mainland, Wakatobi or Menui) differed morphologically, Analysis of Variance (ANOVA) were carried out on principal components with eigenvalues > 1.

4.4. Results

4.4.1. Phylogenetic analyses

Results from our Maximum Likelihood and Bayesian analyses produced highly concordant topologies for both concatenated ND2/ND3 and COI haplotypes. The concatenated ND2/ND3 tree was most informative because more comparative material was available on GenBank (Figure 4.2). Our focal population of *T. c. chloris* lay with the other central Indo-Pacific Collared Kingfisher populations, with a deep split separating them from their closest relatives, the Torresian Kingfisher and Islet Kingfisher in Australia/New Guinea. Within the central Indo-Pacific, Collared Kingfisher populations were broadly split into a Philippines/Palau/Borneo (*T. c. collaris*, *T. c. teraokai* and *T. c. laubmannianus* respectively) population, *T. c. humii* in Singapore and the *T. c. chloris* population on Sulawesi. Individuals from central Sulawesi (sampled by

Andersen *et al.* (2015b)) and from our study population on mainland South-east Sulawesi, and its large continental islands, grouped together (Figure 4.2 and Table S4.1). However the Wakatobi population was entirely distinct, sharing none of the haplotypes present on mainland Sulawesi (Figure 4.3). Our COI tree (Figure 4.4) provided further evidence of the separation of Wakatobi and Sulawesi mainland Collared Kingfisher populations, and the strong separation between Sulawesi and Philippine populations of Collared Kingfisher.

No clear phylogeographic pattern was seen in the Sacred Kingfisher (Figures 4.2 and 4.4). Some structure was evident, with haplotypes S05, S13, S15 and S21 forming a discrete clade for concatenated ND2/ND3, and haplotype S06 for COI. However the separation was weak, with only 1-3 mutations separating even the most divergent haplotypes from other haplotypes (Figure 4.3). No obvious geographical splits were apparent, except perhaps distinctiveness in the Western Australian breeding population.

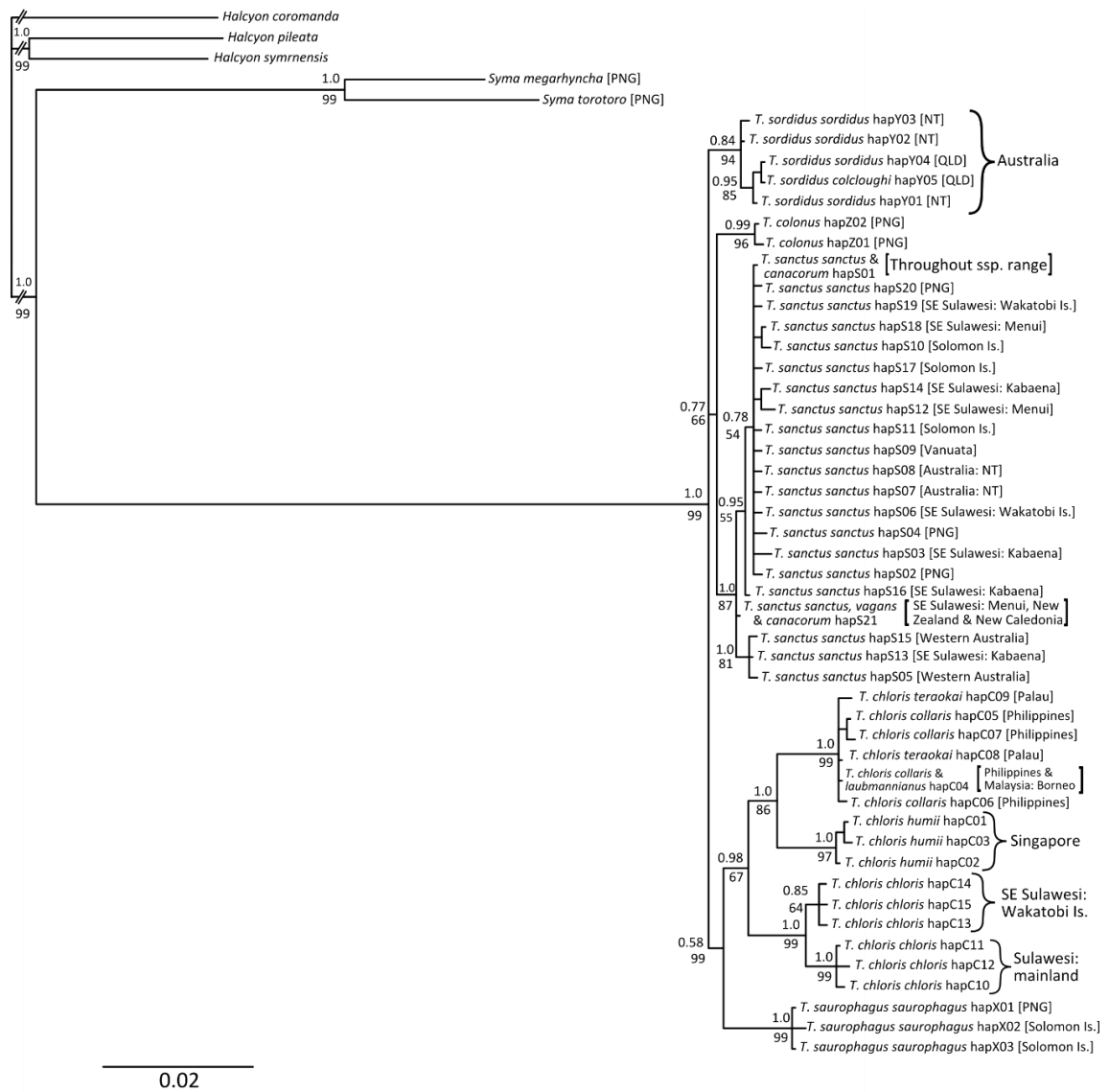


Figure 4.2: Bayesian consensus tree for concatenated ND2 and ND3 haplotypes, showing Bayesian posterior probabilities (above) and bootstrap values from our maximum likelihood analysis (below) for each node. Populations are listed as their currently described subspecies (Gill and Donsker 2018), the haplotype they represent and the geographic range for each haplotype. Square brackets are used for geographic range when referring to a single node. A curly bracket is used for geographic range when referring to more than one node. Where a haplotype is shared between subspecies this is noted. Branch lengths for *Halcyon* were reduced to save space. Geographic abbreviations: PNG, Papua New Guinea; SE Sulawesi, South-east Sulawesi; Is., Islands; NT, Northern Territory; QLD, Queensland.

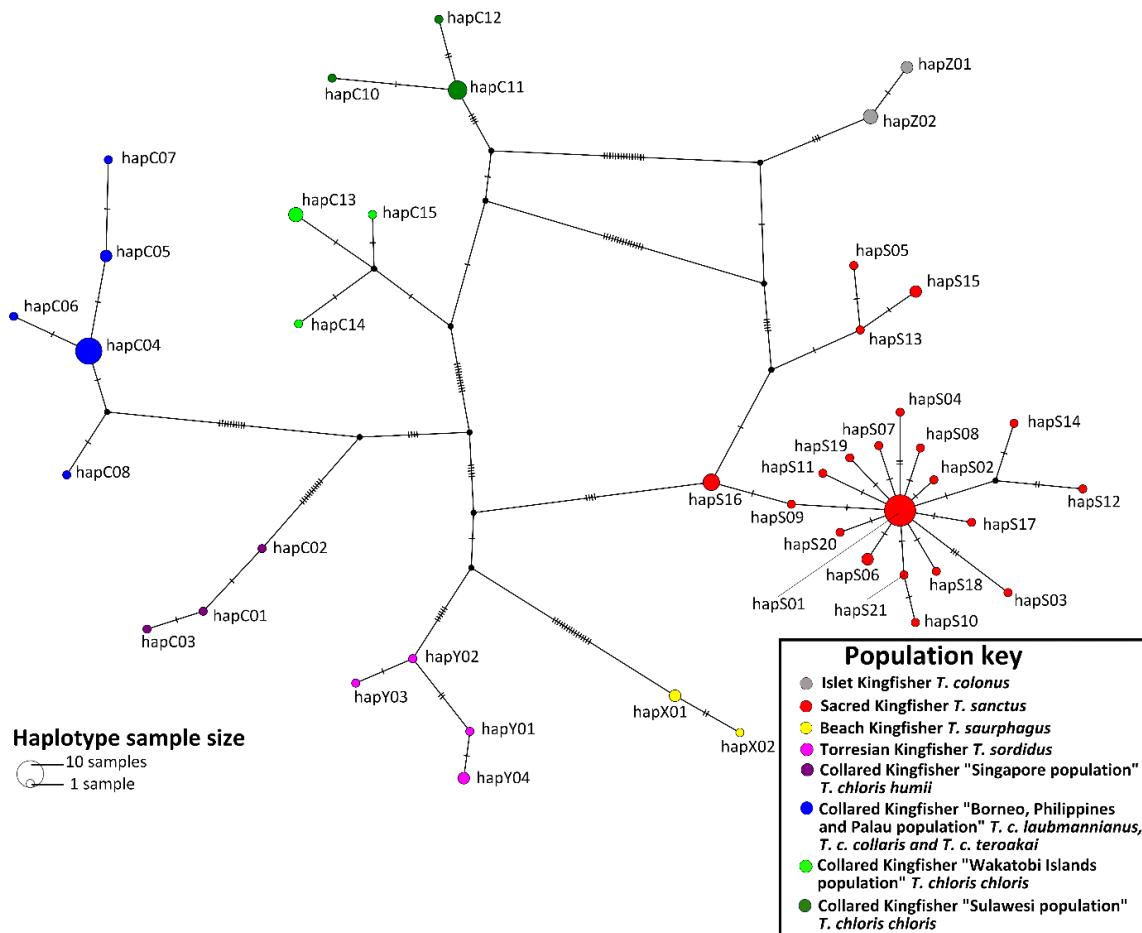


Figure 4.3: Haplotype network of *Todiramphus* populations samples, based on concatenated ND2/3 sequences. One bar indicates one mutation, black nodes are hypothetical ancestral states and the size of the circles corresponds to the number of sampled individuals sharing that haplotype. Individual haplotype labels correspond to haplotype numbers listed in Table S4.1.

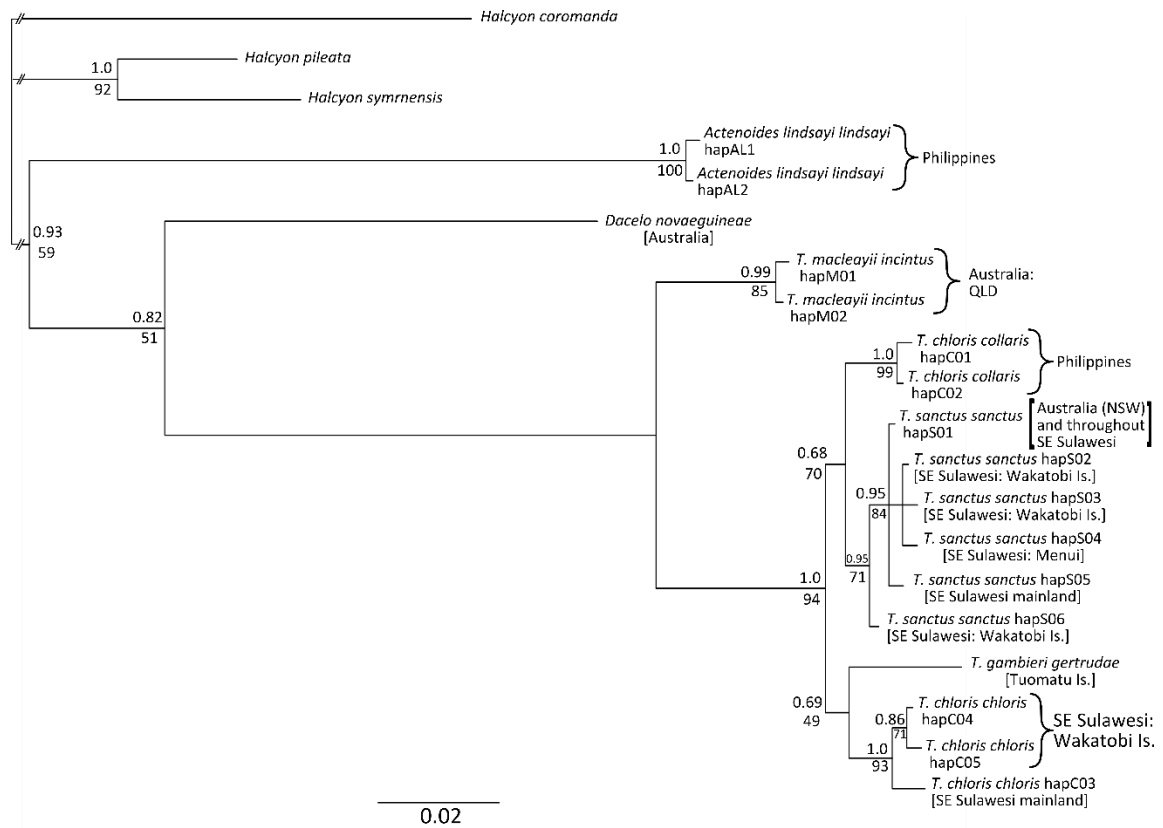


Figure 4.4: Bayesian consensus tree for COI haplotypes, showing Bayesian posterior probabilities (above) and bootstrap values from our maximum likelihood analysis (below) for each node. Populations are listed as their currently described subspecies (Gill and Donsker 2018), the haplotype they represent and the geographic range for each haplotype. Square brackets are used for geographic range when referring to a single node. A curly bracket is used for geographic range when referring to more than one node. Branch lengths for *Halcyon* were reduced to save space. Geographic abbreviations: SE Sulawesi, South-east Sulawesi; Is., Islands; NSW, New South Wales; QLD, Queensland.

4.4.2. Genetic distance

Collared Kingfisher: Calculations of pairwise genetic distance provided an indication of the level of divergence between the populations described in our phylogenetic trees (supplementary material Tables S4.3 and S4.4). Divergence values between the *T. c. chloris* mainland Sulawesi population and the Sacred Kingfisher (ND2: 1.3%) and Beach Kingfisher (ND2: 1.4%) provide an indication of the levels of divergence found between *Todiramphus* species which have been established as taxonomically distinct. Comparisons between the Collared Kingfisher populations sampled showed that *T. c. chloris* on mainland Sulawesi has diverged from both *T. c. humii* in Singapore (ND2: 1.3% divergence) and the subspecies covering the Philippines, Palau and Borneo *T. c. collaris*, *T. c. teraokai* and *T. c. laubmannianus* (ND2: 1.3%). The Philippines/Palau/Borneo population shows minimal divergence within this clade (ND2: 0.0004%). The Philippines/Palau/Borneo population and *T. c. humii* in Singapore differ less from each other (ND2: 0.9%), than either differ from *T. c. chloris*. Within the focal region of South-

east Sulawesi, divergence between the Wakatobi and Sulawesi mainland populations of *T. c. chloris* is smaller (ND2: 0.4%) although this ‘across group’ value is much greater than that of within group divergence (Wakatobi - ND2: 0.0007%; mainland Sulawesi - ND2: 0.0003%).

Sacred Kingfisher: Genetic divergence within the Sacred Kingfisher was minimal. The within group divergence for all samples (and all three subspecies sampled) was only 0.0001% for ND2.

COI was not available for all populations, but followed the same pattern as ND2 where available (Supplementary material, Table S4.4).

4.4.3. Morphological analyses

A summary of the raw morphological measurements collected for this analysis is shown (Table 4.1).

Table 4.1: Morphological measurements, showing mean values \pm standard error.

Variable	Collared Kingfisher		Sacred Kingfisher		
	Mainland (<i>N</i> = 15)	Wakatobi (<i>N</i> = 10)	Mainland (<i>N</i> = 7)	Wakatobi (<i>N</i> = 8)	Menui (<i>N</i> = 3)
Wing length (mm)	102.2 \pm 0.6	113.4 \pm 0.9	89.5 \pm 1.2	92.0 \pm 1.6	89.2 \pm 1.8
Bill length (mm)	47.2 \pm 0.6	54.0 \pm 0.8	42.2 \pm 0.9	44.6 \pm 0.5	43.2 \pm 1.2
Skull length (mm)	27.3 \pm 0.3	28.0 \pm 0.5	24.3 \pm 0.4	25.2 \pm 0.2	24.3 \pm 0.7
Mass (g)	60.6 \pm 1.3	71.2 \pm 2.1	39.1 \pm 1.3	40.9 \pm 1.4	40.3 \pm 2.2

DFA incorporating wing, bill, skull and mass measurements proved 100% successful at categorising the South-east Sulawesi *Todiramphus* kingfishers into the taxonomic groupings suggested by our molecular phylogenies; ‘mainland’ Collared Kingfishers, ‘Wakatobi’ Collared Kingfishers and Sacred Kingfishers (Table S4.5).

The first two principal components explained the majority of the variation seen in both species (Table 4.2) and were the components taken forward for further analysis. Principal component one (PC1) gave an overall indication of body size. Principal component two (PC2) was most strongly influenced by bill length and skull length, giving an indication of bill to skull ratio.

Table 4.2: Summary of the loading of the different variables in the first two PCs of the PCA and the proportion of the variance these PCs explained.

Variable	PC1	PC2
Wing length	-0.534	0.071
Bill length	-0.485	0.608
Skull length	-0.454	-0.790
Mass	-0.523	0.049
Proportion of variance	84.6%	11.5%

Wakatobi Collared Kingfishers were significantly larger than those from the mainland (PC1, ANOVA: $F_{1,23} = 82.91$, $P < 0.001$) (Figure 4.5 and Table 4.2). Collared Kingfisher populations were not found to differ in bill to skull ratio (PC2). In contrast, there was no difference in morphology between Sacred Kingfisher populations (mainland, Wakatobi and Menui) in either PC1 or PC2.

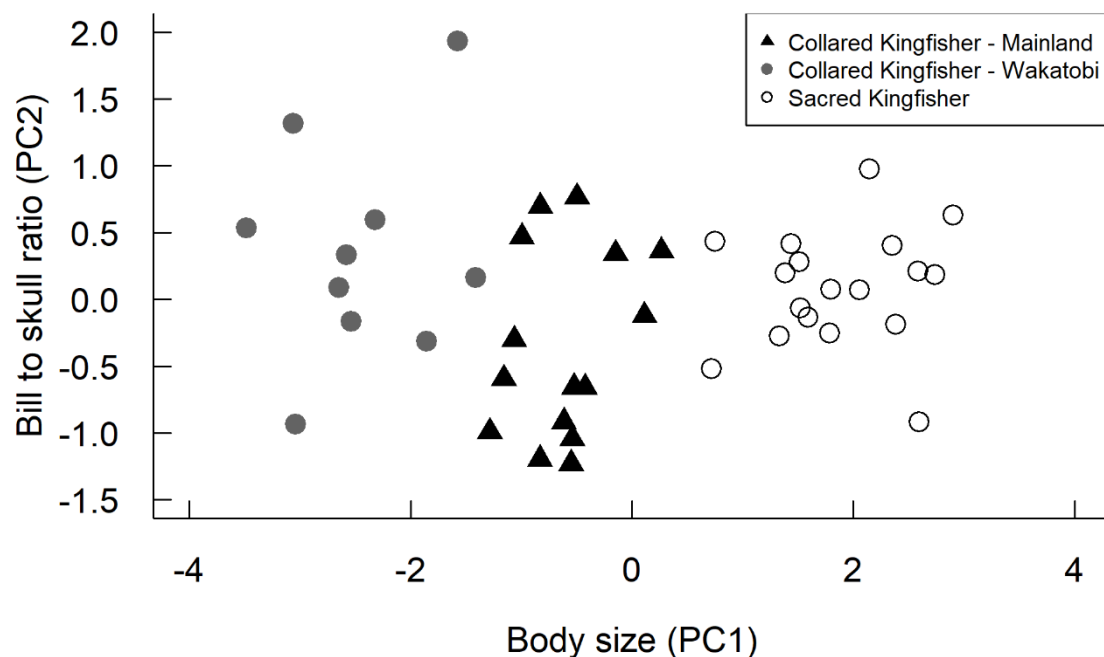


Figure 4.5: Scatterplot of the first two principal components of kingfisher morphology for the Sacred Kingfisher, the Collared Kingfisher mainland population and the Collared Kingfisher Wakatobi Islands population. PC1 reflects body size and PC2 reflects bill/skull ratio. Note: negative values denote larger size in morphological traits for PC1.

4.5. Discussion

Our results demonstrated a clear split in Collared Kingfishers between the South-east Sulawesi mainland population and the Wakatobi Islands population in both genetics and morphology. Genetically the mainland and Wakatobi populations were reciprocally monophyletic with respect to both concatenated ND2/ND3 and COI sequences. The mainland South-east Sulawesi population (this study) grouped with the central Sulawesi population (Andersen *et al.* 2015b), while all the Wakatobi birds represented an independent evolutionary lineage. The Wakatobi birds are significantly larger than those from the Sulawesi mainland, suggesting ecological adaptation to the local conditions on these small islands. While a number of vouchered specimens of Collared Kingfisher (then named *Halcyon chloris*) were collected by Kühn in the early 20th century (Table S4.6) (Hartert 1903), morphological differences in the Wakatobi population have not been previously described.

In addition, our results bring further resolution to the Collared Kingfisher populations of the central Indo-Pacific, giving deeper insight into the Sulawesi populations and corroborating the findings of Andersen *et al.* (2015b). Our analyses confirm that the central Indo-Pacific Collared Kingfisher populations separate into three distinct groups; 1) *T. c. chloris* in Sulawesi (with a more recent separation between mainland Sulawesi and the Wakatobi Islands), 2) *T. c. humii* in Singapore and 3) *T. c. collaris* in the Philippines, *T. c. teraokai* in Palau and *T. c. laubmannianus* in Borneo. As outlined in Andersen *et al.* (2015b) there was almost no divergence between the *T. c. collaris*, *T. c. teraokai* and *T. c. laubmannianus* subspecies on the Philippines, Palau and Borneo respectively. By contrast, the Sulawesi *T. c. chloris* population was clearly distinct (Figures 4.2-4.4). The distinctiveness of the *T. c. chloris* population on Sulawesi could be explained by the isolating effect of the deep water trench that underlies Wallace's Line. This trench ensured Sulawesi was isolated by a water barrier during the last glacial maximum, when the islands to the west of Sulawesi were connected to mainland South-east Asia (Esselstyn *et al.* 2010), and separates *T. c. chloris* from all other Collared Kingfisher subspecies (Figure 4.1).

Unlike the Collared Kingfisher, the migratory Sacred Kingfisher shows no consistent phylogenetic structure, mirroring the results of Andersen *et al.* (2015b). While our phylogenetic work documented 21 haplotypes (concatenated ND2/ND3) within the Sacred Kingfisher, there was little differentiation between these haplotypes (Figure 4.3). Both of the haplotypes found in sedentary populations (hapS01 and hapS21) were also found in migratory populations. Haplotype S01 was the most common haplotype sampled representing 14/39 individuals (Figure 4.3 and Table S4.1). Within South-east Sulawesi we found representative haplotypes from the

full breeding range of the migratory *T. s. sanctus* subspecies (Western, Eastern and Northern Australia), in addition to haplotypes which match the supposedly sedentary *T. s. canacorum* and *T. s. vagans*. Additionally Sacred Kingfishers from South-east Sulawesi showed no difference in morphology between Sulawesi, Wakatobi and Menui birds, suggesting either that these birds were from the same breeding population, or the Sacred Kingfisher shows remarkable morphological uniformity across its range.

It is possible that the radiation of Sacred Kingfisher populations is so recent that genetic differentiation is still minimal, or that there is continuing gene flow between these populations facilitated by the migratory nature of many Sacred Kingfisher populations (Andersen *et al.* 2015b). The lack of diversification in such a widespread bird seems remarkable, particularly considering the level of diversification in the Collared Kingfisher species complex (Andersen *et al.* 2015b) and several other vagile taxa (Cibois *et al.* 2014; Andersen *et al.* 2015a; Garcia-R *et al.* 2017) over the same area as the Sacred Kingfisher's range. However these findings for the Sacred Kingfisher tally with those of Pedersen *et al.* (2018), who found that populations of the Slender-billed Cicadabird species complex (*E. t. pellingi* and *E. t. obiense*) remained morphologically and genetically similar, despite being separated by 500 km of deep ocean. One population of the Slender-billed Cicadabird (*E. t. tenuirostre*) also migrates between Australia and New Guinea (Taylor and Kirwan 2018). The migratory nature and population connectedness over large water barriers seen in the Sacred Kingfisher, and populations of the Slender-billed Cicadabird species complex (this complex also includes distinct isolated populations), may indicate that these populations are still in an early 'colonisation phase' (stage 1) of their taxon cycle (Mayr and Diamond 2001). The taxon cycle concept (TCC), was developed by Wilson (1961) for Melanesian ants, but applied to birds by Ricklefs and Cox (1972) and Diamond *et al.* (1976). The TCC describes how taxa go through a cycle of decreasing vagility as the taxon ages, starting with a colonisation phase and ending with endemism. It helps explain the paradox of the great speciators, how species capable of such wide differentiation stop spreading and begin to diverge in isolation (Diamond *et al.* 1976). The Sacred Kingfisher's preference for coastal edge habitats (Woodall and Kirwan 2018b) match those expected of a species early in its taxon cycle (Mayr and Diamond 2001). These results further highlight the need for wider assessment of Sacred Kingfisher populations, in both their breeding and wintering range, to understand the relationships between the different populations.

A number of factors may explain the divergence seen in the Wakatobi Collared Kingfisher population. We cannot rule out pure genetic drift (Runemark *et al.* 2010) or founder

effect (Spurgin *et al.* 2014) as origins for the changes seen in the Wakatobi Collared Kingfishers. However, the distance between the Wakatobi Islands and mainland is relatively short (27 km) (Kelly *et al.* 2014) and Collared Kingfishers are highly vagile (Woodall 2018a). Therefore it appears unlikely that the Wakatobi population is sufficiently geographically isolated for drift or founder effect alone to be viable explanations (though see Mayr (1942), Diamond (1998), Leisler and Schulze-Hagan (2015) and Andersen *et al.* (2015a) for examples of species from other bird groups with excellent dispersal abilities, Zosteropidae, Acrocephalidae and Monarchidae respectively, isolated by smaller water barriers). Ecologically divergent habitats (such as mainland Sulawesi and the Wakatobi) can create barriers to gene flow (Orsini *et al.* 2013). Under these conditions neutral loci (such as the mitochondrial genes used in this study) can diverge by genetic drift, even between populations which are not separated by strong geographical boundaries. This process is known as Isolation By Adaptation (IBA) (Nosil *et al.* 2009; Orsini *et al.* 2013).

The Wakatobi Islands present a very different habitat to the ecologically complex mainland. The Wakatobi Islands are uplifted coral islands that sit atop a platform of Australian origin and have never been connected to mainland Sulawesi (Milsom and Ali 1999). This seems to have resulted in a change in habitat use by Collared Kingfishers between the mainland and the Wakatobi Islands. Our observations indicated the Collared Kingfisher partitioned habitat with the Sacred Kingfisher on the mainland; the Collared Kingfisher was found inland in scrub, farmland and plantations, and the Sacred Kingfisher occupied a thin coastal strip, always adjacent to water and mostly in mangrove habitats. Of the *Todiramphus* kingfishers mist-netted at mainland sites during this research, 15/16 Collared Kingfishers were mist-netted inland (one in coastal mangrove) and 7/7 Sacred Kingfishers were netted in coastal mangrove. In contrast, on the Wakatobi Islands, both the Collared Kingfisher ($N = 11$) and Sacred Kingfisher ($N = 15$) were exclusively caught in coastal habitats, particularly mangrove.

While the inland habitats typical for Collared Kingfishers are present on the Wakatobi Islands, the small land area of each island means that habitat diversity is low, with a predominance of coastal scrub. It is probable that the marine edge influence dominates the whole of these islands. This is reflected in the depauperate fauna on the Wakatobi Islands in comparison to the larger islands in South-east Sulawesi (Kelly and Marples 2010; Martin *et al.* 2012; O'Connell *et al.* 2017), as species which depend on the greater habitat richness of larger islands cannot persist there (Pimm *et al.* 1988). To persist on the Wakatobi Islands, the Collared Kingfisher population may have had to adapt to a more general habitat niche. The decrease in

land area the Wakatobi Islands would have experienced due to sea level rises in the late Quaternary may have accelerated this process (Weigelt *et al.* 2016). Larger body size in island birds (particularly bill size) has been associated with a more generalist niche in several island bird groups (Grant 1965; Scott *et al.* 2003; Leisler and Schulze-Hagen 2011). Leisler and Winkler (2015) found longer bills in several Pacific island warblers, which allow birds to handle a greater range of prey sizes (Herrera 1978). The increase in body and bill size seen in the Wakatobi Collared Kingfisher (Table 4.1) may reflect such a shift to a more generalist niche.

More thorough surveys of *Todiramphus* species density at both mainland and Wakatobi sites would be needed to confirm this proposed expansion of habitat use. However our observations tally with the habitat descriptions given for these species by White and Bruce (1986), stating that the Collared Kingfisher is most common in gardens, plantations and open wooded country in Sulawesi, Buton and Muna, and is much less associated with mangroves in Wallacea than elsewhere in its range, while the Sacred Kingfisher is mostly associated with mangroves. The habitat on the Wakatobi Islands may more closely mirror that seen on small islands like Palau, where the Collared Kingfisher is also associated with mangroves (Woodall 2018a). Therefore the different selection pressures experienced on mainland Sulawesi and the Wakatobi may be promoting reproductive isolation between Collared Kingfisher populations on the mainland and on the Wakatobi Islands.

While a difference in habitat may be enough to account for the morphological divergence seen in the Collared Kingfisher Wakatobi population, a lack of habitat partitioning between Collared and Sacred Kingfishers on the Wakatobi Islands may bring these two species into closer competition. Such ecologically similar species are likely to have to partition resources to co-exist (Schoener 1974; Jonsson *et al.* 2008; Robertson *et al.* 2014). While the Collared Kingfisher is larger than the Sacred Kingfisher on mainland Sulawesi, a small difference in body size between competing species does not guarantee complete competitive dominance, perhaps necessitating the habitat partitioning between these species seen on the mainland (Reif *et al.* 2018). As outlined by Grant (1968), competing species on islands must segregate by at least one of: 1) habitat, 2) habitat use, 3) food size, 4) food type. Sympatric kingfisher species partition foraging niche by body size (Kasahara and Katoh 2008; Borah *et al.* 2012), since larger kingfishers are able to take larger prey. The *Todiramphus* kingfishers on the Wakatobi Islands are not experiencing competitive exclusion, so the accentuated difference in body size between these species may allow them to partition their niches by food size. This means the Wakatobi population of the Collared Kingfisher may have experienced ecological character displacement,

with selection favouring individuals which differed most from the Sacred Kingfisher (Brown and Wilson 1956; Dayan and Simberloff 2005; Stuart and Losos 2013).

In South-east Sulawesi the only kingfisher species which is both larger than the Collared Kingfisher and found in coastal habitats, is the Black-billed Kingfisher *Pelargopsis melanorhyncha*. The Black-billed Kingfisher is absent from the Wakatobi Islands (Woodall and Kirwan 2018a), so those kingfishers present experience no competition for larger prey. Members of the Collared Kingfisher species complex show remarkable niche flexibility elsewhere in their range, depending on which competitors are present. The Collared Kingfisher is restricted to the coast when in sympatry with the Talaud Kingfisher or Rusty-capped Kingfisher (Eaton *et al.* 2016; del Hoyo *et al.* 2018b; Woodall 2018b) on the small islands of Talaud and Palau, respectively. The Melanesian Kingfisher (a member of the Collared Kingfisher species complex) segregates habitat with the Beach Kingfisher, being restricted to inland areas where the Beach Kingfisher is present (Mayr and Diamond 2001). Mayr and Diamond (2001) also note that the Melanesian Kingfisher and Sacred Kingfisher partition resources ecologically, in Melanesia, by body size and the Sacred Kingfisher's preference for more open habitats. Diamond and Marshall (1977) found that on Santo and Malakula Islands, the Pacific Kingfisher partitions habitats with the Vanuatu Kingfisher, being confined to coastal areas, clearings and open spaces, while the Vanuatu Kingfisher is found in closed forest, but when the Vanuatu Kingfisher is absent on Efate, Erromanga and Tanna Islands, the Pacific Kingfisher is found throughout those habitats. However this pattern does not always hold, Andersen *et al.* (2017) found these two species in sympatry inland on Malakula on the edge of primary forest, in disturbed habitats near human habitation. Potentially the Pacific Kingfisher's tolerance for disturbed areas has allowed it to move further inland. Clearly the presence/absence of competitors is of great ecological importance within this species complex and differences in habitat structure can influence these interactions.

Similar patterns are seen in other widely-distributed, island-colonising taxa, as multiple colonisation events force congeneric species to segregate niche or face competitive exclusion (Mayr and Diamond 2001). Andersen *et al.* (2013) noted that *Ceyx* kingfishers segregate by habitat when in sympatry in the Philippines. Lack (1971) noted that two species of white-eye are seldom found in sympatry on the mainland, generally partitioning altitudinally, or by habitat choice. However sympatric pairs of white-eyes are found on multiple Indian Ocean Islands, where they partition morphologically, with one species larger than the other (Gill 1971; Lack 1971; Warren *et al.* 2006). Wijesundara and Freed (2018) found that the endemic Sri Lankan

White-eye *Zosterops ceylonensis* increased in bill and body size when in sympatry with the widespread Oriental White-eye *Zosterops palpebrosus*. Our results suggest a similar process may occur in sympatric pairs of *Todiramphus* kingfisher.

Two main factors may explain why the Sacred Kingfisher has not experienced selection pressures in a similar way to the Collared Kingfisher in South-east Sulawesi; its consistent habitat choice and its migratory lifestyle. The Sacred Kingfisher is found in mangrove habitat throughout the region, regardless of island size (though with the addition of the Collared Kingfisher as a potential competitor on smaller islands). While wintering grounds have strong carry-over effects on breeding success (Bearhop *et al.* 2004; Latta *et al.* 2016; Rockwell *et al.* 2017), and Sacred Kingfisher individuals are known to be faithful to the same wintering site (Woodall and Kirwan 2018b), the ability of the Sacred Kingfisher to adapt to its wintering grounds will be limited by the constraints placed upon the population by the demands of its breeding grounds and its migration route. In contrast, the resident Collared Kingfisher need only adapt to its local conditions.

Our genetic and morphological findings suggest that the Wakatobi Collared Kingfisher may represent an undescribed subspecies and we recommend investigations of plumage (facilitated by the previously collected type specimens Table S4.6) and song differences to confirm this (Uy *et al.* 2009). This study relied on mitochondrial DNA to separate populations of *Todiramphus* kingfishers. While mitochondrial DNA barcoding approaches have proved successful in species delimitation (Hebert *et al.* 2004b; Kerr *et al.* 2007; Hebert *et al.* 2016), mitochondrial and nuclear DNA have been shown to infer different evolutionary histories in many cases (Rubinoff and Holland 2005; Phillimore *et al.* 2008b). Introgression of mtDNA and sex-biased asymmetries can affect phylogenies that depend solely on mitochondrial DNA, particularly when attempting to infer older evolutionary relationships (Toews and Brelsford 2012). However Andersen *et al.* (2015b) found ND2 and ND3 to provide the best phylogenetic resolution for *Todiramphus* kingfishers, with nuclear genes largely uninformative due to the shallow scale of the *Todiramphus* diversification.

This research illustrates a possible mode of divergence at the early stages of speciation in an isolated *Todiramphus* population. Our results also highlight how much is still to be resolved about the relationships between Sacred Kingfisher populations, and their distribution on their wintering grounds. Assessing the populations of 'great speciator' lineages such as the Collared Kingfisher provides the opportunity to contribute both taxonomic revision and insight into the

early stages of speciation. Their rapid speed of evolutionary change, ability to colonise islands and the frequency with which they are found in secondary sympatry makes 'great speciators' ideal groups in which to study speciation. This work is given impetus by the looming biodiversity crisis that threatens South-east Asia (Sodhi *et al.* 2004; Wilcove *et al.* 2013). Much biodiversity, and the evolutionary lessons it can teach us, faces extinction before being formally recognised.

5. A sympatric pair of undescribed white-eye species with very different origins

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Author contributions: DOC, DJK, NMM, KA and AK conceived this study and carried out fieldwork. DOC, NL and DJK carried out the lab work. DOC conducted genetic analyses, extracted the song data and led the writing. DOC and KOB conducted the song and morphological analyses. DOC and DJK conducted plumage comparisons. FOM screened batches of recordings for clear *Zosterops* songs. All authors contributed to revising and improving the manuscript

Status: This manuscript was accepted for publication in the Zoological Journal of the Linnean Society on 17 February 2019 and is in press. doi: 10.1093/zoolinnean/zlz022

5.1. Abstract

Research in the Indo-Pacific region has contributed massively to the understanding of speciation. White-eyes (Aves: Zosteropidae: *Zosterops*), a lineage containing both widespread 'supertramp' species and a high proportion of island endemics, have provided invaluable models. Molecular tools have increased speciation research, however delimiting species remains problematic. We investigated the evolutionary history of *Zosterops* species in South-east Sulawesi using mitochondrial DNA, morphology, song and plumage analyses, to draw species limits and assess which techniques offer best resolution. Our investigation revealed a novel *Zosterops* species, the 'Wangi-wangi White-eye', >3000km from its closest relative. Additionally, we demonstrated unanticipated diversity in the alleged 'supertramp' the Lemon-bellied White-eye *Zosterops chloris* and propose the Wakatobi Islands subspecies (*Z. c. flavissimus*) deserves promotion to full species status. Furthermore, we provide the first molecular and phenotypic assessment of the Sulawesi endemic the Pale-bellied White-eye *Zosterops consobrinorum*. While local populations of this species vary in either genetics or morphology, none show consistency across measures. Therefore we propose no change to the Pale-bellied White-eye taxonomy. Our results indicate changes in dispersal ability associated with the different stages of island colonisation. This study gives insight into one of the great Indo-Pacific radiations and demonstrates the value of using multiple lines of evidence for taxonomic review.

5.2. Introduction

Islands have long been key to our understanding of evolution, providing discrete units to study patterns of speciation and the processes which underlie these patterns (Darwin 1859; Wallace 1869). The islands of the Indo-Pacific have been particularly important in the last half century for laying down many of the fundamental principles underpinning our understanding of island biogeography and speciation (MacArthur and Wilson 1967; MacArthur *et al.* 1972; Diamond 1974; Diamond *et al.* 1976; Diamond 1998). This region is home to thousands of islands and several widespread species radiations, perfect for studying evolution in multiple closely-related populations (Mayr and Diamond 2001). Modern molecular tools have bolstered this work, uncovering cryptic species (Lohman *et al.* 2010; Irestedt *et al.* 2013) and elucidating the evolutionary history of island colonisations (Cibois *et al.* 2011; Andersen *et al.* 2013; Cibois *et al.* 2014; Andersen *et al.* 2014). However, questions still remain on how best to delimit species in widespread radiations (Tobias *et al.* 2010; Andersen *et al.* 2014) and which processes allow some populations to maintain connectivity over large distances, while others become isolated endemic taxa (Andersen *et al.* 2015b; Pedersen *et al.* 2018).

Zosterops white-eyes are one of the lineages of major importance to the study of avian speciation. *Zosterops* have a wide distribution across the Indo-Pacific, South Asia and Africa (van Balen 2008). They are supreme island colonisers and are found throughout the Indo-Pacific, with 73 of the 96 currently recognised *Zosterops* species being found on islands in this region (Mees 1961; Mees 1969; Mayr and Diamond 2001; Warren *et al.* 2006; van Balen 2018a). *Zosterops* show one of the fastest speciation rates of any vertebrate (Moyle *et al.* 2009), rivalled only by cichlid fish (Meyer 1993; Genner *et al.* 2007; Elmer *et al.* 2010). This rapid rate of diversification has earned them the label as one of the Indo-Pacific's 'great speciator', taxa marked out by their remarkable speciation rates (Mayr and Diamond 2001; Moyle *et al.* 2009; Cornetti *et al.* 2015; Lim *et al.* 2018). The radiation includes extremely widespread species such as the Japanese White-eye *Zosterops japonicus* and Oriental White-eye *Zosterops palpebrosus*, containing multiple well-defined races (Lim *et al.* 2018), 'supertramp' edge species such as the Louisiade White-eye *Zosterops griseotinctus* which are found on many small islands, varying little throughout their range (Mayr and Diamond 2001), and a large number of single island endemics (van Balen 2008).

Zosterops species embody the paradox of ‘great speciators’; how do taxa that are sufficiently vagile to be such successful island colonisers become isolated and diverge into endemic species (Diamond *et al.* 1976)? Diamond *et al.* (1976) proposed that this pattern may arise from rapid shifts in dispersal ability in populations. The phylogeographic pattern of *Zosterops* species in Moyle *et al.* (2009) appeared consistent with this thesis. The taxon cycle concept (TCC) may help explain the pattern seen in the ‘great speciators’. The TCC describes how taxa go through a cycle of decreasing vagility as the taxon ages, starting with a colonisation phase and ending with endemism. The TCC was developed by Wilson (1961) for Melanesian ants, but was applied to birds by Ricklefs and Cox (1972) and Diamond *et al.* (1976). Many taxa do not conform to the expectations of the TCC (Mayr and Diamond 2001), but it provides a useful framework for considering how dispersal ability can be lost. Older lineages in island archipelagos have had longer to adapt to local conditions, and may experience selection that leads to a loss of dispersal ability (Losos and Ricklefs 2009; Gillespie *et al.* 2012). Pedersen *et al.* (2018) recently showed the expected relationship between taxon age and decreased dispersal ability in a ‘great speciator’, the Slender-billed Cicadabird *Edolisoma tenuirostre* species complex, adding support to the concept.

Recent molecular work has begun to re-draw the taxonomy and evolutionary relationships of widespread *Zosterops* species (Habel *et al.* 2013; Cox *et al.* 2014; Husemann *et al.* 2015; Habel *et al.* 2015a; Round *et al.* 2017; Wells 2017; Lim *et al.* 2018) and show unexpected divergence within supposedly ‘supertramp’ lineages (Linck *et al.* 2016). However there are still few studies addressing phenotypic and song evolution, processes key to species isolation (Uy *et al.* 2009), though see Phillimore *et al.* (2008b), Baker (2012), Potvin (2013), Husemann *et al.* (2014) and Habel *et al.* (2015b). An understanding of how phenotype and song diverge in comparison to molecular markers, in isolated populations, would give greater insight into this rapidly evolving lineage (Jønsson *et al.* 2014), and provide more effective species delimitation (Dong *et al.* 2015; Liu *et al.* 2016; Wood *et al.* 2016).

In the heart of the Wallacea region, the south-eastern peninsula of Sulawesi provides an excellent study system to test the effect of isolation on *Zosterops* species (Figure 5.1). There are continental islands (Buton, Muna, Kabaena and Wawonii) which were connected to Sulawesi at the time of the last glacial maximum, around 20,000 years ago (Voris 2000; Yokoyama *et al.* 2000; Clark *et al.* 2009) and oceanic islands (the Wakatobi Islands and Runduma Island) which have never been connected to the Sulawesi mainland (Milsom and Ali 1999; Nugraha and Hall 2018). The region has been fruitful for recent speciation research. While the Wakatobi Islands

are only separated from Buton by 27 km, they are home to six endemic bird subspecies (Kelly and Marples 2010; Collar and Marsden 2014) and a proposed new species of flowerpecker (Kelly *et al.* 2014). Kabaena Island, only 16 km from the mainland, is also home to an endemic subspecies of Red-backed Thrush *Geokichla erythronota kabaena* (Robinson-Dean *et al.* 2002).

Current taxonomy identifies two *Zosterops* species, the Lemon-bellied White-eye *Zosterops chloris* and Pale-bellied White-eye *Zosterops consobrinorum* in South-east Sulawesi (van Balen 2018a). The natural history of these species is still being uncovered. The Lemon-bellied White-eye is a typical ‘supertramp’ species (Mayr and Diamond 2001; Eaton *et al.* 2016), occupying small islands, mangroves and edge habitats where it avoids stronger competitors. It is found on small islands from the east coast of Sumatra to the west coast of Papua, and in coastal areas and edge habitats on larger islands in the Lesser Sundas and on Sulawesi (van Balen 2018b). The different races of the Lemon-bellied White-eye are not thought to be very distinct, with significant overlap in phenotypic traits (Eaton *et al.* 2016). The subspecies *Z. c. flavissimus* is found on the Wakatobi Islands and the subspecies *Z. c. intermedius* is found on Buton, Muna and Kabaena (van Balen 2018b). The newly discovered Lemon-bellied White-eye population on the mainland of South-east Sulawesi has been proposed to be either *Z. c. intermedius* (Kelly *et al.* 2010) or *Z. c. mentoris* which is found in northern and central Sulawesi (Trochet *et al.* 2014). The Pale-bellied White-eye is restricted to the south-eastern peninsula of Sulawesi, Buton and Kabaena (Wardill 2003; van Balen 2008; O’Connell *et al.* 2017). The Buton Island population has been suggested as a potentially separate subspecies (Wardill 2003). A potentially novel *Zosterops* species is present on only the northern most Wakatobi Island (Wangi-wangi) (Figure 5.1). It has been provisionally assigned as a population of the Pale-bellied White-eye (van Balen 2018c), and proposed as a novel species by Eaton *et al.* (2016), the ‘Wangi-wangi White-eye’ *Zosterops sp. nov.* This prospective *Zosterops* species first received scientific recognition when it was identified by DJK, NMM and Martin Meads in 2003 (Kelly and Marples 2010) and has been awaiting molecular work to confirm its status. The South-east Sulawesi study system provides the opportunity to firstly clarify the understudied taxonomy of these populations, and secondly investigate the impact of isolation on a widespread ‘supertramp’ and regional endemic *Zosterops* species.

To achieve the aims of this study our research goals were to; 1. assess the ‘supertramp’ Lemon-bellied White-eye by comparing populations for divergence in mitochondrial DNA, morphology or song, 2. assess populations of the regional endemic Pale-bellied White-eye using the same methods, with a particular focus on the undescribed ‘Wangi-wangi White-eye’, which

has been provisionally assigned to this species, 3. estimate divergence times to gain insight into the evolutionary relationships of the *Zosterops* taxa in the region and 4. examine the morphological traits associated with dispersal ability to gain insight into the relationship between dispersal ability and population isolation.

5.3. Methods

5.3.1. Study site and sampling

Sampling was carried out throughout South-east Sulawesi (Figure 5.1), on research expeditions undertaken between 1999 and 2017 in the months of June-September by NNM, DJK, AK, KA and DOC. *Zosterops* species were sampled on 12 islands throughout the region. For additional details on sampling locations see supplementary material (Table S5.1). Mist-nets were used to trap birds for sampling. Birds trapped were colour ringed for easy identification if re-trapped. Coates and Bishop (1997) and Eaton *et al.* (2016) were used for species identification and aging of birds trapped. The morphological measurements; wing length (maximum chord), tarsus length (minimum), bill length (tip of bill to the base of the skull), skull length (base of the bill to the notch at the back of the head), bill depth (measured at the nares), tail length (longest tail feather from base to tip) and weight (grams) were taken (Svensson 1992; Redfern and Clark 2001). All measurements were taken by a single recorder (NNM). Only adult birds were included in morphological analyses. The *Zosterops* species of South-east Sulawesi are sexually monomorphic (van Balen 2018b; van Balen 2018c), so sexes were not separated for morphological analyses. Approximately 5-10 contour feathers were plucked from the flank of each bird and stored in sealed paper envelopes. Contour feathers were sampled to minimise the risk of injury to the birds and avoid disruption to flight ability and plumage-based visual signals (McDonald and Griffith 2011). Mist-netting was carried out in a variety of habitats used by *Zosterops* species including plantation, forest edge, farmland and mangroves.

Zosterops songs were recorded using a Zoom H2 Handy Recorder with a Sennheiser Me62 Omni-Directional Condenser Microphone Capsule with a K6 power supply. The microphone was mounted on a Telinga V2 Foldable Parabolic Reflector to minimise background noise. Songs were saved in a Waveform Audio File Format for maximum song quality. As the song of different *Zosterops* species is similar, the microphone operator was accompanied by another team member with binoculars to identify the species of each individual recorded. Recording was mainly carried out just after dawn and just before dusk, at the peaks of singing

activity. To ensure each recording was of a separate individual, the song recording team walked a new 1km transect route during each recording session and observed *Zosterops* flocks to ensure that the same individuals were not being recorded multiple times. In addition to these recordings, the Xeno-Canto bird sound collection (<http://www.xeno-canto.org>) was searched to source further recordings of our study species.

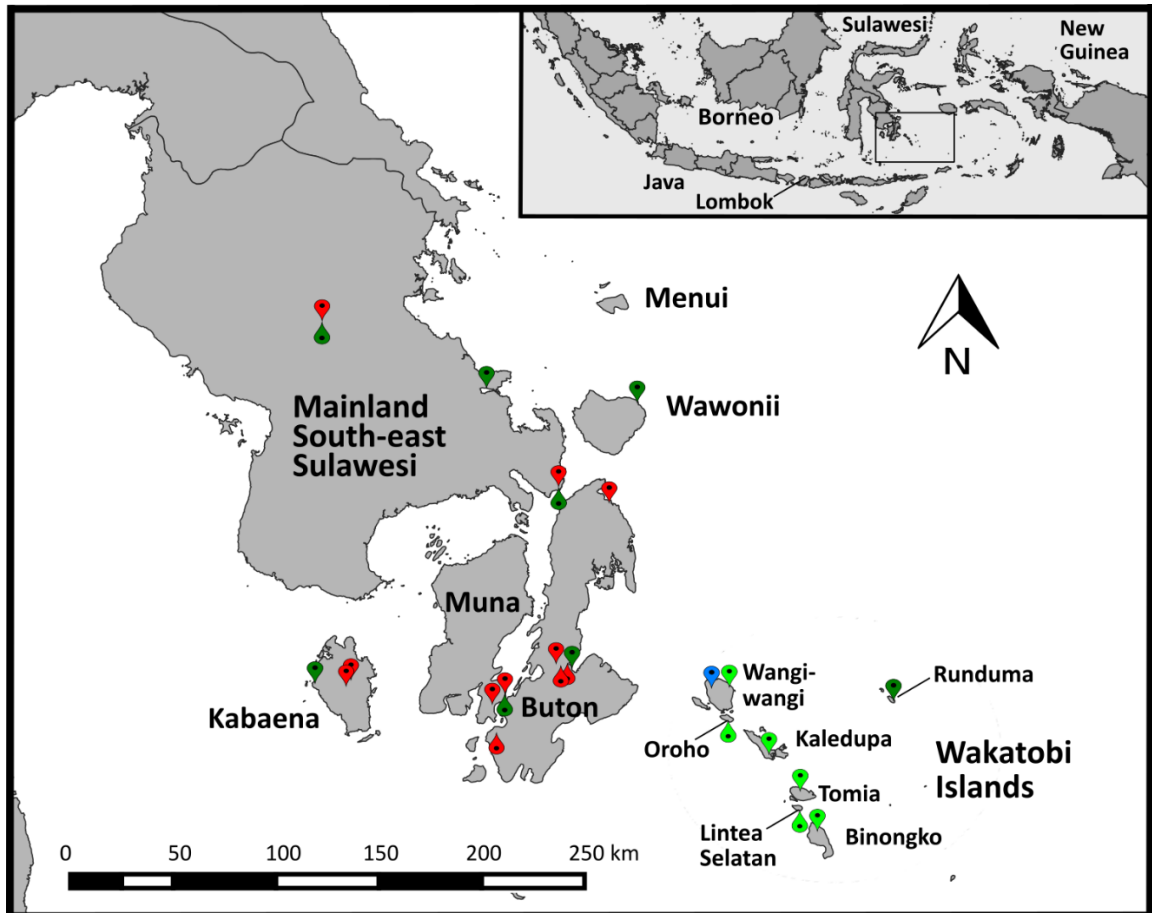


Figure 5.1: Map showing the study region of South-east Sulawesi (main panel) and the Sulawesi region of Indonesia (top right panel). Sites where *Zosterops* were sampled indicated by coloured pins; red indicates the Pale-bellied White-eye, blue indicates the 'Wangi-wangi White-eye' and green indicates the Lemon-bellied White-eye, with the *Z. c. flavissimus* subspecies indicated by lime green.

5.3.2. DNA sequencing

DNA was extracted from feathers using a Qiagen DNeasy Blood and Tissue Kit (Qiagen, California, USA), following Kelly *et al.* (2014). We sequenced three mitochondrial genes; the entire second (1041bp) and third (351bp) subunits of mitochondrial nicotinamide adenine dinucleotide dehydrogenase (ND2 and ND3, respectively) and a 615bp region of the cytochrome c oxidase subunit one (COI) gene. Several novel primers were developed for use in this study to amplify the selected regions (supplementary material, Table S5.2). The established primer

L10755 was also used for ND3 (Chesser 1999). The polymerase chain reaction (PCR) procedure was adapted from Kelly *et al.* (2014). All PCR amplifications were performed in 20 µl reactions, consisting of 8.1 µl double-distilled H₂O, 0.4 µl 10 mM deoxynucleoside triphosphates (dNTPs), 2 µl 10x PCR reaction buffer, 2.4 µl 25 mM MgCl₂, 1 µl 10 µM forward primer, 1 µl 10 µM reverse primer, 0.1 µl Taq polymerase (New England Biolabs) and 5 µl template DNA. All reactions were amplified under the following thermal cycler conditions: 4 min at 94 °C followed by 45 cycles of 1 min at 94 °C, 1.5 min at the gene specific annealing temperature (53 °C for ND2, 50 °C for ND3 and 55 °C for COI) and 1.5 min at 72 °C, finishing with 5 min at 72 °C. Amplified PCR products were screened on 2% agarose gels stained with Gel Red. Sanger sequencing was carried out in both directions by GATC Biotech (Cologne, Germany) using an ABI 3730xl DNA analyser system. All sequences were submitted to GenBank (Benson *et al.* 2013). The sequences produced for this study were given the accession numbers MH492798-MH492939 (Table S5.1).

5.3.3. Taxon sampling

In addition to our focal study populations in South-east Sulawesi, sequence information for *Zosterops* species and other comparison groups were sourced from GenBank (Benson *et al.* 2013) (accession numbers provided in Table S5.1). ND2, ND3 and COI are widely used genes, allowing for comparisons with a large amount of published material to elucidate the evolutionary history of our target species. ND2 and ND3 sequences were concatenated and analysed separately to COI sequences, due to a much wider sample of *Zosterops* ND2 and ND3 genes being available on GenBank (Moyle *et al.* 2009; Wickramasinghe *et al.* 2017). Moyle *et al.* (2009) provided the only published sequences for an individual of our focal *Zosterops* species, a Lemon-bellied White-eye sampled in South Sulawesi. The ND2/ND3 analyses included 137 samples (56 produced by this study, 81 sourced from GenBank) representing 62 species; 51 Zosteropidae along with three Timaliidae, four Pellorneidae, one Passeridae, two Leiotrichidae and one Muscicapidae to serve as out group taxa (Tables S5.1 and S5.3). COI analyses included 108 samples (30 produced by this study, 78 sourced from GenBank) representing 22 species; 16 Zosteropidae along with four Timaliidae, one Vireonidae and one Muscicapidae to serve as out group taxa (Tables S5.1 and S5.4). Sample sizes of sequences used for each species are available in the supplementary material (Tables S5.3 and S5.4). All taxonomy was based on current Handbook of the Birds of the World Alive designations (del Hoya *et al.* 2018).

5.3.4. Phylogenetic and genetic analyses

Sequences were assembled by producing a contig from a forward and a reverse sequence read then aligned using ClustalW multiple alignment in BioEdit 7.2.5 (Hall 1999) and the ND2 and ND3

genes were concatenated using MESQUITE 3.40 (Maddison and Maddison 2018). Only one representative of each haplotype for ND2/ND3 and COI was included in the construction of the phylogenetic trees for the sampled species, a full list of the samples and their haplotypes is provided (Table S5.1). The aligned ND2/ND3 samples were partitioned by gene, and both concatenated ND2/ND3 and COI were partitioned by codon position for model selection (Angelis *et al.* 2018). Samples were partitioned by codon position, to allow for different substitution rates between positions (Shapiro *et al.* 2006). Modeltest was performed with MEGA X (Kumar *et al.* 2018). Using Bayesian information criterion (BIC) (Jhvueng *et al.* 2014), implemented in the 'Find best DNA model' tool (Kumar *et al.* 2018) the optimal nucleotide substitution model for each partition of the concatenated ND2/ND3 and COI data was selected and sequence summary information was produced (Table S5.5).

Using the partitioned model scheme selected (Table S5.5), we carried out maximum likelihood analysis and Bayesian phylogenetic inference on our concatenated ND2/ND3 and COI data separately. Maximum likelihood (ML) heuristic tree searches were performed using GARLI 2.01 (Zwickl 2006). To avoid local optima, 250 independent searches were performed, each starting from a random tree following Andersen *et al.* (2014). Searches were terminated when no topological improvements were found after 100 000 generations. All other parameters were left at default settings. Statistical support for the ML topology was assessed with 1000 nonparametric bootstrap replicates (Felsenstein 1985) and a 50% majority-rule tree was generated in PAUP* 4.0b10 (Swofford 2002). Bayesian phylogenetic inference (BI) was carried out using MrBayes 3.2.6 (Ronquist and Huelsenbeck 2003). We used two independent Markov chain Monte Carlo (MCMC) runs, with four chains per run, sampling every 1000 generations. Burnin and convergence were assessed using TRACER 1.7.1 (Rambaut *et al.* 2018), burnin was set at 25% with convergence in runs accepted when the average standard deviation in split frequencies (ASDSF) reached 0.01 (Ronquist *et al.* 2012) and the effective sample size (ESS) of model parameters exceeded 200 (Drummond *et al.* 2006). The model of concatenated ND2/ND3 reached ASDSF 0.01 and an ESS of >200 for all model parameters after four million generations. The model for COI reached ASDSF 0.01 and an ESS of >200 for all model parameters after seven million generations. Phylogenetic tree topology was taken from the BI, with a 50% majority rule tree produced in FigTree 1.4.3 (Rambaut 2016). Annotations were added in INKSCAPE 0.48.5 (Team Inkscape 2018).

TCS haplotype networks of the sampled Sulawesi *Zosterops* species were constructed with concatenated ND2/ND3 and with COI sequences using POPART (Leigh and Bryant 2015). This allowed the connections between populations and haplotype sample sizes to be visualised.

Pairwise comparisons were carried out in MEGA X to calculate maximum, minimum and mean uncorrected proportional genetic distances (p-distances) within and between sampled populations, for both longer mitochondrial genes; ND2 and COI.

5.3.5. Molecular dating

We estimated divergence time in BEAST 2.4.8 (Drummond *et al.* 2002; Bouckaert *et al.* 2014). Concatenated ND2/ND3 sequences were used for divergence dating due to the wide array of comparison *Zosterops* species (Moyle *et al.* 2009). The same partitioning scheme and model set was used as in the phylogenetic analysis (Table S5.5). To allow different substitution models to be implemented for each partition, nucleotide substitution models were unlinked. Rates of evolution were set at 0.029 and 0.024 for ND2 and ND3 respectively following Linck *et al.* (2016), representing the number of substitutions per site per million years, derived from estimates produced by Lerner *et al.* (2011). We used the estimated date of the divergence of *Zosteropidae* and *Zosterornis* (formerly *Stachyris*) from related taxa, given as 5.01 Ma (4.46-5.57 MA) by Moyle *et al.* (2009) based on geological data, as a point calibration. This calibration was set as a normal distribution with mean 5.01 and sigma 0.555 (Wickramasinghe *et al.* 2017). Clock and Tree models were linked between sites (Drummond and Bouckaert 2015). Following Baele *et al.* (2012) path sampling and stepping-stone sampling were carried out in BEAST to test for clock-like rates, by computing the marginal likelihood for each clock model (Lartillot and Philippe 2006; Xie *et al.* 2011). A Relaxed Clock Log Normal clock model was found to have the highest marginal likelihood and was selected for use (Baele *et al.* 2012; Baele *et al.* 2013). A Yule speciation process was assumed for the tree model, following Wickramasinghe *et al.* (2017). We ran 10 independent MCMC chains for 100 million generations, sampling every 20,000 generations. We assessed burnin and convergence using TRACER 1.7.1 (Rambaut *et al.* 2018) to confirm acceptable mixing, likelihood stationarity and ESS > 200 for all estimated parameters. Burnin was set at 25% for all runs. We used TreeAnnotator 2.4.8 (Bouckaert *et al.* 2014) to summarise the posterior sample of phylogenetic time-trees produced by BEAST into a maximum clade credibility tree. This tree was visualised in FigTree 1.4.3 (Rambaut 2016), displaying 95% highest posterior density (HPD) bars showing the estimate of node ages.

5.3.6. Song data extraction

Zosterops recordings were separated into calls and songs. Songs were selected to be analysed as they are of principal importance in mediating species recognition (Uy *et al.* 2009). Sonograms were prepared and analysed using RAVEN PRO 1.5 (Bioacoustics Research Program 2018). Contrast and brightness were set to an equal level and the sharpness was set at 2000, all other settings were left at default (Ng *et al.* 2016). Recordings with clear sonograms, containing at least 2 discrete bursts of song, were chosen for analysis. Standard song traits were measured from the sonograms following Tobias *et al.* (2010): 1. total number of notes, 2. duration of song, 3. pace (number of notes divided by duration), 4. maximum frequency, 5. minimum frequency, 6. bandwidth (maximum minus minimum frequency) and 7. Peak frequency (the frequency with the greatest amplitude) (Figure 5.2). To account for intra-individual variation, intra-individual means were computed from an average of 6.13 songs (range 2-14) per individual (Potvin 2013; Ng *et al.* 2016). These means were then used as sample points.

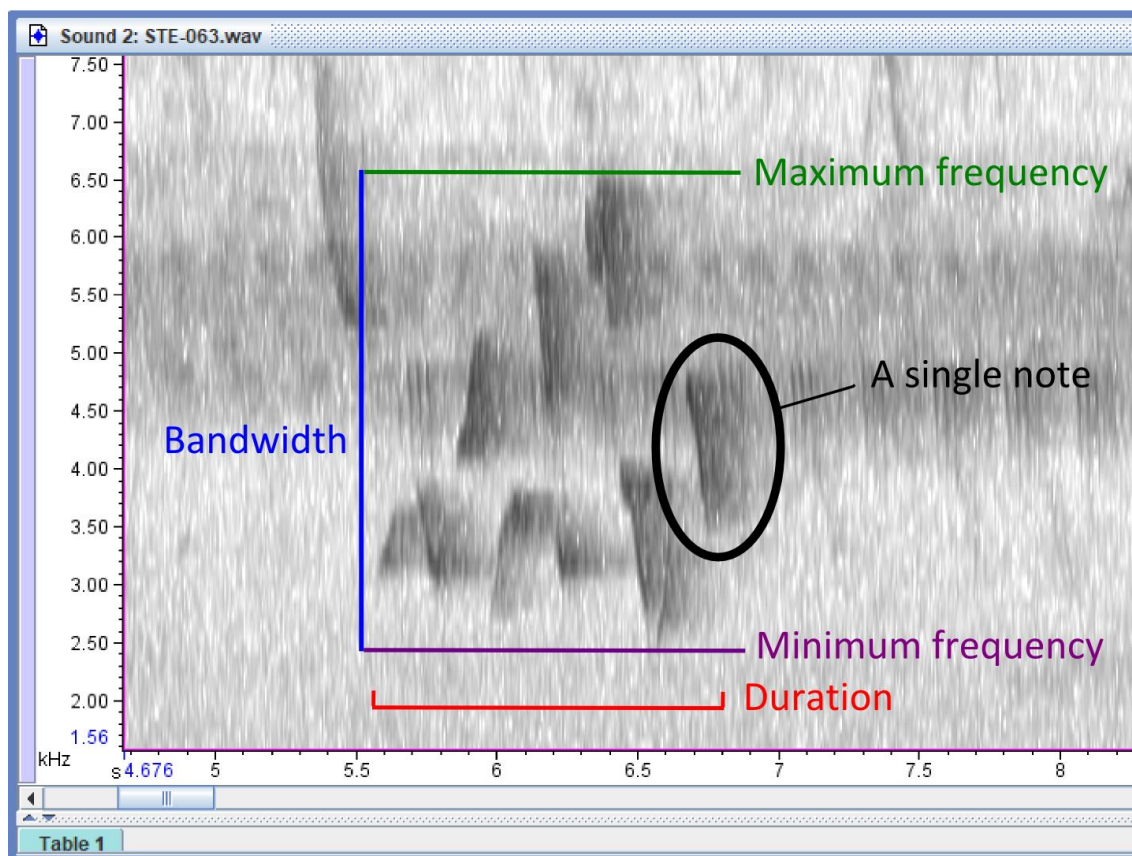


Figure 5.2: a typical *Zosterops* song burst as viewed in RAVEN PRO 1.5, illustrating some of the traits measured in this study. The individual shown was a Pale-bellied White-eye from Kabaena Island.

5.3.7. Morphological and song analyses

All morphological and song statistical analyses were carried out in R Software 3.4.2 (R Development Core Team 2017). Histograms of each trait were first plotted to ensure normal distributions. Two types of analyses were carried out for both the morphological and song data (separately), Principal Component Analysis (PCA) and Discriminant Function Analysis (DFA). PCA was carried out to capture the variance in the morphological and song traits in a smaller number of principal components. A PCA was carried out for each of the analysis groups; 1. Lemon-bellied White-eye morphology, 2. Lemon-bellied White-eye song, 3. Pale-bellied White-eye and the 'Wangi-wangi White-eye' morphology and 4. Pale-bellied White-eye song. As the traits in each PCA were on different scales, all were re-scaled for inclusion in the PCA using the scale function in R, such that their means were = 0 and their variances were = 1 (Thomas *et al.* 2017). To test whether the different populations of our focal *Zosterops* species differed from each other in morphology or song, Analysis of Variance (ANOVA) were carried out on principal components with eigenvalues > 1. To ensure that the assumption of normality was not violated, Q-Q plots of the residuals of each ANOVA test were inspected. Tukey's Honest Significant Difference (HSD) tests were used as post-hoc tests for ANOVAs which returned significant results. The Tukey HSD posthoc allowed for pairwise comparisons to be carried out between each comparison group, and this method corrected for multiple comparisons (Maxwell and Delaney 2018).

DFA, conducted with package 'MASS' (Ripley *et al.* 2016), was used to identify axes that provided the most effective separation between pre-defined groups. For the DFA analyses the groupings were taken from our molecular phylogenies and our analyses assessed how well (% grouping accuracy) the morphology and song data for our study populations supported the phylogenetic groupings. DFA was carried out using the same groupings as in the PCA.

5.3.8. Tobias scoring of species status

To assess the species status of potentially novel *Zosterops* species addressed in this study, a Tobias scoring was carried out for any populations showing potential species level genetic separation. The Tobias scoring system is used by the Handbook of the Birds of the World and Birdlife International for their taxonomic assessments (del Hoyo *et al.* 2018d), based on the criteria outlined by Tobias *et al.* (2010). This system assesses phenotypic characteristics only; morphology, song and plumage, and does not take genetic results into account. A population must reach a Tobias score of seven to be considered a separate species. A detailed description of the criteria is supplied in the Appendices (Section 5.1)

5.3.9. Dispersal ability

To understand speciation in populations an estimate of their dispersal ability is useful (Claramunt *et al.* 2012). Wing length itself is not informative of dispersal ability (Dawideit *et al.* 2009), however it can be used to calculate wingspan. Using studies where both wing length and wingspan were available, Garrard *et al.* (2012) developed a formula to calculate wingspan (where L = wing length and S = wingspan):

$$S = 1.91L + 0.06$$

Wingspan is likely to scale with body mass (m) such that for every unit increase in body mass, wingspan would increase by the power of three, if scaling is isometric (Schmidt-Nielsen 1984). Therefore, following Garrard *et al.* (2012), we created a shape parameter describing ‘wingspan to weight ratio’ (S^3/m) for all *Zosterops* sampled in this study. This allowed an investigation of variation in wingspan not accounted for by body mass. An ANOVA with Tukey’s HSD tests was used to assess differences in ‘wingspan to weight ratio’ between the focal *Zosterops* populations. This provided a rough proxy for the relative dispersal ability of different populations. Q-Q plots of the residuals of this ANOVA were used to ensure the assumption of normality had not been violated.

5.4. Results

5.4.1. Range extension

This study provided the first record of the Lemon-bellied White-eye on Runduma Island (van Balen 2018b) (Figure 5.1).

5.4.2. Sequence production

Sequencing of our focal *Zosterops* species focused on the ND2 and ND3 genes, as they allowed for comparison with the largest array of published *Zosterops* sequences (Moyle *et al.* 2009; Wickramasinghe *et al.* 2017), including ND2/ND3 sequenced for the Lemon-bellied White-eye from South Sulawesi. All individuals sequenced for ND2 were also sequenced for ND3, with a smaller sample of individuals sequenced for COI (Table 5.1, Table S5.1).

Table 5.1: Number of sequences produced for each of our focal species, for ND2/ND3 and for COI. The Sulawesi mainland and its continental islands are highlighted in bold, Wakatobi Islands are highlighted in italics and Runduma is treated as a separate oceanic island. Location for each individual sampled and GenBank accession numbers provided in Table S5.1.

Island	Lemon-bellied White-eye		Pale-bellied White-eye		'Wangi-wangi White-eye'	
	ND2/ND3	COI	ND2/ND3	COI	ND2/ND3	COI
Mainland Sulawesi	12	4	6	2	-	-
Buton	5	2	5	3	-	-
Muna	4	-	1	-	-	-
Kabaena	4	2	4	2	-	-
Wawonii	1	-	-	-	-	-
Runduma	2	2	-	-	-	-
<i>Wangi-wangi</i>	2	2	-	-	4	4
<i>Kaledupa</i>	2	4	-	-	-	-
<i>Tomia</i>	2	-	-	-	-	-
<i>Binongko</i>	2	3	-	-	-	-
Total	36	19	16	7	4	4

5.4.3. Phylogenetic analyses

Results from our Maximum Likelihood and Bayesian analyses produced highly concordant topologies for well supported nodes for both concatenated ND2/ND3 and COI haplotypes. The concatenated ND2/ND3 tree was most informative because more comparative material was available on GenBank. The Lemon-bellied White-eye and Pale-bellied White-eye are close relatives, sharing a node with the Black-crowned White-eye *Zosterops atrifrons* (Figure 5.3). For the Lemon-bellied White-eye, there was a clear split between the *Z. c. flavissimus* population on the Wakatobi Islands and all other Lemon-bellied White-eye populations in ND2/ND3 (Figure 5.3). All individuals from mainland South-east Sulawesi and the adjacent continental islands (Buton, Muna, Kabaena and Wawonii) grouped closely together. However the mainland South-east Sulawesi population showed some divergence from the population on the southern peninsula of Sulawesi. The Runduma population was also distinct from the mainland South-east Sulawesi population, though the split was shallower than that between the mainland South-east Sulawesi and South Sulawesi populations. The four groupings of Lemon-bellied White-eye; 1. Wakatobi *Z. c. flavissimus*, 2. South Sulawesi, 3. South-east Sulawesi mainland and continental islands and 4. Runduma Island, showed little within group variability, but distinct splits between

populations (Figure 5.4). The majority of the ‘mainland South-east Sulawesi’ individuals shared the same haplotype (ND2/ND3: hapCH02) (Figure 5.4, Table S5.1). The COI tree provided additional support for the taxonomic pattern seen in the Lemon-bellied White-eye (Figure 5.5), with a strong split between the *Z. c. flavissimus* population on the Wakatobi Islands and mainland South-east Sulawesi populations, and a further shallower split between the Runduma Island population and the individuals sampled on mainland Sulawesi and its continental islands. There was little within group variability between haplotypes and distinct splits between these groups (Figure 5.6, Table S5.1).

The Pale-bellied White-eye displayed an unusual pattern (Figures 5.3 and 5.4). All mainland Sulawesi individuals grouped closely together and showed only minor divergence from the most isolated Pale-bellied White-eye population on Kabaena Island in ND2/ND3. However the Buton and Muna populations proved distinct. Within this population there was a further deeper split between individuals with the haplotypes hapCO11-12 ($N = 2$ from Buton) which were more closely related to the Kabaena and Sulawesi populations, and individuals with haplotypes hapCO10 and hapCO13 ($N = 3$ from Buton and $N = 1$ from Muna) which were much more distinct (Figure 5.4). Individuals from both of these divergent Buton/Muna populations were found at the same site on Buton (Kusambi, 5.153°S 122.895°E) (Table S5.1). The mainland Sulawesi and Kabaena populations showed no difference in COI, sharing the same haplotypes (Figures 5.5 and 5.6, Table S5.1). The COI phylogeny also separated Buton birds from those on mainland Sulawesi and Kabaena, but with a shallower split than for ND2/ND3.

The ‘Wangi-wangi White-eye’ was not closely related to the Pale-bellied White-eye, as had been provisionally suggested (van Balen 2018c) (Figure 5.3). It was a highly distinct taxon, most closely related to the Kolombangara White-eye *Zosterops murphyi*, Rennell White-eye *Zosterops rennellianus* and the Louisiade White-eye *Zosterops griseotinctus*, taxa found in the Solomon Islands (>3000km distant). The COI tree lacked the depth of sampling within the *Zosterops* genus to provide any further insight into the evolutionary history of the ‘Wangi-wangi White-eye’, but confirmed its difference from sequenced taxa (Figure 5.5).

In addition to our focal species, the phylogenetic analyses illustrated deep separations within several widespread *Zosterops* species; the Oriental White-eye, Japanese White-eye and African Yellow White-eye *Zosterops senegalensis* (Figure 5.3 and 5.5).

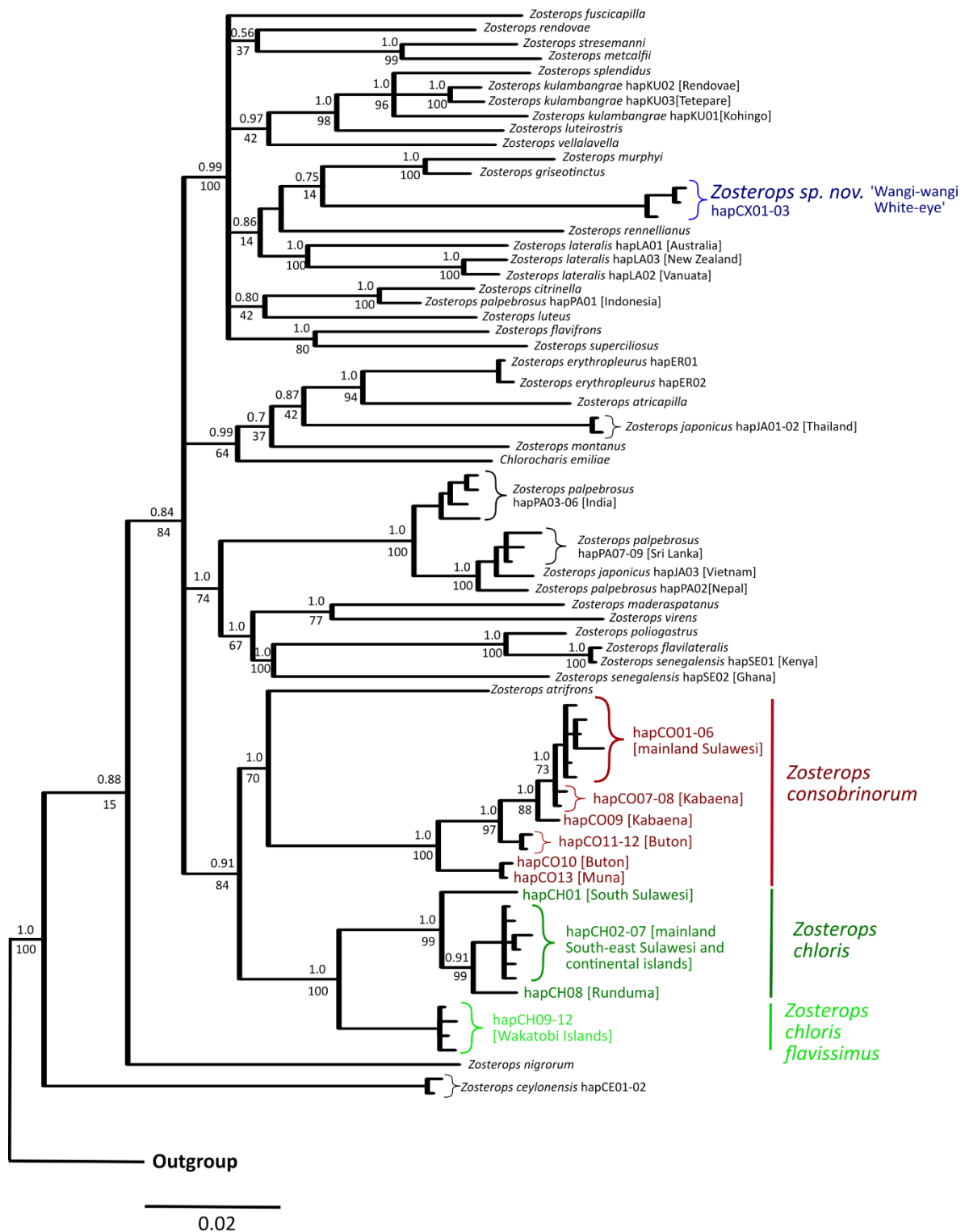


Figure 5.3: Bayesian consensus tree for concatenated ND2/ND3 haplotypes, showing Bayesian posterior probabilities (above) and bootstrap values from our maximum likelihood analysis (below) for each node. Haplotype number was given when there was more than one representative of a single taxon, with geographic information added with square brackets (single node) or curly brackets (multiple nodes) when that was informative to the pattern seen. Full tree with outgroups shown available in supplementary material (Figure S5.1).

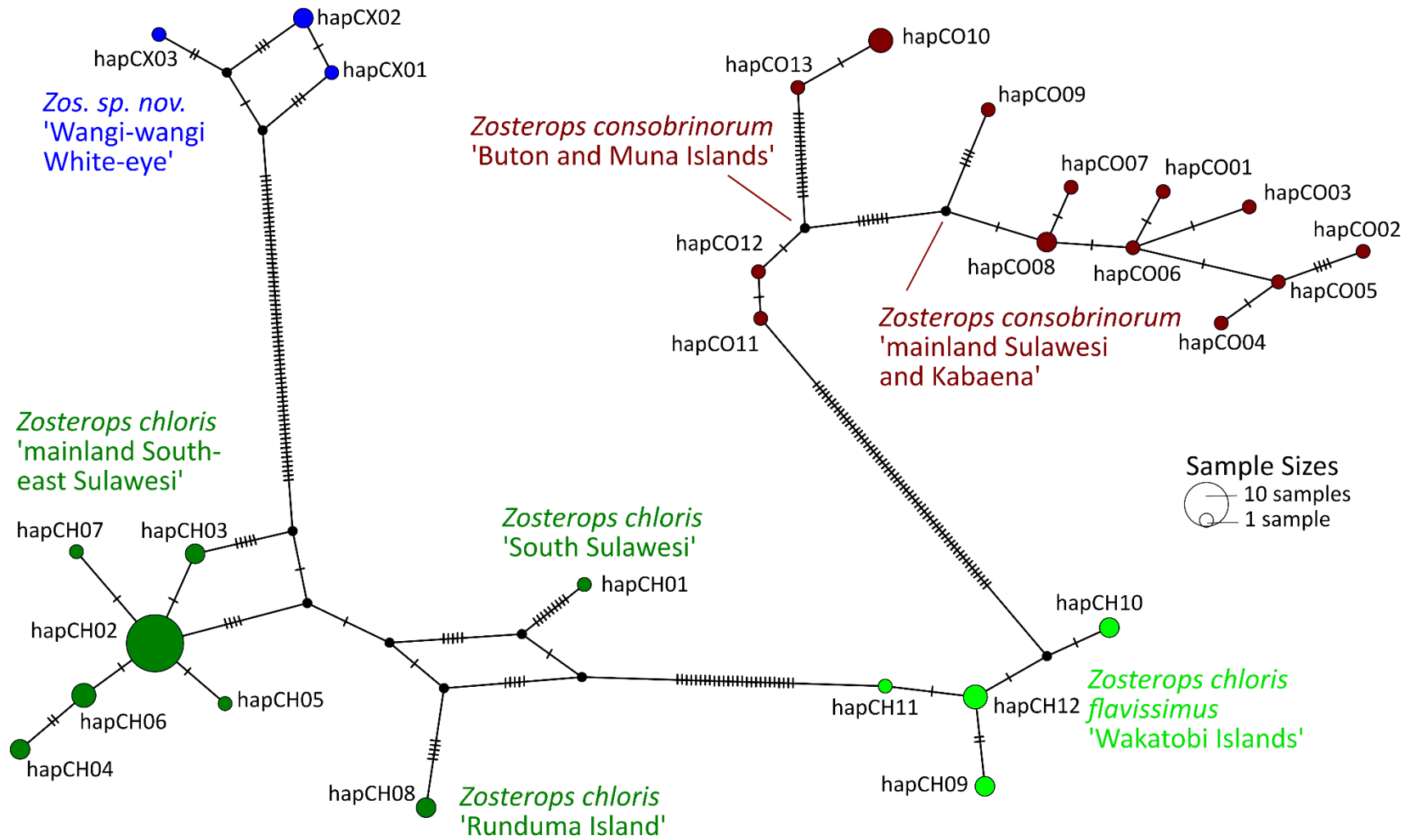


Figure 5.4: Haplotype network of sampled Sulawesi *Zosterops* populations samples, based on concatenated ND2/3 sequences. One bar indicates one mutation, black nodes are hypothetical ancestral states and the size of the circles corresponds to the number of sampled individuals sharing that haplotype.

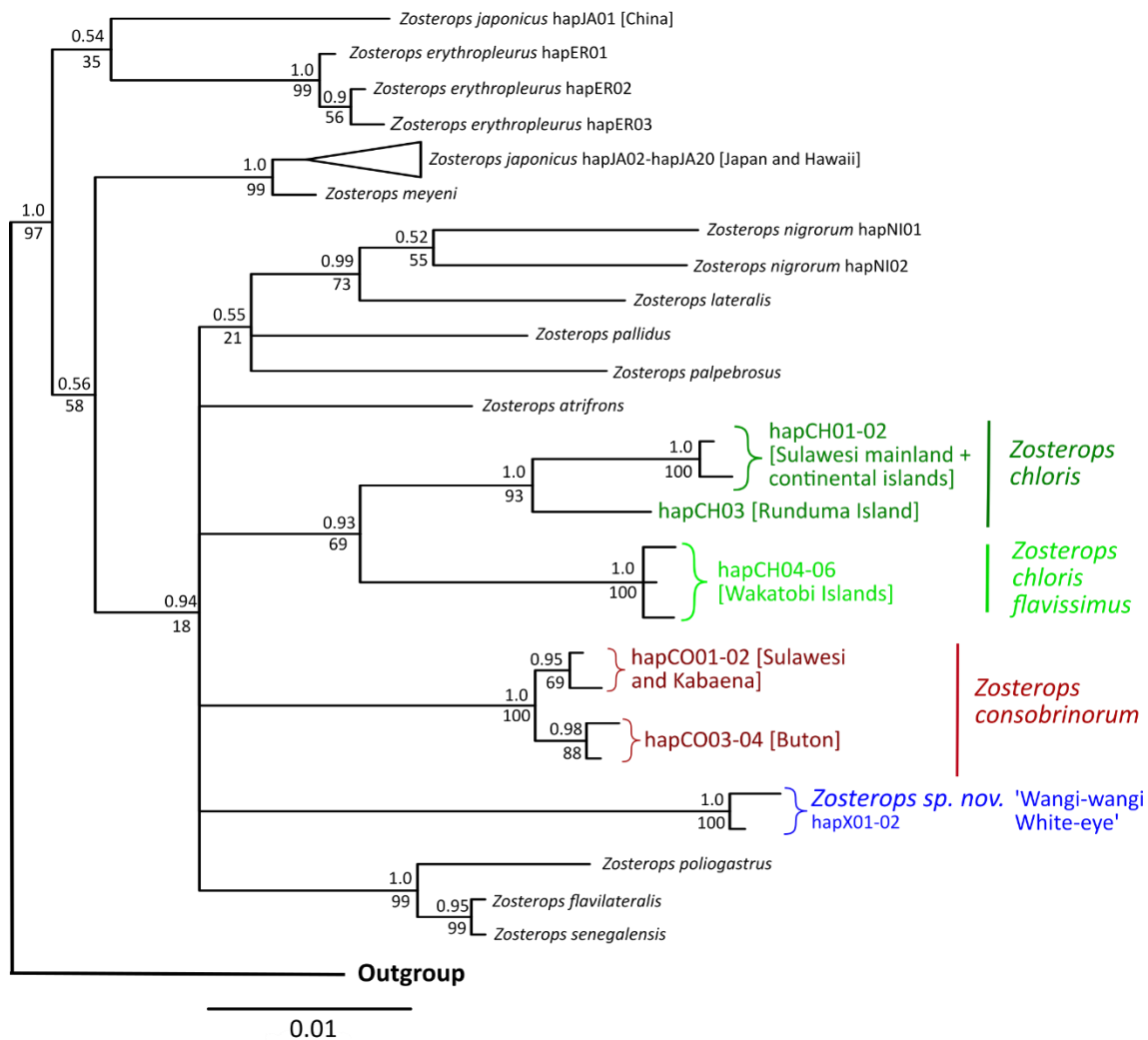


Figure 5.5: Bayesian consensus tree for COI haplotypes, showing Bayesian posterior probabilities (above) and bootstrap values from our maximum likelihood analysis (below) for each node. Haplotype number was given when there was more than one representative of a single taxa, with geographic information added with square brackets (single node) or curly brackets (multiple nodes) when that was informative to the pattern seen. The core Japanese White-eye *Zosterops japonicus* lineage was collapsed as it was monophyletic. Full tree with outgroups shown available in supplementary material (Figure S5.2).

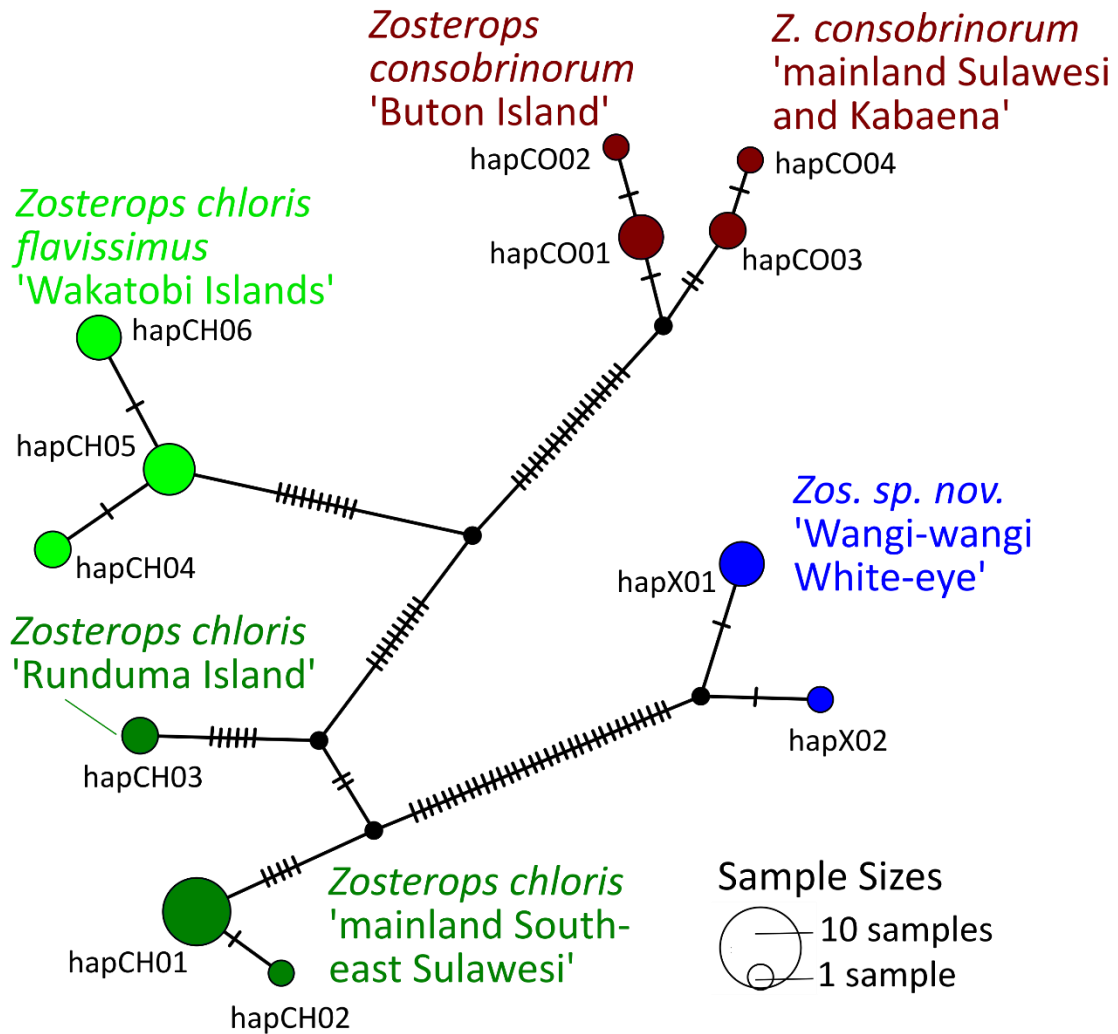


Figure 5.6: Haplotype network of sampled Sulawesi *Zosterops* populations samples, based on COI sequences. One bar indicates one mutation, black nodes are hypothetical ancestral states and the size of the circles corresponds to the number of sampled individuals sharing that haplotype.

5.4.4. Divergence dating

Our molecular clock showed the *Zosterops* radiation to have begun ~1.8 Myr ago (Figure 5.7) as demonstrated in Moyle *et al.* (2009) and Wickramasinghe *et al.* (2017). Within our focal species, the 'Wangi-wangi White-eye' was estimated to have diverged 0.7-1.23 Myr ago. Precise dating for this taxon was difficult, as its closest relatives are Solomon Islands endemics, separated by a large geographic distance. The Lemon-bellied White-eye diverged from the Black-crowned White-eye *Zosterops atrifrons* and Pale-bellied White-eye 0.77-1.36 Myr ago. *Zosterops c. flavissimus* on the Wakatobi Islands diverged from the Lemon-bellied White-eye mainland Sulawesi populations 0.38-0.8 Myr ago. This may mark the colonisation of the Wakatobi Islands by the Lemon-bellied White-eye. The South Sulawesi and South-east Sulawesi populations of

Lemon-bellied White-eye then diverged 0.17-0.38 Myr ago, with a later divergence of the Runduma Island population from South-east Sulawesi mainland populations 0.08-0.22 Myr ago.

The Pale-bellied White-eye diverged from the Black-crowned White-eye 0.57-1.21 Myr ago (Figure 5.7). The unusual population structure within the Pale-bellied White-eye population from Buton and Muna made estimating divergence dates challenging. Individuals with the ND2/ND3 haplotypes hapCO10 and hapCO13 (Buton and Muna) diverged from other populations 0.22-0.51 Myr ago. The remaining Buton individuals diverged 0.08-0.22 Myr ago. Divergence dating of the Kabaena population was also unclear and too shallow to offer sensible estimates.

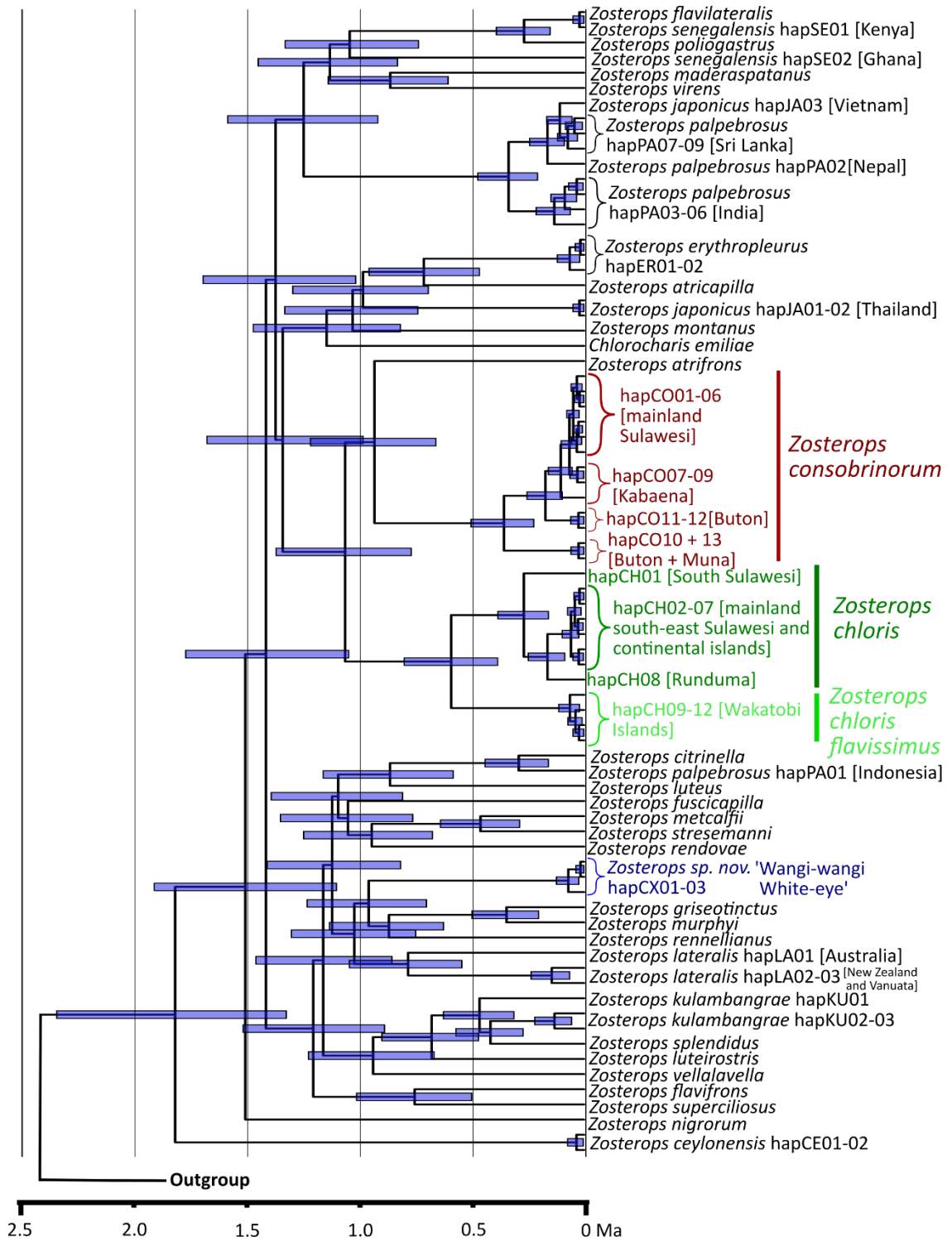


Figure 5.7: Divergence dating of *Zosterops* species based on BEAST analysis on concatenated ND2/ND3 genes. The blue bars indicate 95% Highest Posterior Density (HPD) intervals.

5.4.5. Genetic distance

Calculations of pairwise genetic distance provided an indication of the level of divergence between the populations described in our phylogenetic trees. COI samples were not available for all populations, but COI distances are given where available. Pairwise distances between all *Zosterops* species sampled are available in the supplementary material (Tables S5.6 and S5.7).

Lemon-bellied White-eye: Mainland South-east Sulawesi (including continental islands) and South Sulawesi populations showed divergence (ND2: 1.22%) as demonstrated by our phylogenetic work. Within the focal region, mainland South-east Sulawesi and the Wakatobi population were strongly divergent (ND2: 2.5%, COI: 4.9%). The Wakatobi population also differed from South Sulawesi (ND2: 2.05%) and Runduma (ND2: 2.35%, COI: 4.66%). The most closely-related population to Runduma was mainland South-east Sulawesi (ND2: 0.73%, COI: 2.22%). Each population showed low within group variability; mainland South-east Sulawesi (ND2: 0.09%, COI: 0.04%), Runduma (ND2: 0%, COI: 0%), Wakatobi Islands (ND2: 0.04%, COI: 0.14%).

Pale-bellied White-eye: The Buton/Muna population differed in ND2 from the Sulawesi population (2.1%) and Kabaena population (1.9%), though the Buton population showed less difference in COI to Sulawesi/Kabaena (0.59%). Sulawesi and Kabaena populations differed little (ND2: 0.31%, COI: 0%). The Buton/Muna population showed high within group variability for ND2 (ND2: 1.09%) in comparison to Sulawesi (ND2: 0.12%) and Kabaena (ND2: 0.29%) populations. COI was much less variable, with Buton populations showing only 0.11% within group variation and the undifferentiated Sulawesi and Kabaena populations showing 0.08%.

‘Wangi-wangi White-eye’: The ‘Wangi-wangi White-eye’ was strongly distinct from all Pale-bellied White-eye populations (ND2: 6.23% and COI: 8.35% at a minimum) and all Lemon-bellied White-eye populations (ND2: 5.24% and COI: 7.17% at a minimum). The most closely-related populations were the Louisiade White-eye (ND2: 5.08%) and Lowland White-eye *Zosterops meyeri* (COI: 6.78%). The ‘Wangi-wangi White-eye’ showed minor within group variability (ND2: 0.29%, COI: 0.16%).

5.4.6. Morphological analyses

A total of 752 *Zosterops* individuals from 11 islands were measured for these analyses; 575 Lemon-bellied White-eyes, 139 Pale-bellied White-eyes and 38 ‘Wangi-wangi White-eyes’ (Supplementary information, morphological trait summaries Tables S5.8-S5.11). For analysis the

sampled individuals were grouped along the splits provided by the molecular phylogenies. Lemon-bellied White-eye individuals were classified into the groupings; mainland (Sulawesi mainland and the continental islands $N = 168$), Wakatobi (the six Wakatobi Islands $N = 362$) and Runduma ($N = 45$). Pale-bellied White-eye individuals were split into mainland Sulawesi ($N = 48$), Buton and Muna ($N = 68$) and Kabaena ($N = 23$) groups. 'Wangi-wangi White-eyes' ($N = 38$) were analysed with Pale-bellied White-eyes to establish the level of separation between them.

For Lemon-bellied White-eye morphology, PC1 (78% of the variance) and PC2 (8.3% of the variance) had eigenvalues > 1 and were carried forward for analyses. PC1 was loaded equally between the seven morphological traits, giving a general indicator of body size (Table S5.12). PC2 was largely loaded by bill length and skull length, giving a general indicator of bill to skull ratio. The Lemon-bellied White-eye populations were significantly different from each other in body size (PC1, ANOVA: $F_{2,572} = 554.5$, $P < 0.001$), with the mainland, Wakatobi and Runduma populations all significantly different from each other (Tukey HSD, $P \text{ adj.} < 0.001$ for all comparisons). Runduma individuals were the largest, followed by mainland individuals, with Wakatobi individuals being the smallest (Figure 5.8, Tables S5.8 and S5.9). Lemon-bellied White-eye populations also significantly differed in bill to skull ratio (PC2, ANOVA: $F_{2,572} = 17.56$, $P < 0.001$), with the Runduma population differing from mainland (Tukey HSD, $P \text{ adj.} < 0.001$) and Wakatobi (Tukey HSD, $P \text{ adj.} < 0.001$) populations (Figure 5.8). Mainland and Wakatobi populations did not differ for PC2.

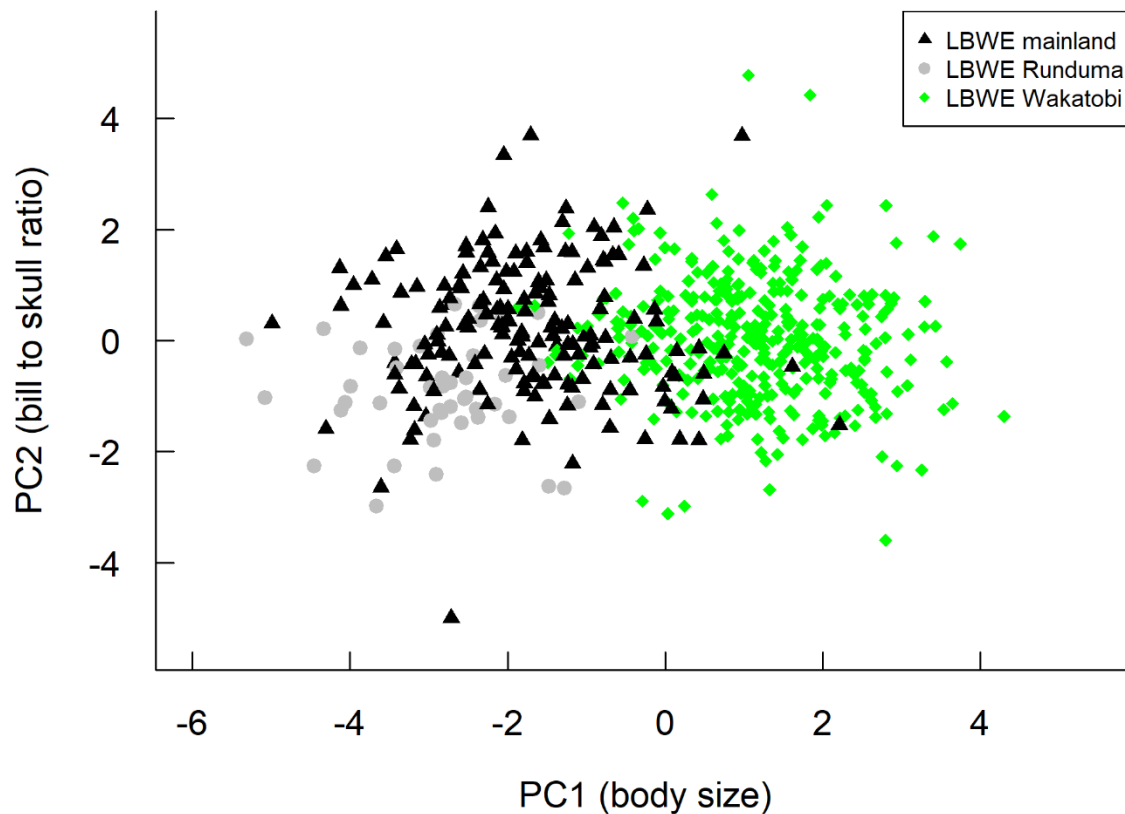


Figure 5.8: Scatterplot of Lemon-bellied White-eye (LBWE) morphological PCA. Black triangles represent individuals from mainland South-east Sulawesi and its continental islands, grey circles represent individuals from Runduma Island, green diamonds represent individuals from the Wakatobi Islands. Variance explained: PC1 - 78.3%, PC2 - 8.3%. Negative values for PC1 indicates larger body size.

For Pale-bellied White-eye and 'Wangi-wangi White-eye' morphology, only PC1 (88.7% of the variance) had an eigenvalue > 1 and was carried forward for analysis (Table S5.12). PC1 was equally weighted between all seven morphological traits and provided a general indicator of body size. The Pale-bellied White-eye populations and 'Wangi-wangi White-eye' differed significantly in body size (PC1, ANOVA: $F_{3, 173} = 918.1$, $P < 0.001$) (Figure 5.9, Tables S5.10 and S5.11). The 'Wangi-wangi White-eye' was larger than all Pale-bellied White-eye populations (Tukey HSD, $P_{adj.} < 0.001$ for all comparisons). The Pale-bellied White-eye Kabaena population was significantly larger than both the mainland Sulawesi and Buton/Muna population (Tukey HSD, $P_{adj.} < 0.001$ for both comparisons). The mainland Sulawesi and Buton/Muna population did not differ in morphology.

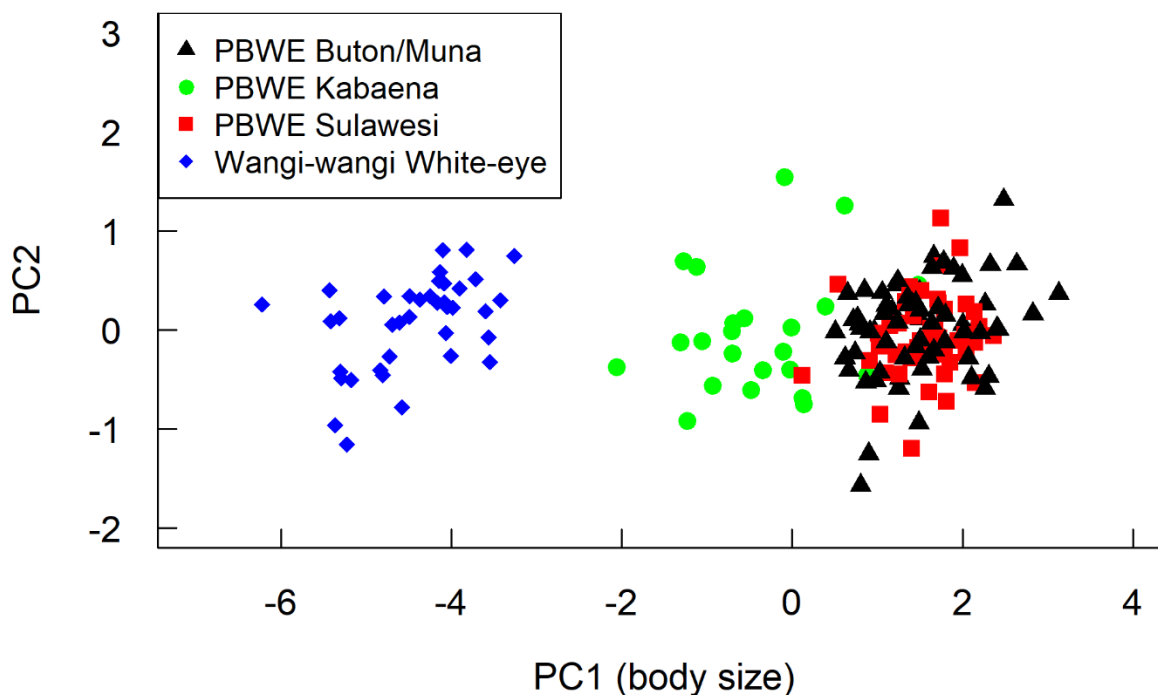


Figure 5.9: Scatterplot of Pale-bellied White-eye (PBWE) and 'Wangi-wangi White-eye' morphology PCA. Black triangles represent Pale-bellied White-eye individuals from Buton and Muna Islands, red squares represent Pale-bellied White-eye individuals from mainland Sulawesi, green circles represent Pale-bellied White-eye individuals from Kabaena Island, blue diamonds represent the 'Wangi-wangi White-eye'. Variance explained: PC1 - 88.7%, PC2 - 3.2%. Negative values for PC1 indicates larger body size.

5.4.7. Song analyses

A total of 120 *Zosterops* individuals from seven islands had their song recorded for these analyses; 52 Lemon-bellied White-eyes and 68 Pale-bellied White-eyes (Supplementary information, song trait summaries Tables S5.13-S5.16). No 'Wangi-wangi White-eye' songs were recorded. An additional three recordings were sourced from Xeno-Canto; two *Z. chloris maxi* recordings taken on Lombok Island (XC166854 and XC166855) and one Pale-bellied White-eye recording from Buton Island (XC333521). As with the morphological analyses, for the song analyses Lemon-bellied White-eye individuals were split into mainland ($N = 24$) and Wakatobi ($N = 28$) groups, with the addition of a Lombok group ($N = 2$). Pale-bellied White-eye individuals were split into mainland Sulawesi ($N = 11$), Buton and Muna ($N = 31$) and Kabaena ($N = 27$) groups.

For Lemon-bellied White-eye song, PC1 (39.8% of the variance), PC2 (24.0%) and PC3 (16.4%) had eigenvalues > 1 and were carried forward for analyses (Table S5.15). PC1 was most heavily loaded by the number of notes, duration, maximum frequency and bandwidth. PC2 was

most heavily loaded by the temporal traits duration and pace. PC3 was most heavily loaded by minimum frequency and pace. The Lemon-bellied White-eye populations differed significantly in all comparisons (PC1, ANOVA: $F_{2,51} = 52.89$, $P < 0.001$; PC2, ANOVA: $F_{2,51} = 6.073$, $P < 0.005$; PC3, ANOVA: $F_{2,51} = 3.196$, $P < 0.05$). All three populations were distinct (Figure 5.10 and Tables S5.13-S5.15). The Lemon-bellied White-eye mainland population differed significantly from the Wakatobi population in PC1 (Tukey HSD, $P_{adj.} < 0.001$) and from the Lombok population in PC1 and PC2 (Tukey HSD, $P_{adj.} < 0.001$ and $P_{adj.} < 0.05$ respectively). The Wakatobi and Lombok populations differed significantly in PC2 and PC3 (Tukey HSD, $P_{adj.} < 0.01$ and < 0.05 respectively).

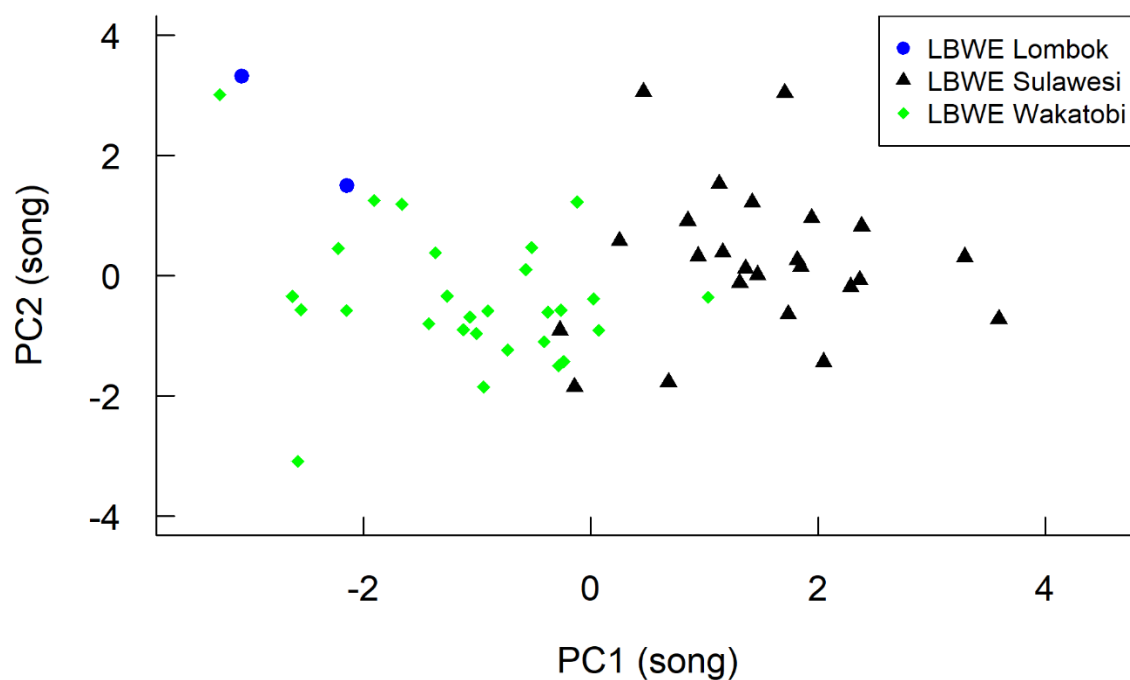


Figure 5.10: Scatterplot of Lemon-bellied White-eye (LBWE) song PCA. Black triangles represent individuals from mainland South-east Sulawesi and its continental islands, green diamonds represent individuals from the Wakatobi Islands, blue circles represent individuals from Lombok. Variance explained: PC1 - 39.8%, PC2 - 24.0%.

For Pale-bellied White-eye song, PC1 (41.7% of the variance), PC2 (21.8%) and PC3 (16.2%) had eigenvalues > 1 and were carried forward for analyses (Table S5.17). PC1 was most heavily loaded by duration, maximum frequency and bandwidth. PC2 was most heavily loaded by pace and peak frequency. PC3 was most heavily loaded by the number of notes, maximum frequency and bandwidth. The Pale-bellied White-eye Kabaena and Buton/Muna populations

differed significantly in song PC1 (PC1, ANOVA: $F_{2,66} = 4.133$, $P < 0.05$; Tukey HSD, $P_{adj.} < 0.05$) (Figure 5.11). There were no other significant differences in Pale-bellied White-eye song.

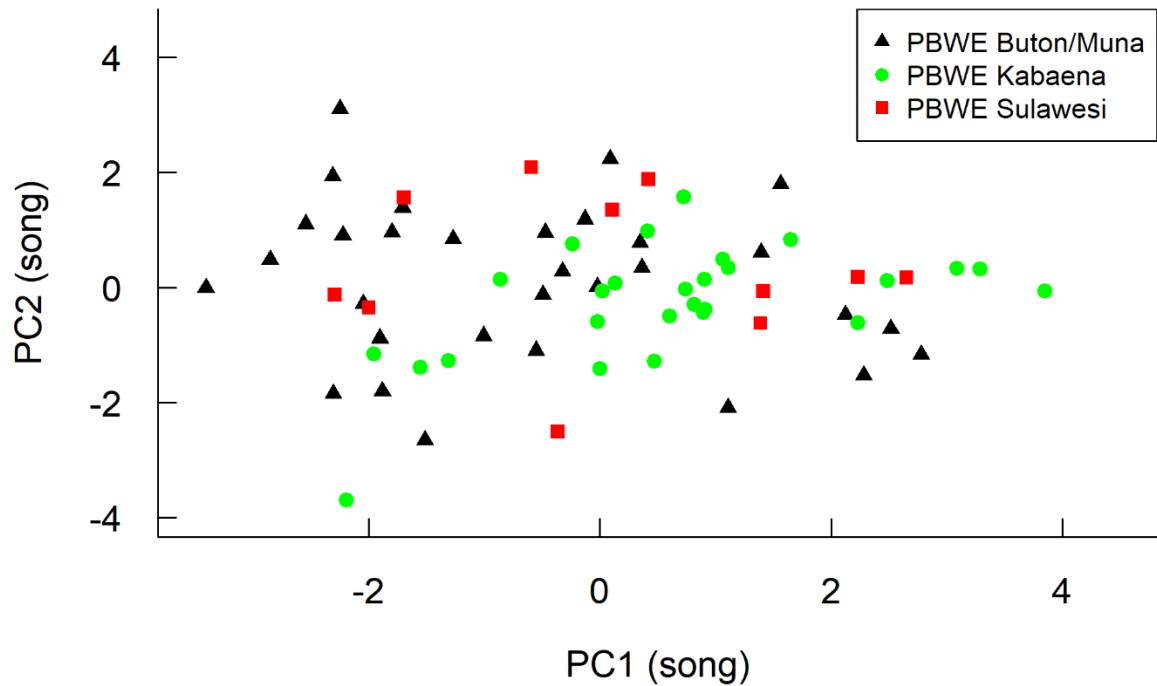


Figure 5.11: Scatterplot of the Pale-bellied White-eye (PBWE) song PCA. Black triangles represent Pale-bellied White-eye individuals from Buton and Muna Islands, red squares represent Pale-bellied individuals from mainland Sulawesi, green circles represent Pale-bellied White-eye individuals from Kabaena Island. Variance explained: PC1 - 41.7%, PC2 - 21.8%.

5.4.8. Classification based on morphological and song traits

DFA classification of Lemon-bellied White-eye individuals suggested a close match of morphological and song traits for the taxonomic groupings identified in our molecular phylogeny (Table 5.2, Figure 5.3-5.6). The sampling location of the majority of individuals could be accurately predicted from these traits.

Table 5.2: Percentage classification accuracy of the DFA for morphology and song of Lemon-bellied White-eyes (LBWE). Sample sizes given are: N = morphological sample size / song sample size. A dash indicates no sample available for that population. Results given indicate the % of individuals classified in that category, with morphological results before the slash (/) and song results after. Shaded grey squares are the predicted result, i.e. the population from which the individual was sampled. All seven morphological traits; wing, tail, tarsus, skull and bill length, bill depth and weight, were used. All seven song traits; number of notes, duration, pace, maximum, minimum and peak frequency, and bandwidth, were used.

	LBWE "mainland"	LBWE "Wakatobi"	LBWE "Runduma"	LBWE "Lombok"
LBWE "mainland SE Sulawesi + continental islands" ($N = 168 / 24$)	89.29 / 95.83	8.92 / 4.17	1.79 / -	- / 0
LBWE "Wakatobi Islands" ($N = 362 / 28$)	3.6 / 0	96.4 / 100	0 / -	- / 0
LBWE "Runduma" ($N = 45 / -$)	2.22 / -	2.22 / -	95.56 / -	- / -
LBWE "Lombok" ($N = - / 2$)	- / 0	- / 0	- / -	- / 100

The 'Wangi-wangi White-eye was 100% distinguishable in morphology from all Pale-bellied White-eye populations in the DFA analysis (Table 5.3). There was only a weak distinction between Pale-bellied White-eye populations. The Kabaena Pale-bellied White-eye was the most accurately classified in morphology, and the Buton/Muna population showed the greatest classification accuracy in song, however both showed a large degree of overlap with other Pale-bellied White-eye populations. The mainland Sulawesi population could not be accurately classified, particularly with song traits. More Sulawesi individuals were classified as belonging to other islands than to Sulawesi.

Table 5.3: Percentage classification accuracy of the DFA for morphology and song of Pale-bellied White eyes (PBWE) and the ‘Wangi-wangi White-eye’. Sample sizes given are: N = morphology sample size / song sample size. A hyphen (-) indicates no sample available for that population. Results provided are: % of individuals classified in that category, with morphological results before the slash (/) and song results after. Shaded grey squares are the predicted result, i.e. the population from which the individual was sampled. Morphological traits wing, tail, tarsus, skull and bill length, bill depth and weight used. All seven song traits; number of notes, duration, pace, maximum, minimum and peak frequency, and bandwidth, were used.

	PBWE “mainland”	PBWE “Buton/Muna”	PBWE “Kabaena”	“Wangi-wangi White-eye”
PBWE “mainland Sulawesi” ($N = 48 / 11$)	58.33 / 18.18	41.67 / 45.45	0 / 36.36	0 / -
PBWE “Buton/Muna” ($N = 68 / 31$)	20.6 / 0	77.94 / 74.19	1.47 / 25.81	0 / -
PBWE “Kabaena” ($N = 23 / 27$)	4.35 / 0	13.0 / 33.33	82.61 / 66.66	0 / -
“Wangi-wangi White- eye” ($N = 38 / -$)	0 / -	0 / -	0 / -	100 / -

5.4.9. Tobias scoring

For the Tobias scoring of phenotypic traits the Wakatobi *Z. c. flavissimus* population was compared to the Lemon-bellied White-eye mainland South-east Sulawesi and continental islands population and the ‘Wangi-wangi White-eye’ was compared to the Pale-bellied White-eye. Both *Z. c. flavissimus* (Tobias score: nine) and the ‘Wangi-wangi White-eye’ (Tobias score: seven) were identified as distinct species. Detailed scoring is provided in the Appendices (Sections 5.1.1 and 5.1.2).

5.4.10. Assessment of dispersal ability

South-east Sulawesi *Zosterops* populations differed significantly in their inferred dispersal ability, indicated by the Wingspan to Weight ratio (S^3/m) dispersal ability proxy (ANOVA: $F_{6, 745} = 35.66$, $P < 0.001$) (Figure 5.12). Much of this difference was accounted for by the Lemon-bellied White-eye Runduma population, which had a significantly longer wingspan for its body mass than any of the other *Zosterops* populations (Tukey HSD, $P_{adj.} < 0.001$ for all comparisons). The Lemon-bellied White-eye mainland population also had a significantly longer wingspan for its body mass than any of the other *Zosterops* populations (Tukey HSD, $P_{adj.} < 0.05$ for all comparisons), apart from the Lemon-bellied White-eye Runduma population. There were no

significant differences between the Lemon-bellied White-eye Wakatobi Islands population, 'Wangi-wangi White-eye' and any of the Pale-bellied White-eye populations.

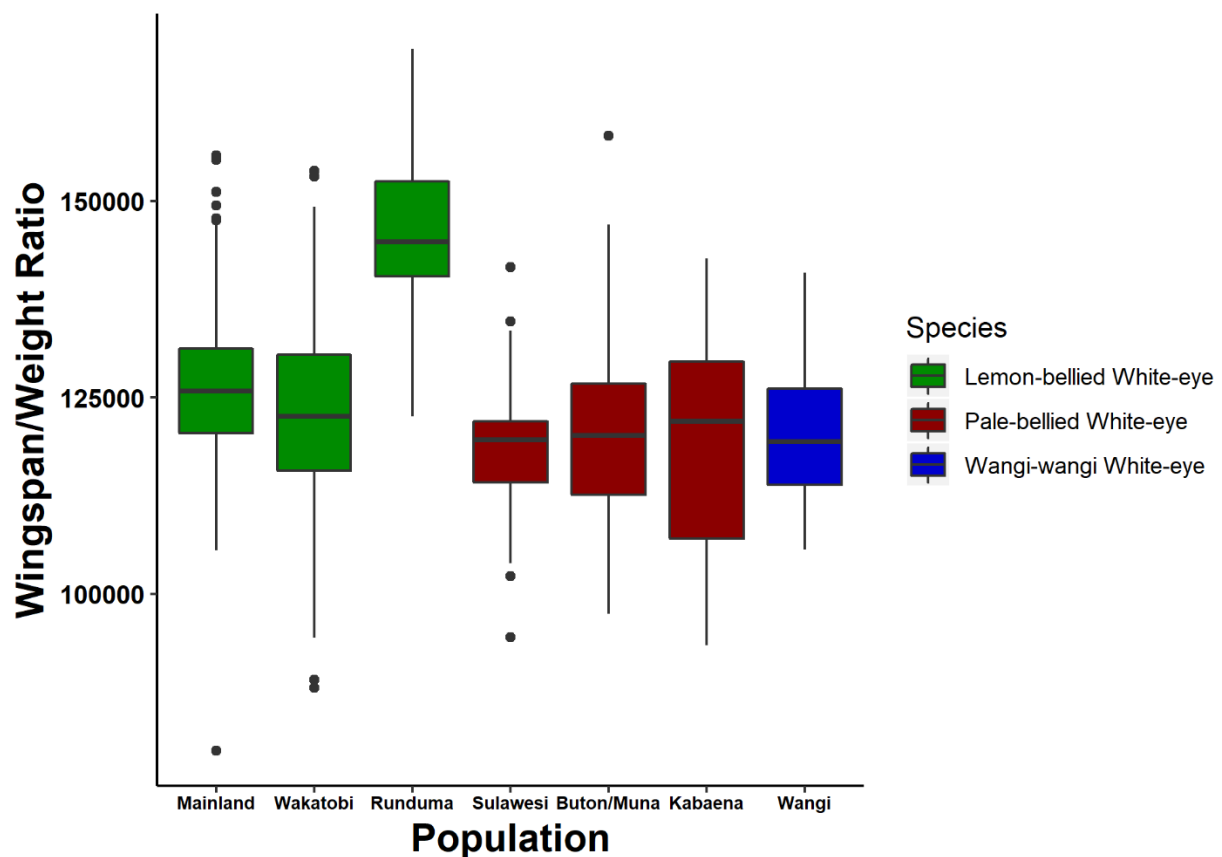


Figure 5.12: The Wingspan/Weight ratio of each *Zosterops* population identified in this study, providing a proxy for their dispersal ability.

5.5. Discussion

Our results present evidence for the recognition of two new species of *Zosterops* from the same island archipelago in Sulawesi. The 'Wangi-wangi White-eye' is a phenotypically-distinct species in need of recognition. It is reciprocally monophyletic from all other sampled *Zosterops* species. *Zosterops c. flavissimus* proved distinct in genetics, morphology and song and we believe it should be promoted to full species status. The proposal to recognise these two new species is also supported by the Tobias taxonomic scoring criteria (Appendices - Section 5.1 Tobias scoring, Tables S5.18 and S5.19) (Tobias *et al.* 2010). Our results suggest that Sulawesi Lemon-bellied White-eye subspecies are in need of further revision. We do not recommend any change to the taxonomy of the Pale-bellied White-eye, as populations of this species did not show consistent variation between genetic and phenotypic measures. Our results also demonstrate differences

in dispersal ability between *Zosterops* populations in an early colonisation period, and populations which have become isolated, endemic species.

5.5.1. *Zosterops* sp. nov. - the 'Wangi-wangi White-eye'

The discovery of unrecorded novel vertebrate species (i.e. not by splitting documented populations) has become increasingly rare. Due to its unique biogeographic position (Esselstyn *et al.* 2010), Sulawesi has particularly high endemism (Michaux 2010). It also remains relatively poorly studied (Cannon *et al.* 2007) and novel taxa have been found on Sulawesi in recent years (Indrawan and Rasmussen 2008; Esselstyn *et al.* 2012). However, these taxa were found in remote forested areas or on more isolated islands. The fact that the 'Wangi-wangi White-eye' was found on a densely populated, environmentally degraded island was particularly remarkable. Most Wakatobi bird species descriptions date from the expedition of Heinrich Kühn (1901-1902) (Hartert 1903). This single island endemic must have been overlooked.

The 'Wangi-wangi White-eye' occurs in mixed species flocks with the Lemon-bellied White-eye on Wangi-wangi, and exhibits the same generalist foraging habits common to *Zosterops* (van Balen 2008; Kelly 2014). The 'Wangi-wangi White-eye' was a much larger bird than the Lemon-bellied White-eye (Table S5.9 and S5.11), likely facilitating niche partitioning between these congeneric species. It was relatively common on Wangi-wangi; in the 18 mist-netting sessions conducted on that island, 20% of birds caught were 'Wangi-wangi White-eyes' and 39% were Lemon-bellied White-eyes. All netting was carried out in the scrub and forest edge habitats which are the most common ecosystems on the island. 'Wangi-wangi White-eyes' showed tolerance of disturbed habitats, though they did not show the flexibility in habitat preference of Lemon-bellied White-eyes (present in all habitats on the Wakatobi Islands), and were not present in mangroves. Concern for the future of the 'Wangi-wangi White-eye' is amplified by the small size of Wangi-wangi island (155km²) and that extensive surveys in South-east Sulawesi have shown it to be the only home of the 'Wangi-wangi White-eye' (it was even absent from Wangi-wangi's satellite islands; Oroho and Kapota). The authors recommend the collection of type specimens so that this species can be officially named and recognised, coupled with detailed surveys of Wangi-wangi Island to assess this species' distribution and density, and any conservation action required. A series of photos of this species are supplied in the supplementary material to aid future field identification of this new taxon.

The provisional classification of the 'Wangi-wangi White-eye' as a population of the Pale-bellied White-eye (van Balen 2018c) is understandable; both are pale-chested *Zosterops*

separated by a short distance (27km between Buton and Wangi-wangi). However our Tobias scoring of the 'Wangi-wangi White-eye' versus the Pale-bellied White-eye (del Hoyo *et al.* 2018d), shows that these species are phenotypically distinct, and the 'Wangi-wangi White-eye' should be considered a separate species (Appendices, section 5.1.2). Our phylogenetic work shows the closest relatives of the 'Wangi-wangi White-eye' are found in the Solomon Islands; the Kolombangara White-eye and Rennell White-eye (single island endemics), and the Louisiade White-eye which is restricted to a series of small islands (van Balen 2018a). These taxa are all >3000km distant from Wangi-wangi and are phenotypically distinct, all having yellow/green chests. The nodes placing the 'Wangi-wangi White-eye' in this clade have low support (Figure 5.3), so its evolutionary origins remain uncertain. Sequencing of other Indo-Pacific *Zosterops* species which have not yet had their genetic data assessed, such as the Black-ringed White-eye *Zosterops anomalus* from South Sulawesi, may shed light on this situation. The 'Wangi-wangi White-eye' may be a remnant of an older *Zosterops* radiation and represent a relict taxon.

5.5.2. Lemon-bellied White-eye - independent colonisations and the 'Wakatobi White-eye'

This study clarified a number of features about Sulawesi Lemon-bellied White-eye populations, while raising further questions. It appears from our data that the South-east Sulawesi mainland and its continental islands form a continuous population, rather than *Z. c. intermedius* being present on the continental islands and *Z. c. mentoris* on the mainland as had been suggested in Trochet *et al.* (2014). The mainland South-east Sulawesi population of Lemon-bellied White-eyes was closely related to the South Sulawesi population (*Z. c. intermedius*), but shows sufficient divergence (ND2: 1.22%) that further investigation is required to clarify their taxonomy. Currently there is insufficient genetic or phenotypic data to classify the Lemon-bellied White-eyes from the mainland South-east Sulawesi population as either *Z. c. intermedius* or *Z. c. mentoris*. *Zosterops c. intermedius*, as currently defined includes populations from South Sulawesi, the continental islands of South-east Sulawesi and much of the Lesser Sundas (van Balen 2018a). An assessment of the different populations currently assigned to *Z. c. intermedius*, and *Z. c. mentoris* (isolated populations in Central and Northern Sulawesi) are needed to clarify the taxonomy of Lemon-bellied White-eyes on mainland Sulawesi.

Within South-east Sulawesi, the Runduma population of Lemon-bellied White-eyes (first noted by this study) represents a recent independent colonisation from a mainland South-east Sulawesi source population (Figure 5.7), not from the Wakatobi Islands. This was an unexpected discovery, as the shortest distance between Runduma and the closest mainland population

(Buton) is 123km (Figure 5.1). The distance between Runduma and its nearest Wakatobi Island neighbour is only 61km (Daft Logic 2018b). The Runduma population of another small passerine, the Olive-backed Sunbird *Cinnyris jugularis*, appears to have colonised Runduma via the shorter distance from the Wakatobi Islands (Kelly 2014). Given Runduma's isolation and tiny size (c. 5.5 km²) (Daft Logic 2018a), it was unsurprising that it was colonised much later than the Wakatobi Islands (Figure 5.7). Runduma Lemon-bellied White-eyes are morphologically distinct from other Lemon-bellied White-eye populations, showing the largest body size and longest bill length (Figure 5.8, Table S5.8). Larger bill and body size has been repeatedly observed to evolve in bird populations as an adaptation to a more generalist niche on small islands (Grant 1965; Clegg *et al.* 2002; Clegg and Owens 2002; Scott *et al.* 2003). Runduma was almost entirely covered in coconut plantation, and the Lemon-bellied White-eye population has been observed to feed on coconut nectar more regularly on Runduma than elsewhere (DJK, pers. obs.). Thus the longer bill may be an adaptation allowing the population to take advantage of an abundant resource in an ecologically constrained habitat. Such changes can be rapid and quickly come to fixation in a population (Bosse *et al.* 2017). This morphological difference, coupled with the pairwise genetic distance (ND2: 0.73%, COI: 2.22%), between mainland Sulawesi and Runduma populations indicates there may be a subspecies level difference between them (Hebert *et al.* 2004b). Future collection of song recordings and type specimens for assessment of more subtle plumage differences might prove useful in determining the taxonomic status of this population.

Zosterops c. flavissimus (Wakatobi Islands) proved the most distinct of the Lemon-bellied White-eye populations sampled. It appears to have diverged much earlier (0.38-0.8 Myr ago) than any of the other Sulawesi populations of Lemon-bellied White-eye (Figure 5.7). This was an older date of divergence than that of several recognised *Zosterops* species (Figure 5.7). *Zosterops c. flavissimus* was morphologically distinct from other Lemon-bellied White-eye populations (Figure 5.8, Tables S5.8 and S5.9), being significantly smaller. Its song was highly distinct from mainland South-east Sulawesi Lemon-bellied White-eyes (Figure 5.10), with a generally higher maximum frequency and number of notes (Tables S5.13 and S5.14), which would be expected for a population with a smaller body size (Potvin 2013). Wakatobi *Z. c. flavissimus* were also distinct from mainland South-east Sulawesi Lemon-bellied White-eyes in plumage, with a more vibrant yellow head and paler bill (Supplementary information: Tobias scoring, Table S5.18). The pairwise difference between Wakatobi *Z. c. flavissimus* and mainland South-east Sulawesi Lemon-bellied White-eyes (ND2: 2.5%, COI: 4.9%) was much larger than the average species difference (COI: 2.7%) Hebert *et al.* (2004b) found between North American birds, and is much more than 10 times the intra-group variation. It also compares favourably

with the pairwise differences found between well differentiated *Zosterops* species in this study (Tables S5.7 and S5.8). Our Tobias scoring of Wakatobi *Z. c. flavissimus* versus mainland Sulawesi Lemon-bellied White-eyes (del Hoyo *et al.* 2018d), showed *Z. c. flavissimus* to be phenotypically distinct, supporting its status as a full species (Appendices, section 5.1.1). All of this evidence makes a strong case for the recognition of *Z. c. flavissimus* as a full species. Several type specimens of the Wakatobi *Zosterops*, currently designated *Z. c. flavissimus*, are in the American Museum of Natural History's collection (Table S5.20). Based on these specimens Hartert (1903) originally described *Z. c. flavissimus* as an independent species, *Zosterops flavissimus*, but this species was subsumed into the Lemon-bellied White-eye in later taxonomic revisions. We hope the availability of these specimens will facilitate the promotion of *Z. c. flavissimus* to full species.

Zosterops c. maxi (Lombok) was also significantly different in song from other Lemon-bellied White-eye populations, though with a tiny sample size ($N = 2$). A much larger sample size and investigation of further traits would be needed to form a greater understanding of the relationship of *Z. c. maxi* to other Lemon-bellied White-eye populations.

5.5.3. Pale-bellied White-eye - inconsistent variation between measures

By providing the first detailed assessment of the Pale-bellied White-eye, this study gives a first insight into its evolutionary history and emphasises the need to use a combined approach when studying systematics and evolution. The fact that the Black-crowned White-eye *Z. atrifrons* was the Pale-bellied White-eye's closest relative from the species sampled was unsurprising. The Black-crowned White-eye is a pale-chested white-eye endemic to central and northern Sulawesi, showing geographic and phenotypic similarity (van Balen 2008). The unusual patterns of divergence between Pale-bellied White-eye populations emphasises how easily incorrect inferences can be drawn in phylogenetic studies, particularly when using a small number of mitochondrial genes. Due to unavoidable logistical constraints, many phylogeographic studies have relied on a small number of museum specimens from each individual population, or a single line of evidence, for assessing populations (genetic, phenotypic or acoustic). While phenotypic and genetic measures often provide the same answer (García *et al.* 2016), there are cases where they have been shown to differ (Phillimore *et al.* 2008b; Potvin *et al.* 2013).

While the Kabaena population of Pale-bellied White-eyes was distinct in morphology and song (Figure 5.9 and 5.11), it was almost inseparable from the mainland Sulawesi population in mitochondrial DNA (Figures 5.3-5.7). This population has only been separated from mainland Sulawesi since the last glacial maximum (Voris 2000). Kabaena was the smallest island (873 km²)

that the Pale-bellied White-eye was found on. This may have presented a more ecologically constrained environment for the Kabaena Pale-bellied White-eye population in comparison to the mainland (Lomolino and Weiser 2001). The larger body size of the Kabaena Pale-bellied White-eye population (Figure 5.9), may have been an adaptation to life on a smaller island (Clegg and Owens 2002). Morphological adaptation to new environmental conditions can occur rapidly in birds and may not be related to change in neutral genetic markers like mitochondrial DNA, particularly over the short time span Kabaena has been isolated (Nussey *et al.* 2005; Charmantier *et al.* 2008; Lande 2009). As well as adaptation to local conditions, genetic drift can play a role in phenotypic change in island populations, and may lead to rapid change in small populations on islands (Clegg *et al.* 2002; Runemark *et al.* 2010).

The unusual population structure of the Buton/Muna Pale-bellied White-eye population was more difficult to explain. Initial observations of the song and phenotype of the Buton population prompted suggestions it could be an independent subspecies (Wardill 2003). This would be unexpected for an island only 6km from Sulawesi, but not unprecedented (Mayr 1942; Mayr and Diamond 2001). This study found no such differences, but strong genetic divergence in ND2/ND3 in half of the Buton birds and the single Muna bird sampled. That such genetically divergent individuals could be found at the same site on Buton (Kusambi, 5.153°S 122.895°E) seems strange. The regular trading of *Zosterops* species as pets within Indonesia (Harris *et al.* 2017) may also have confused the pattern. Pale-bellied White-eyes sing the most readily of our study species (pers. obs.) and are popular pets. It is entirely possible that the Buton/Muna population was originally more genetically distinct, but escaped Pale-bellied White-eye pets with mainland Sulawesi heritage may have bred with the local population, reducing overall genetic divergence between Buton and Sulawesi (Laikre *et al.* 2010). There was no morphological distinction between Sulawesi, Buton or Muna birds, so a deeper genomic sampling would be needed to understand this pattern. The lack of morphological divergence between the Buton and Muna populations may reflect the fact they inhabit larger, more diverse islands than Kabaena (Buton - 4,408 km²; Muna - 2890 km²), which are only separated by 0.6 km at their closest point. These two diverse islands may provide a less ecologically-constrained environment (Lomolino and Weiser 2001). Sampling from a larger number of sites, in a wider diversity of habitats, would allow greater understanding of the Buton and Muna populations, and assess whether they are uniform in morphology throughout those islands. Considering all traits together we recommend no change to the taxonomy of the Pale-bellied White-eye.

5.5.4. Other *Zosterops* species considered

The wider results of our phylogenetic work give further credence to attempts to bring greater resolution to widespread taxa, such as the African Yellow White-eye, Oriental White-eye and Japanese White-eye (Husemann *et al.* 2016; Round *et al.* 2017; Wells 2017; Lim *et al.* 2018). The superficial phenotypic similarity of *Zosterops* species means that many populations may have been inaccurately assigned. This is likely to be the case in many taxa in the Indo-Pacific, as island colonisation has led to a huge amount of diversification. The species diversity of Monarchidae (Andersen *et al.* 2015a), *Pachycephala* (Andersen *et al.* 2014; Jønsson *et al.* 2014) and *Macropygia* (Ng *et al.* 2016) has been shown to have been vastly underestimated in many cases, as have other radiations.

5.5.5. The effect of isolation on taxa with differing dispersal ability

Assessing the evolutionary history of three *Zosterops* lineages in the same island archipelago allowed for a consideration of the effects of island colonisation, and how dispersive populations of ‘great speciators’ become isolated. Our study species included an apparent ‘supertramp’ (the Lemon-bellied White-eye), a regional endemic (the Pale-bellied White-eye) and a single island endemic (‘Wangi-wangi White-eye’). The ability of the Lemon-bellied White-eye to colonise even small, remote islands like Runduma, its broad habitat preference and its widespread, largely island-based range, have led to it being described as a ‘supertramp’ (Diamond 1974; Eaton *et al.* 2016). However this study found significant geographic structure to Lemon-bellied White-eye populations. The panmixia that would be expected of a true ‘supertramp’ was not apparent, and the current Lemon-bellied White-eye taxonomy contains unrecorded endemism. This tallies with the recent assessment of the classic ‘supertramp’, the Louisiade White-eye, by Linck *et al.* (2016), who found significant geographic and population structure. This may be an illustration of the rapid shifts in dispersal ability inferred to explain the paradox of ‘great speciator’ lineages (Diamond *et al.* 1976; Moyle *et al.* 2009). Loss of dispersal ability has been documented in many island-colonising taxa (Bellemain and Ricklefs 2008; Losos and Ricklefs 2009).

An assessment of the inferred dispersal ability of the *Zosterops* species in South-east Sulawesi provides insight into this phenomenon (Figure 5.12). The Runduma Lemon-bellied White-eye population showed the greatest potential dispersal ability, with a longer wingspan for its body mass than the other populations, typical of a very recent colonist (Mayr and Diamond 2001). The mainland Sulawesi Lemon-bellied White-eye population also showed a long

wingspan for its body mass, perhaps because of its restriction to edge habitats, typically a thin coastal strip of mangrove, by the stronger competitor, the Pale-bellied White-eye (Kelly *et al.* 2010; O'Connell *et al.* 2017). The 'Wangi-wangi White-eye' and the Pale-bellied White-eye might be assumed to be relatively poor dispersers due to their endemism and their absence from very isolated islands (Ricklefs and Cox 1972; Mayr and Diamond 2001). This appears to be the case, as they had a significantly shorter wingspan for a given body mass than either the Runduma or South-east Sulawesi mainland Lemon-bellied White-eye populations (Figure 5.12). Strikingly the Wakatobi *Z. c. flavissimus* population seemed to have lost its dispersal capability, showing the same wingspan for body mass ratio as the 'Wangi-wangi White-eye' and the Pale-bellied White-eye. Dispersal ability can be lost in island taxa, when adaptation to local environmental conditions favours traits other than dispersal ability (Gillespie *et al.* 2012). The Wakatobi Islands are a more ecologically constrained, species depauperate environment (Kelly and Marples 2010; O'Connell *et al.* 2018), than the mainland and continental islands, which have a greater diversity of species and habitats (Catterall 1996; Martin *et al.* 2012; O'Connell *et al.* 2017). Selection for traits that increased local adaptation to the environment of the Wakatobi Islands, may have led to reduced dispersal ability in *Z. c. flavissimus*.

The differences in dispersal ability between our *Zosterops* taxa illustrates a route by which the rapid shifts in dispersal ability in *Zosterops* species may occur. Increased adaptation to local conditions may lead to reduced dispersal ability, potentially resulting in the large numbers of small island endemics seen in the group. The 'Wangi-wangi White-eye' appears to fit the model of a late stage taxon (stage 4) in the taxon cycle (Wilson 1961), being: 1) the first species of its genus to colonise the island (Figure 5.7), 2) restricted to the island interior, and 3) endemic to a single island (Ricklefs and Cox 1972; Mayr and Diamond 2001). By comparison, the mainland South-east Sulawesi Lemon-bellied White-eye population (and the recent offshoot from this population on Runduma) seem to represent the early stages (stages 1-2) of the taxon cycle, being: 1) generalist, 2) associated with edge habitats and mangroves, 3) good dispersers and 4) found on widely separated islands. Pale-bellied White-eyes and *Z. c. flavissimus* may represent an intermediate point (stages 2-3), being: 1) regional endemics, 2) not restricted to just edge habitats and 3) relatively poor dispersers.

5.5.6. Conclusions

This study documents unrecorded endemism and different evolutionary histories in multiple *Zosterops* taxa. Our results highlight the importance of using multiple measures of divergence to understand speciation. Studying 'great speciator' lineages of the Indo-Pacific, like *Zosterops*

white-eyes, provides an excellent opportunity for both taxonomic revision and the examination of evolution processes. The diversity of taxa within 'great speciator' lineages; single island endemics, widespread colonisers and small island 'supertramps', provides opportunities to analyse how taxa with very different life history traits adapt to island colonisation and isolation. Our taxonomic considerations are given impetus by the discovery of a novel species on a small ecologically-degraded island, although the 'Wangi-wangi White-eye' (first noted in 2003) still awaits formal description. This illustrates the administrative delays that can occur in conservation biology. We hope this study will prompt a deeper consideration of the birds of South-east Sulawesi and, in particular, the conservation of the endemic bird populations of the Wakatobi Islands.

6. Island-like processes in urban populations of a ‘great speciator’

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Author contributions: DOC, DJK, NMM, KA and AK conceived this study. DOC, DJK, NMM, SS, SBAK and AK carried out fieldwork. DOC carried out the analyses and led the writing. All authors contributed to revising and improving the manuscript

Status: This manuscript is being prepared for submission to Journal of Evolutionary Biology.

6.1. Abstract

Island populations often occupy a wider ecological niche and show increased population density in comparison to mainland populations. This is attributed to decreased interspecific competition due to low species richness, coupled with increased intraspecific competition, as island population densities tend to be high. Urban areas may act as ecological islands, as they replicate these features of true geographical islands. We investigated this effect in the *Zosterops* species of South-east Sulawesi, Indonesia. The Lemon-bellied White-eye *Zosterops chloris* is found on small oceanic islands, on the coastal fringe of larger landmasses, and in urban areas. It is replaced inland on larger islands by the Pale-bellied White-eye *Zosterops consobrinorum*. The two species are found in sympatry in coastal areas on large islands. Here we investigated the niche space and population density of the two *Zosterops* species at sites where they were found in allopatry and sites where they were found in sympatry. We used n -dimensional hypervolumes, incorporating several measures, to represent morphological niche. The Lemon-bellied White-eye showed increased morphological niche hypervolume and population density at sites where they were in allopatry, both in urban areas and on the small island Runduma. The Pale-bellied White-eye showed no difference in niche hypervolume or population density between sites of allopatry and sympatry. This suggests the weaker competitor, the Lemon-bellied White-eye, is experiencing character release in allopatry. This study reveals the potential of urban areas to act as ecological islands.

6.2. Introduction

Oceanic islands have lower species richness than adjacent mainland areas (MacArthur and Wilson 1967). One reason for this lower species richness is that islands support less habitat diversity (Kier *et al.* 2009). However for successful island colonists, this reduction of interspecific competition may provide access to a greater array of resources (Olesen and Valido 2003). Island populations frequently display a wider ecological niche than mainland relatives, potentially taking advantage of the resources used by interspecific competitors on the mainland (Lister, 1976; Blondel *et al.*, 1988; Eberhard, 1989; Scott *et al.*, 2003). This reduction in interspecific competition has also been linked to higher densities in island populations, known as density compensation (MacArthur *et al.* 1972; Nilsson 1977; Rodda and Dean-Bradley 2002; Buckley and Jetz 2007; O'Connell *et al.* 2019). Higher levels of intraspecific competition in high density island populations (Robinson-Wolrath and Owens 2003) may be a driver of the wider niches seen in island populations (Svanbäck and Bolnick 2007).

Urban areas may act as ecological islands, promoting similar adaptations to those on true geographical islands. Urban areas typically have lower species richness, but those species that succeed in urban environments are often found in higher densities than in 'natural' habitats (Shochat *et al.* 2006). Urban colonisation promotes phenotypic change in populations (Alberti *et al.* 2017a) and selects for good colonisers (Parris and Hazell 2005) as well as adaptable, efficient foragers (Petren and Case 1996; Shochat *et al.* 2004). Heavily modified urban core areas are typically dominated by introduced synanthropic species, which live commensally with humans worldwide (McKinney 2006). Suburban areas and urban fringes are often occupied by native 'edge' species (Pickett *et al.* 2016). These 'edge' species are generalists which can take advantage of the fragmented habitats of urban fringes and become regionally abundant (McKinney 2006; Ries and Sisk 2010).

Classic niche theory predicts that interspecific competitors will evolve adaptations to minimise niche overlap and reduce direct competition in sympatry (Gause 1934; Hardin 1960; MacArthur and Levins 1967). In species-depauperate areas one would anticipate less niche partitioning, as interspecific competition would be reduced (Grant 1972). However, the degree to which species divergence is caused by competition in sympatry, or by sorting of pre-existing variation evolved in allopatry, remains controversial (Rice and Pfennig 2007; Pigot and Tobias 2013). The strongest evidence that interspecific competition plays an important role in shaping the niche space of populations is found amongst closely related species (McCormack *et al.* 2010; Benítez-López *et al.* 2014). Indeed, the principle of phylogenetic niche conservatism dictates

they are likely to have similar niches (Lee-Yaw and Irwin 2015). Niche partitioning in sympatry can be achieved by divergence in phenotype (Grant and Grant 2006; Norberg and Norberg 2015), spatial or temporal segregation of foraging (Albrecht and Gotelli 2001; Robertson *et al.* 2014) or a combination of partitioning strategies (Reifová *et al.* 2011; Reif *et al.* 2018; Sottas *et al.* 2018). Phenotypic divergence of sympatric populations due to interspecific competition is known as ecological character displacement (Brown and Wilson 1956; Schluter and McPhail 1992; Stuart and Losos 2013).

The reverse of character displacement is character release (Grant 1972; Arthur 1982). If a competitor is absent from an ecosystem, the remaining species may be able to expand their niche, to take advantage of the vacated niche space (Boag and Grant 1984). Decreased interspecific competition provides the opportunity for character release (Bolnick *et al.* 2010), but increased intraspecific competition is necessary to drive niche expansion (Svårdson 1949; Roughgarden 1974; Svanbäck and Bolnick 2007). While the effects of interspecific competition have been relatively well studied (reviewed in, Dayan and Simberloff 2005; Stuart and Losos 2013; Beans 2014), the potential effects of niche release from competition has received less attention, particularly in mainland systems (though see, Fjeldså 1983; Robinson and Wilson 1994). In addition many studies have discussed character release as a directional change in individual traits (e.g. increased bill length in birds) (Grant 1972), rather than an increase in overall niche width, as might be more accurately predicted from niche theory (Van Valen 1965). Few studies have provided any evidence of increased intraspecific competition driving niche expansion (though see, Robinson-Wolrath and Owens 2003).

In the heart of the Wallacea region, the south-eastern peninsula of Sulawesi provides an excellent study system to test the adaptations of closely related species when in allopatry and in sympatry (Figure 6.1). The region is home to two species of the *Zosterops* avian 'great speciator' lineage, which are among the fastest evolving of all vertebrate groups (Moyle *et al.* 2009). The Pale-bellied White-eye *Zosterops consobrinorum*, is a regional endemic restricted to the south-eastern peninsula of Sulawesi and the continental islands of Buton, Muna and Kabaena (O'Connell *et al.* 2017; van Balen 2018c). The Lemon-bellied White-eye *Zosterops chloris* is a typical 'supertramp' species (Mayr and Diamond 2001; Eaton *et al.* 2016), occupying small islands, mangroves and edge habitats where it avoids stronger competitors. It is found on small islands from the east coast of Sumatra to the west coast of Papua, and on the coastal fringes of larger islands in the Lesser Sundas and Sulawesi (van Balen 2018b).

Within South-east Sulawesi the Lemon-bellied White-eye is restricted to small islands and the coastal fringe of mainland Sulawesi and the larger continental islands, while the Pale-bellied White-eye is found inland (Kelly *et al.* 2010; O'Connell *et al.* 2017). The two species are found in sympatry in coastal areas, but the Lemon-bellied White-eye is largely restricted to within c. 1km of the coast (pers. obs.). However Wardill (2003) noted that the Lemon-bellied White-eye replaces the Pale-bellied White-eye in urban areas such as Kendari city (the region's capital). This may be due to the Lemon-bellied White-eye having a greater tolerance for human modified habitat than the Pale-bellied White-eye, which dominates in more pristine habitats (Martin and Blackburn 2010). Two *Zosterops* species are seldom found in sympatry on large landmasses, they generally partition altitudinally, or by habitat choice (Lack 1971). Wijesundara and Freed (2018) found that the endemic Sri Lankan White-eye *Zosterops ceylonensis* increased in bill and body size when in sympatry with the widespread Oriental White-eye *Zosterops palpebrosus*, showing evidence of character displacement. Therefore the Lemon-bellied White-eye and the Pale-bellied White-eye are likely to have partitioned their niches when found in sympatry and may experience niche release when in allopatry.

We hypothesised; 1. the two *Zosterops* species in our study region would have partitioned niche in sympatry and may experience character release when in allopatry, and 2. release from interspecific competition would allow allopatric white-eye populations to reach higher density than sympatric populations, likely increasing intraspecific competition. To investigate these hypotheses, our research goals were to; 1. measure the morphological niche of both *Zosterops* species in our study area and test for any difference in morphological niche volume between sites of allopatry and sympatry, 2. assess the abundance of *Zosterops* species at each site, to test for any difference in density between sites of allopatry and sympatry.

6.3. Methods

6.3.1. Study site and sampling

Sampling was carried out in South-east Sulawesi (Figure 6.1), on research expeditions undertaken between 1999 and 2017 in the months of June-September by NMM, DJK, AK, SBAK, SS and DOC. All sites where Lemon-bellied White-eyes and Pale-bellied White-eyes were sampled are included in this analysis, apart from the *Z. c. flavissimus* population on the Wakatobi Islands, as this likely represents a separate species (O'Connell *et al.* in press). Three sites were sampled where Lemon-bellied White-eyes and Pale-bellied White-eyes were in sympatry in coastal areas; Rumburumba, mainland Sulawesi (4.428°S 122.811°E), Labundobundo, Buton

(5.189°S 122.931°E) and Kamama Mekar, Muna (5.313°S 122.642°E). Three sites were sampled where the Lemon-bellied White-eye was found in allopatry; two urbanised sites Kendari, mainland Sulawesi (4.014°S 122.526° E) and Sikeli, Kabaena (5.276°S 121.798°E), and one small island site Runduma Island (5.334°S 124.336°E). Four sites were sampled where the Pale-bellied White-eye was found in allopatry; Kusambi, Buton (5.156°S 122.897°E), Kaikalu, Buton (5.175°S 122.894°E), Enano, Kabaena (5.247°S 121.957°E) and Tangkeno, Kabaena (5.274°S 121.921°E). Mist-nets were used to trap birds for sampling. Netting was carried out for between one and three weeks at each site, at multiple locations centred around the coordinates provided. Birds trapped were colour ringed for easy identification if re-trapped. Coates and Bishop (1997) and Eaton *et al.* (2016) were used for species identification and aging of birds. The morphological measurements; wing length (maximum chord), bill length (tip of bill to the base of the skull), and weight (grams) were taken (Svensson 1992; Redfern and Clark 2001). Bill length is a key indicator of feeding niche in birds, wing length and weight indicate body size (Grant 1965). All measurements were taken by a single recorder (NMM). Only adult birds were included in morphological analyses. The *Zosterops* species of South-east Sulawesi are sexually monomorphic (van Balen 2018b; van Balen 2018c), so sexes were not separated for morphometric analyses. Mist-netting was carried out in a variety of habitats used by *Zosterops* species including plantation, forest edge, farmland and mangroves.

To establish *Zosterops* population densities where they were mist netted, line-transects were carried out in the vicinity of mist-netting sites, in the same habitats. Transects were carried out at all sites except Kaikalu. Transects were 1 km in length and only *Zosterops* species up to 25 m either side of this transect were recorded. Therefore each transect surveyed an area of five hectares. Transects were carried out from 06h00-08h30, during the peak of bird activity. Each transect was surveyed only once. The yellow chest of the Lemon-bellied White-eye and the off-white chest of the Pale-bellied White-eye made these species readily identifiable from each other. DOC, SBAK, DJK, SS and AK carried out the transects, ensuring at least two recorders participated in each transect and walking at a recommended pace of 1-2 km/hr (Bibby *et al.* 2000). A GPS unit was used to measure the length and mark the location of each transect.

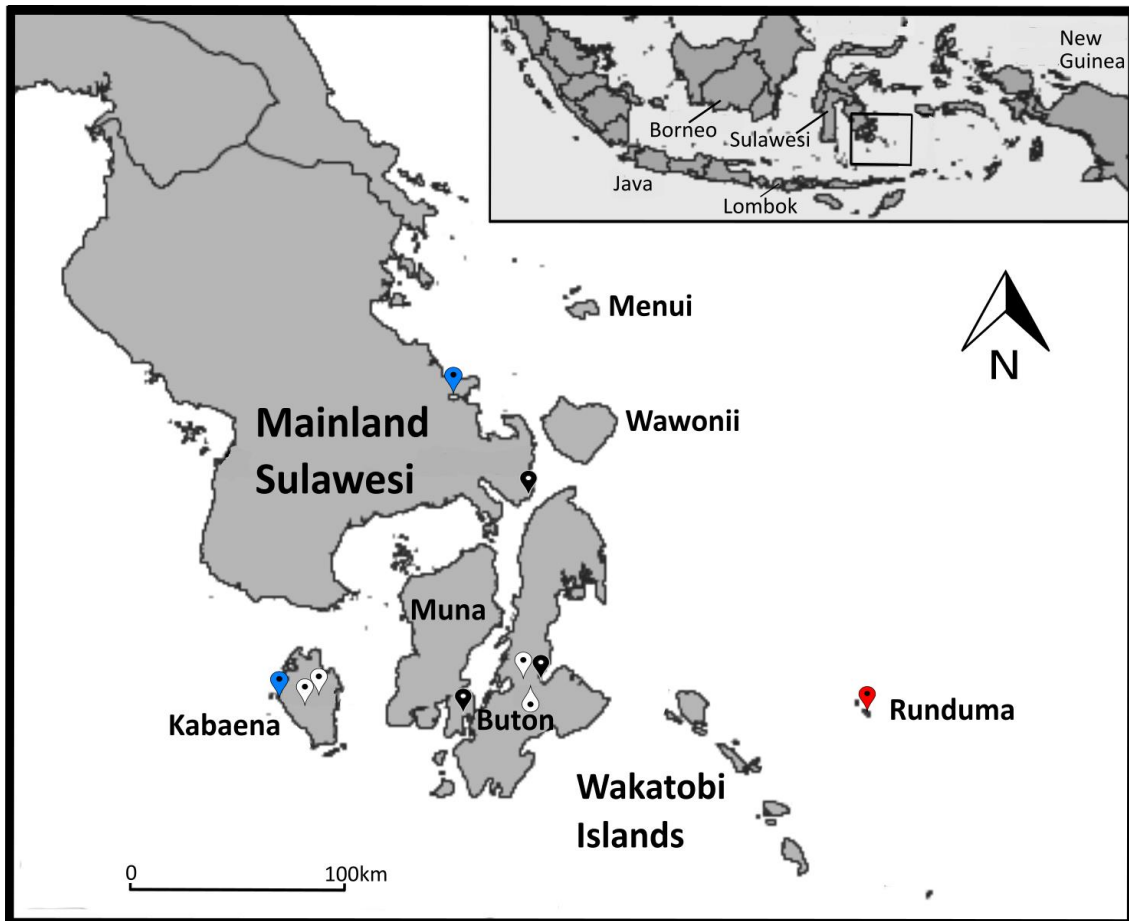


Figure 6.1: Map showing the study region of South-east Sulawesi (main panel) and the Sulawesi region of Indonesia (top right panel). Locations where *Zosterops* species were sampled are marked by pins, black pins indicate sites where the Lemon-bellied White-eye and the Pale-bellied White-eye were in sympatry, white pins indicate where the Pale-bellied White-eye was found in allopatry, blue pins indicate where the Lemon-bellied White-eye was found in allopatry in urban areas and the red pin indicates where the Lemon-bellied White-eye was found in allopatry on a small island.

6.3.2. Quantification of morphological niche hypervolume

All statistical analyses were performed in R software v. 3.5.1 (R Core Team 2018). To quantify morphological niche volume of each population the concept of n -dimensional hypervolumes was utilised (Hutchinson 1957). In this framework we defined the morphological niche as the 3-dimensional hypervolume produced from the combination of the three morphological variables measured. To calculate this hypervolume we used dynamic range boxes implemented in the R package 'dynRB' (Junker *et al.* 2016), which provided a robust nonparametric approach to quantify n -dimensional hypervolumes. For each group assessed, 'dynRB' calculates the size of that group's n -dimensional hypervolume. Hypervolumes were bounded between 0 and 1. This method is robust to sample size differences between populations, once a minimum of $N = 10$ is

attained (Junker *et al.* 2016). This sample size was attained for all populations except the Pale-bellied White-eye Labundobundo population ($N = 5$) (Table S6.1). For a full description of this approach see Junker *et al.* (2016) and Kuppler *et al.* (2017). As each morphological trait was on a different scale, they were first re-scaled using the *scale* function in R (R Core Team 2018).

Using the dynamic range box method we calculated the morphological niche hypervolume for *Zosterops* species at each site. The aggregation method ‘mean’ was utilised in ‘dynRB’ as this is the most suitable for evaluating similarity between niches (Junker *et al.* 2016). A Welch two-sample t-test was carried out to test for a difference in the volume of the morphological niche of both *Zosterops* species, between sites where they were in sympatry, and sites where they were in allopatry. To ensure that the assumption of a normal distribution was not violated, histograms were used to investigate the data distribution and QQ-plots of the residuals of each test were assessed for fit.

6.3.3. Abundance in sites of allopatry and sympatry

Differences in population abundance of *Zosterops* species between sites was tested by modelling transect counts of *Zosterops* species with variations of generalised linear models (GLM) for count data, utilising the R package ‘MASS’ (Venables and Ripley 2002). As a posthoc to the GLMs, a Tukey Honest Significant Difference (HSD) test was carried out using the ‘glht’ function in the R package ‘multcomp’ (Hothorn *et al.* 2008). The Tukey HSD posthoc allowed for pairwise comparisons to be carried out between all sites, and this method corrected for multiple comparisons (Maxwell and Delaney 2018). Year and month were included in the initial model but dropped from the final model after model selection using AIC, R^2 and standard plots of model fit (R Core Team 2018).

6.4. Results

6.4.1. Morphological niche hypervolume

A total of 224 Lemon-bellied White-eyes were sampled across six sites and 142 Pale-bellied White-eyes across seven sites (Table S6.1). Lemon-bellied White-eye populations in allopatry had a significantly larger morphological niche hypervolume than Lemon-bellied White-eye populations in sympatry (Welch t-test $t = 3.088$, $df = 3.779$, $P < 0.05$) (Figure 6.2). Pale-bellied White-eyes showed no difference in morphological niche hypervolume, whether in sympatry or allopatry (Welch t-test $t = 1.543$, $df = 3.940$, $P = 0.199$).

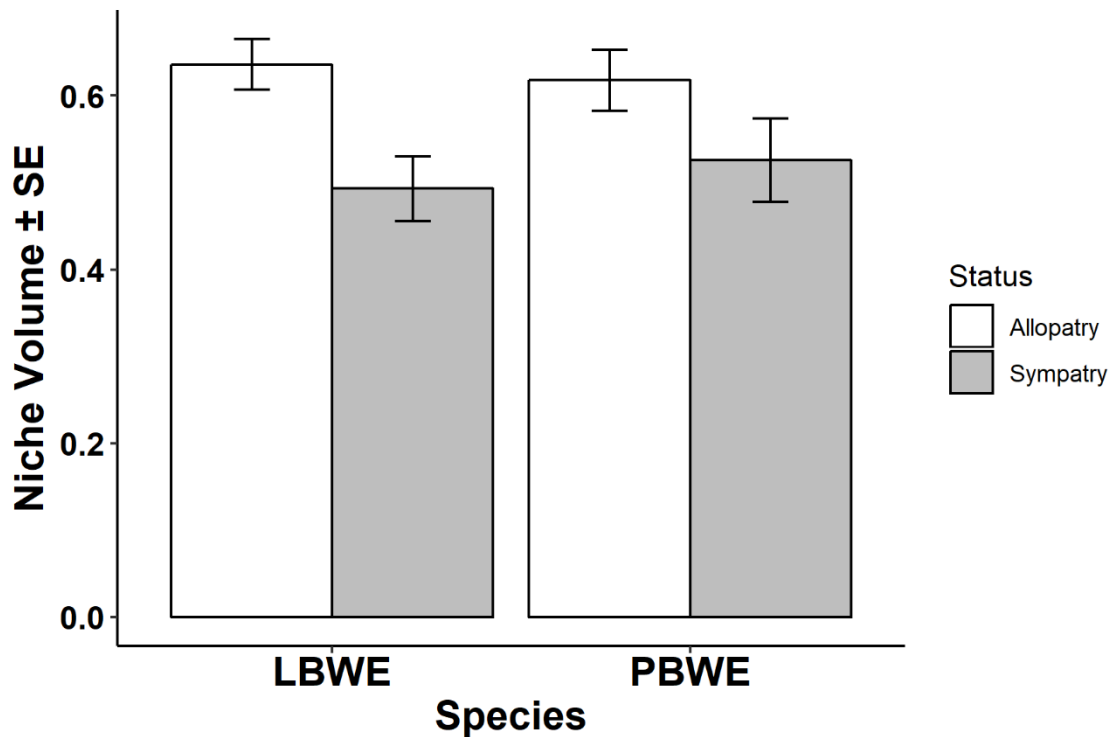


Figure 6.2: Barplot showing the mean morphological niche hypervolume (\pm standard error) for Lemon-bellied White-eye (LBWE) and Pale-bellied White-eye (PBWE) populations, in allopatry and sympatry.

6.4.2. Abundance

A total of 59 transects were carried out across nine of the 10 sites sampled in this study (Table S6.2). There was a significant difference in the abundance of Lemon-bellied White-eye populations between sites (Negative Binomial GLM: *Pseudo* $R^2 = 0.80$, $F_{5, 30} = 24.763$, $P < 0.001$) (Figure 6.3). This difference was accounted for by the Lemon-bellied White-eye having a significantly higher abundance at all sites where it was in allopatry, in comparison to all sites where the Lemon-bellied White-eye was in sympatry (Tukey HSD: $P_{adj.} < 0.001$ for all comparisons) (Table S6.3). There was no difference in the abundance of the Lemon-bellied White-eye at the sites where it was in allopatry. Between the sites where the Lemon-bellied White-eye was in sympatry, Lemon-bellied White-eye abundance was significantly higher in Kamama Mekar than Labundobundo (Tukey HSD: Estimate \pm standard error (SE) = 1.537 ± 0.480 , $P_{adj.} < 0.05$), while there was no difference between Lemon-bellied White-eye abundance in Rumberumba and either Kamama Mekar or Labundobundo (Table S6.3).

Pale-bellied White-eye populations were found to differ significantly in abundance (Quasi-Poisson GLM: *Pseudo* $R^2 = 0.34$, $F_{5, 37} = 3.789$, $P < 0.01$) (Figure 6.3). However this

difference was only found for comparisons involving the Pale-bellied White-eye Labundobundo population. Pale-bellied White-eyes in Labundobundo were significantly less common than in Kusambi (Tukey HSD: Estimate \pm SE = -8.25 ± 2.468 , $P_{adj.} < 0.01$) or Tangkeno (Tukey HSD: Estimate \pm SE = -5.182 ± 1.513 , $P_{adj.} < 0.01$). There were no differences between any of the other sites, regardless of whether the Pale-bellied White-eye was in allopatry or in sympatry with the Lemon-bellied White-eye.

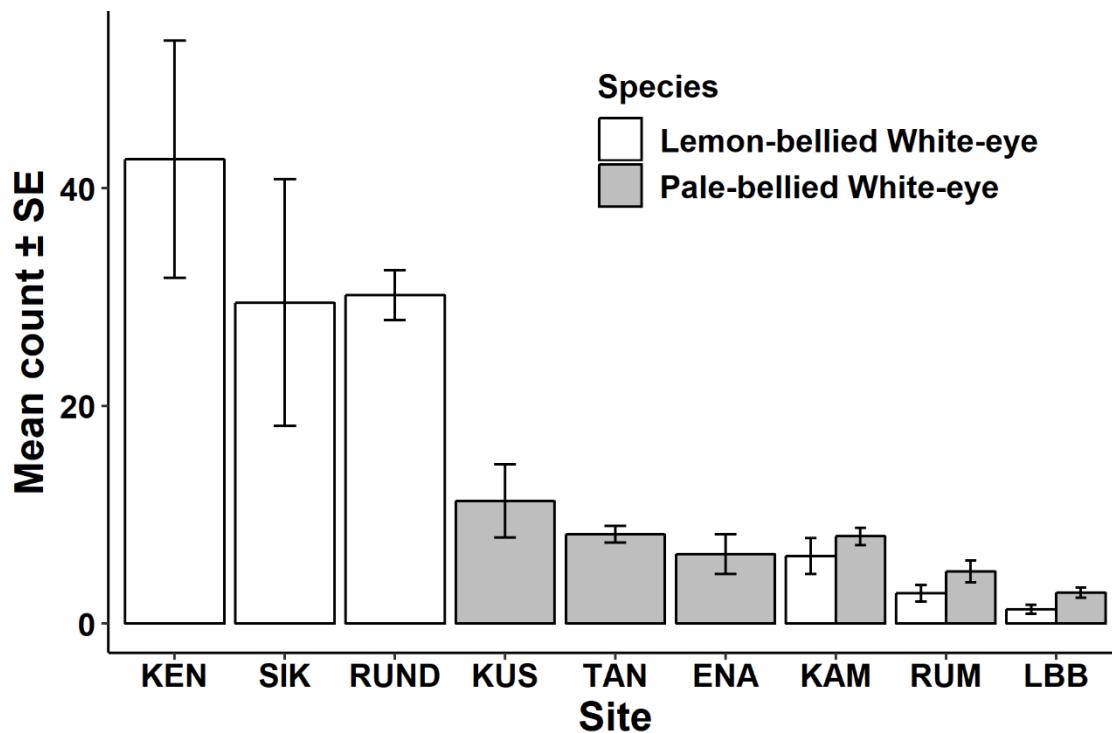


Figure 6.3: Barplot showing the mean transect count (\pm standard error) of *Zosterops* species across the study area. Coastal sites where the Lemon-bellied White-eye and Pale-bellied White-eye were in sympatry; KAM - Kamama Mekar (Muna), RUM - Rumbarumba (Sulawesi), LBB - Labundobundo (Buton). Inland sites where Pale-bellied White-eyes were in allopatry; KUS - Kusambi (Buton), TAN - Tangkeno (Kabaena), ENA - Enano (Kabaena). Island where Lemon-bellied White-eyes were in allopatry; RUND - Runduma Island. Urban areas where Lemon-bellied White-eyes were in allopatry; KEN - Kendari (Sulawesi), SIK - Sikeli (Kabaena).

6.5. Discussion

In this study we demonstrated that Lemon-bellied White-eyes show an increased niche hypervolume and increased abundance in allopatry, both in a small oceanic island population and in two urban populations (Figures 6.2 and 6.3). These results demonstrate that island-like processes can occur in urban populations of an island-colonising species. In contrast, the Pale-bellied White-eye showed no difference in morphological niche hypervolume between sites where it was in allopatry or in sympatry with the Lemon-bellied White-eye, and no consistent

difference in abundance between sites of allopatry and sympatry. Therefore, our results provide evidence supporting both our hypotheses for the Lemon-bellied White-eye, but support neither for the Pale-bellied White-eye. This disparity may be explained if the Pale-bellied White-eye is a stronger competitor than the Lemon-bellied White-eye. If that were so, its morphology or abundance would not be significantly affected by the presence of the Lemon-bellied White-eye.

Lemon-bellied White-eye populations in allopatry showed increased morphological niche hypervolume and abundance in comparison to Lemon-bellied White-eye populations in sympatry with the Pale-bellied White-eye (Figures 6.2 and 6.3). In the absence of a congeneric competitor, the Lemon-bellied White-eye may have access to a wider resource base, allowing it to establish a larger morphological niche and a higher population density (Robinson *et al.* 2000). The high density of the allopatric Lemon-bellied White-eye populations likely also results in higher intraspecific competition, as has been shown in other *Zosterops* species (Robinson-Wolrath and Owens 2003). Increased intraspecific competition may drive niche expansion, into niche space available due to the absence of interspecific competitors (Svårdson 1949; Roughgarden 1974; Svanbäck and Bolnick 2007). Such a pattern in the allopatric Lemon-bellied White-eye populations may represent a case of character release (i.e. niche release in the absence of an interspecific competitor) (Grant 1972).

Character release is traditionally considered to have a genetic basis (Grant 1972; Schluter and McPhail 1992). Despite this, few studies have demonstrated a genetic basis for proposed cases of character release (Stuart and Losos 2013), and this aspect was not investigated in the present study. Therefore the increase in morphological niche seen in allopatric populations of the Lemon-bellied White-eye may be an example of phenotypic plasticity (Pfennig *et al.* 2006). Phenotypic plasticity can produce a rapid adaptive response to different environmental conditions, without genetic change (Turcotte and Levine 2016). However, recent research has suggested that phenotypic plasticity and character release are not mutually exclusive (Pfennig and Pfennig 2010). Phenotypic plasticity might play a key role in the early stages of character release and displacement, producing an adaptive response which may become fixed as the plastic trait is exposed to selection (Pfennig and Pfennig 2010; Levis *et al.* 2017). If plastic change in a trait is adaptive it can be stabilised by the evolution of genetic differences through genetic assimilation (West-Eberhard 2003; Crispo 2007; Pfennig and Martin 2010).

It is striking that the same pattern was observed in Lemon-bellied White-eye populations both on the isolated Runduma Island (c. 5.5km² in size and 61 km from the nearest neighbouring island (Daft Logic 2018b; Daft Logic 2018a)) and in two disjunct urbanised areas. Island-like processes have been noted in mainland populations of emberizid sparrows living in species depauperate marshes and mangroves (Greenberg and Olsen 2010; Luther and Greenberg 2011), but this effect has not previously been noted in urbanised areas. Sulawesi is one of the most thinly populated regions of Indonesia (Biro Pusat Statistik 2010), and most of the sites sampled for this study were thinly populated. The regional capital of South-east Sulawesi, Kendari (>300,000 people) and the town of Sikeli (c. 10,000 people) on Kabaena Island, were the exceptions. The urban areas of South-east Sulawesi are relatively low density, particularly on the outskirts, with housing interspersed with overgrown vacant spaces dominated by invasive shrubs such as *Lantana camara*, and gardens planted with introduced ornamental trees (pers. obs.). Our sampling sites in Sikeli and Kendari were in degraded sites on the suburban fringes, and on the Halu Oleo University campus (Kendari). The campus was a mosaic of overgrown areas and ornamental plantings. These habitats are likely ideal for an edge-adapted generalist like the Lemon-bellied White-eye (Alberti *et al.*, 2017b).

The traits that allow the Lemon-bellied White-eye to colonise small oceanic islands may make it an ideal urban dweller. Møller (2009) found that urban birds in the Western Palearctic had a high propensity for dispersal, high rates of feeding innovation and high fecundity. These traits are characteristic of the widespread island colonising lineages of the Indo-Pacific (Mayr and Diamond 2001). Ward (1968) noted that the replacement of forest areas with suburban gardens in Singapore allowed a widespread island coloniser, the Collared Kingfisher *Todiramphus chloris*, which had previously been restricted to mangrove areas, to move inland and replace the White-breasted Kingfisher *Halcyon smyrnensis* as the dominant kingfisher. Diamond and Marshall (1977) found that another widespread island coloniser, the Pacific Kingfisher *Todiramphus sacer* partitioned habitat with the endemic Vanuatu Kingfisher *Todiramphus farquhari* on Malakula Island, with the Pacific Kingfisher confined to coastal areas, while the Vanuatu Kingfisher was found in closed forest. However, a more recent survey found the Pacific Kingfisher inland in sympatry with the Vanuatu Kingfisher, potentially making use of the roads and other human edge habitats produced by an expanding human population (Friesen 1994; Andersen *et al.* 2017). Human development appears to be creating environments beneficial to widespread edge species, but harmful to more specialised endemics. Such changes facilitate biotic homogenisation (McKinney 2006).

Pale-bellied White-eyes showed no consistent differences between sites of sympatry and allopatry. The only site shown to differ significantly in abundance for Pale-bellied White-eyes, Labundobundo, appeared to have been a generally poor site for *Zosterops*, with the lowest abundance recorded for both species (Figure 6.3). Pale-bellied White-eyes showed no significant difference in morphology between allopatric and sympatric populations (Figure 6.2). The dominance of the Pale-bellied White-eye in less degraded inland habitats (Martin and Blackburn 2010), suggests it is the stronger competitor (Wilson and Keddy 1986; Jonsson *et al.* 2008), which may explain why it shows no morphological changes when it is in sympatry with the Lemon-bellied White-eye (Freshwater *et al.* 2014). We confirmed the observation made by Wardill (2003), that the Pale-bellied White-eye is absent from urban areas. The closest known record of the Pale-bellied White-eye to Kendari city is at Haluoleo Airport (4.077°S 122.417°E), c. 7.3 km south-west of the city outskirts and c. 16.25 km from the coast (James Eaton pers. comm.; Daft Logic 2018b), and the closest to Sikeli village was at 5.270°S, 121.811°E, c. 1.6 km from the outskirts of the village and c. 2.27 km from the coast (pers. obs.; Daft Logic 2018b). This is likely explained by the Pale-bellied White-eye being a poor coloniser, with less tolerance for disturbed habitats than the Lemon-bellied White-eye (Martin and Blackburn 2010; van Balen 2018c).

This study highlights an increase in morphological niche breadth and population density in populations of a widespread island colonising species in allopatry from a congeneric competitor. This phenomenon has previously been observed in island settings, but we found evidence that the same pattern was apparent for both a small island population, and urban populations, of Lemon-bellied White-eyes. Our results support the idea that species-depauperate, urban mainland areas may act as ecological islands for edge species. Further study of this phenomenon may offer great insight into island effects in a rapidly urbanising world. The Indo-Pacific may provide an ideal system for such a study, as it contains several bird lineages (e.g. *Zosterops*, *Todiramphus* and Monarchidae) where widespread island colonising species have partitioned habitat with locally endemic congeneric competitors. It seems likely that generalist edge species are benefiting from human modification of the environment at the expense of more specialised endemic species. Developing an understanding of this phenomenon may be of great importance in the face of increasing human influence and accelerating biotic homogenisation.

7. Female birds crowded out by males on small islands: niche contraction in dense populations of Olive-backed Sunbirds is asymmetric.

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Author contributions: DOC, DJK, NMM, KA and AK conceived this study. DOC, DJK, NMM, SBAK, SS and AK carried out fieldwork. DOC carried out the analyses and led the writing. All authors contributed to revising and improving the manuscript

Status: This manuscript was published in *Emu - Austral Ornithology* on 22 March 2019 for the special issue 'Ornithological advances in New Guinea and the Indo-Pacific'. doi: 10.1080/01584197.2019.1588743

7.1. Abstract

Competition takes place not only between species, but also within them. Intersexual competition for resources may increase sexual dimorphism in body size to minimise ecological niche overlap. Change in the level of sexual dimorphism in a species is a common feature of island radiations. This is often interpreted as ecological release from interspecific competitors absent from small islands, allowing niche expansion by both sexes of a dimorphic species into niche space that would otherwise be taken by interspecific competitors. The Olive-backed Sunbird *Cinnyris jugularis* is a widespread island colonising species found throughout the Indo-West Pacific. Here we investigate sexual dimorphism in morphological niche of Olive-backed Sunbird populations in South-east Sulawesi, Indonesia, for evidence of increased sexual dimorphism on small islands. We used n -dimensional hypervolumes, incorporating multiple traits, to represent morphological niche. We found decreased overlap in morphological niche between females and males on the species-depauperate Wakatobi Islands, in comparison to mainland Sulawesi and its larger continental islands, indicating greater sexual dimorphism on the small islands. This change in sexual dimorphism was associated with a decrease in the morphological niche hypervolume of females, but no change in males. Therefore there was no indication of expansion of niche space in the absence of mainland competitors. However the change in niche overlap was associated with the significantly higher population density of Wakatobi Olive-backed Sunbirds. Therefore this increased sexual dimorphism may serve to alleviate intraspecific competition for resources. This study illustrates adaptations that may facilitate successful island colonising in sexually dimorphic species.

7.2. Introduction

Competition was proposed by Darwin (1859) as a primary driver of diversification. Competition for resources takes place not only between species, but within them (Doebeli 2011; Meiri *et al.* 2014). Where intraspecific competition is strong it can drive increased diversity in resource use within a species (Svanbäck and Bolnick 2007; Sheppard *et al.* 2018). Intraspecific competition is typically at its strongest in high density populations (Robinson-Wolrath and Owens 2003; Pafilis *et al.* 2009). In sexually dimorphic species, strong intersexual competition can promote selection for an accentuation of the size difference between males and females, facilitating resource partitioning between the sexes (Slatkin 1984; Shine 1989; Bolnick and Doebeli 2003) and increasing the overall niche space occupied by a species (Butler *et al.* 2007).

Sexual dimorphism in a species can initially arise through a number of different processes such as natural selection for resource partitioning (Dayan and Simberloff 1994), sexual selection (Gittleman and Valkenburgh 1997) and fecundity selection (selection for larger females with greater reproductive capacity) (Scharf and Meiri 2013; Meiri *et al.* 2014). Regardless of how sexual dimorphism arose originally, a change in selection pressure can lead to differences in the degree of sexual dimorphism between populations of the same species (Butler *et al.* 2007). Increased sexual dimorphism has been noted in the island populations of a diverse range of taxa (Selander 1966; Meiri *et al.* 2014), including woodpeckers (Selander 1966), finches (Ebenman and Nilsson 1982), mustelids (Dayan and Simberloff 1994) and pythons (Pearson *et al.* 2002). The increased sexual dimorphism seen in island populations is thought to be associated with; 1. fewer interspecific competitors, allowing species which succeed in island colonisation to increase in density and diverge into niche space usually occupied by mainland competitors and 2. greater intraspecific competition due to higher population densities, driving intersexual niche divergence (Selander 1966; MacArthur *et al.* 1972; Butler *et al.* 2007; Greenberg and Olsen 2010). A recent meta-analysis by Meiri *et al.* (2014) of sexual dimorphism in lizards and carnivorous mammals found that the number of competitor species was not linked to sexual dimorphism, calling into question whether release from interspecific competition plays a role in increased sexual dimorphism. While increased sexual dimorphism in individual traits has been noted in many species, few studies have quantified dimorphism in multidimensional morphological niche space, or related niche space to population density (though see Butler *et al.* (2007) and Greenberg and Olsen (2010)).

In the heart of the Wallacea region, the south-eastern peninsula of Sulawesi provides an excellent study system to test how natural selection on small islands may affect sexual

dimorphism (Figure 7.1). There are continental islands (Buton, Muna and Kabaena) which were connected to Sulawesi at the time of the last glacial maximum, around 10,000 years ago (Voris 2000), and oceanic islands (including the Wakatobi Islands) which have never been connected to the Sulawesi mainland (Milsom and Ali 1999; Carstensen *et al.* 2012). The region is home to the Olive-backed Sunbird *Cinnyris jugularis*, an extremely successful island coloniser, with a wide range stretching from South-east Asia to North-east Australia (Cheke and Mann 2018e). It shows distinct sexual dimorphism in plumage and body size, with males larger than females. The subspecies *C. j. infrenatus* is found on mainland Sulawesi and its continental islands, while *C. j. plateni* is found on the Wakatobi Islands (Kelly and Marples 2011; O'Connell *et al.* 2017; Cheke and Mann 2018e). On the mainland and continental islands there are seven ecologically similar, generalist small passerine species which may compete directly or indirectly with the Olive-backed Sunbird for resources; the Brown-throated Sunbird *Anthreptes malacensis*, Black Sunbird *Leptocoma aspasia*, Crimson Sunbird *Aethopyga siparaja*, Lemon-bellied White-eye *Zosterops chloris*, Pale-bellied White-eye *Zosterops consobrinorum*, Grey-sided Flowerpecker *Dicaeum celebicum* and Yellow-sided Flowerpecker *Dicaeum aureolimbatum* (Eaton *et al.* 2016). On the Wakatobi Islands there are only three such ecologically similar passerine species present: the Lemon-bellied White-eye and Grey-sided Flowerpecker *Dicaeum celebicum*, which are present throughout the islands (Kelly and Marples 2010), and an unnamed white-eye species (the 'Wangi-wangi White-eye') awaiting formal description which is found only on the most northern Wakatobi Island (Wangi-wangi) (Eaton *et al.* 2016).

We hypothesised; 1. there would be greater sexual dimorphism in Olive-backed Sunbird populations on the Wakatobi Islands than in the mainland system (mainland Sulawesi and the continental islands), 2. greater sexual dimorphism would be accompanied by an expansion in niche volume in both sexes in the absence of interspecific competitors and 3. greater sexual dimorphism would be accompanied by higher population density in Olive-backed Sunbirds, likely increasing intraspecific competition. To investigate these hypotheses our research goals were to 1. measure the overlap in morphological niche between female and male Olive-backed Sunbirds on each island to test for a difference in sexual dimorphism between the mainland system and the Wakatobi Islands, 2. ascertain any differences in morphological niche volumes for female or male Olive-backed Sunbirds between the mainland system and the Wakatobi Islands and 3. assess the population abundance of Olive-backed Sunbirds across the study area.

7.3. Methods

7.3.1. Study site and sampling

Sampling was carried out throughout South-east Sulawesi (Figure 7.1), on research expeditions undertaken between 1999 and 2017 in the months of June-September by NMM, DJK, AK, SBAK, SS and DOC. Olive-backed Sunbirds were sampled on 10 islands throughout the region for this study. Mist-nets were used to trap birds for sampling. Birds trapped were colour ringed for easy identification if re-trapped. Coates and Bishop (1997) and Eaton *et al.* (2016) were used for species identification and for the aging and sexing of birds trapped. The morphological measurements; wing length (maximum chord), bill length (tip of bill to the base of the skull), and mass (grams) were taken (Svensson 1992; Redfern and Clark 2001). Bill length is a key indicator of feeding niche in birds, wing length and mass indicate body size (Grant 1965). All measurements were taken by a single recorder (NMM). Only adult birds were included in morphological analyses. Mist-netting was carried out in habitats used by Olive-backed Sunbirds including a variety of plantation, forest edge, farmland and mangrove habitats.

To establish Olive-backed Sunbird population densities where they were mist netted, line-transects were carried out in the vicinity of mist-netting sites, in the same habitats. Transects were 1 km in length and only Olive-backed Sunbirds up to 25 m either side of this transect were recorded. Therefore each transect surveyed an area of five hectares. Transects were carried out from 06h00-08h30, during the peak of bird activity. Each transect was surveyed only once. All Olive-backed Sunbirds seen or heard within the survey area were recorded. Male, female and unidentified sex (recorded by call) Olive-backed Sunbirds were all added together to give a total count of Olive-backed Sunbirds recorded for the survey area. DOC, SBAK, DJK, SS and AK carried out the transects, ensuring at least two recorders participated in each transect and walking at a recommended pace of 1-2 km/hr (Bibby *et al.* 2000). A GPS unit was used to measure the length and mark the locations of each transect.

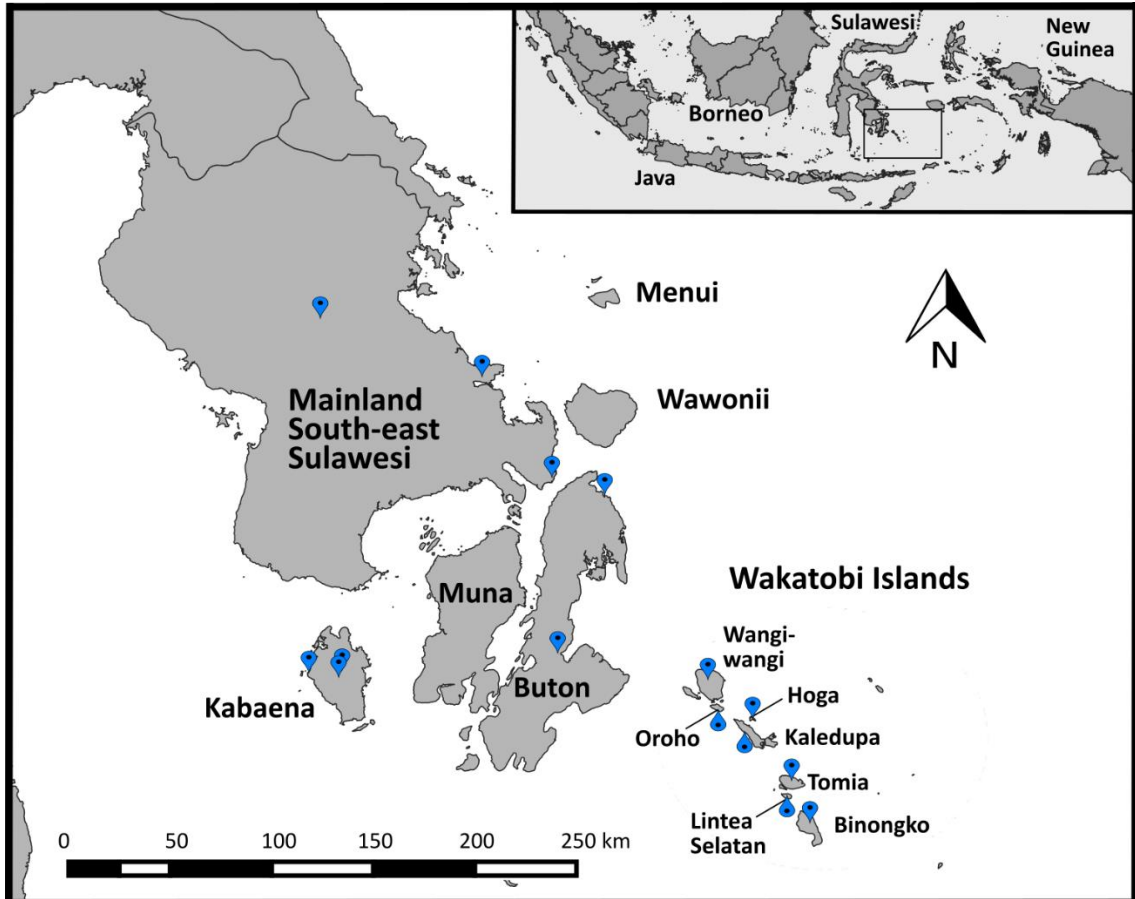


Figure 7.1: Map showing the study region of South-east Sulawesi (main panel) and the Sulawesi region of Indonesia (top right panel). Locations where Olive-backed Sunbirds were sampled for this study marked by a pin.

7.3.2. Quantification of overlap in morphological niche

All statistical analyses were performed in R software v. 3.5.1 (R Core Team 2018). To quantify the overlap in morphological niche, we utilised the concept of n -dimensional hypervolumes (Hutchinson 1957). In this framework we defined the morphological niche as the 3-dimensional hypervolume produced from the combination of the three morphological variables measured. To calculate this hypervolume we used dynamic range boxes implemented in the R package ‘dynRB’ (Junker *et al.* 2016), which provided a robust nonparametric approach to quantify n -dimensional hypervolumes. For each group assessed, ‘dynRB’ calculates the size of that group’s n -dimensional hypervolume, and the proportion of that hypervolume that overlaps with each other group assessed. Hypervolumes and overlap values were bounded between 0 and 1. For a full description of this approach see Junker *et al.* (2016) and Kuppler *et al.* (2017). As each morphological trait was on a different scale, they were first re-scaled using the *scale* function in R (R Core Team 2018).

Using the dynamic range box method we calculated the morphological niche volume for female and male Olive-backed Sunbirds on each island sampled. We utilised the aggregation method 'mean' in 'dynRB' as this is the most suitable for evaluating similarity between two niches (Junker *et al.* 2016). To investigate sexual dimorphism between female and male Olive-backed Sunbirds, the proportion of the morphological niche that overlapped between females and males on each island was calculated. The proportion of morphological niche overlap provided a measure of sexual dimorphism in each population, i.e. less overlap in morphological niche indicated greater sexual dimorphism between female and male Olive-backed Sunbirds. A Welch two-sample t-test was carried out to test for a difference in the proportion of morphological niche overlap between the mainland system, and the Wakatobi Islands populations. In addition, a Welch two-sample t-test was carried out to test for a difference in the total morphological niche volume between the mainland system, and the Wakatobi Islands populations, for both female and male Olive-backed Sunbirds. QQ-plots of the residuals of each test were used to ensure that the assumption of a normal distribution was not violated. The morphological niche overlap values were log transformed to conform to a normal distribution.

7.3.3. Assessing abundance

Differences in population abundance of Olive-backed Sunbirds between islands were tested by modelling transect counts of Olive-backed Sunbirds with a generalised linear model (GLM) with Poisson errors. As a posthoc to the GLM, a Tukey Honest Significant Difference (HSD) test was carried out using the 'glht' function in the R package 'multcomp' (Hothorn *et al.* 2008). The Tukey HSD posthoc allowed for pairwise comparisons to be carried out between all islands, and this method corrected for multiple comparisons (Maxwell and Delaney 2018). Year and month were included in the initial model but dropped from the final model after model selection using AIC, R^2 and standard plots of model fit (R Core Team 2018). QQ-plots of the residuals of each test were used to ensure that the assumption of a normal distribution was not violated.

7.4. Results

7.4.1. Sexual dimorphism in morphological niche volume

A total of 246 Olive-backed Sunbirds (93 female, 153 male) were trapped; 72 (27 female, 45 male) across the mainland system and 174 (66 female, 108 male) across seven of the Wakatobi Islands (Figure 7.1, Table 7.1).

Table 7.1: A summary of the morphological data used in this analysis for Olive-backed Sunbirds *Cinnyris jugularis*, showing mean figures \pm standard error. The Sulawesi mainland and its continental islands are highlighted in bold, Wakatobi Islands are highlighted in italics.

Population	Wing length (mm)	Bill length (mm)	Mass (g)
Sulawesi Female (N = 8)	52.06 \pm 0.7	20.65 \pm 0.34	7.2 \pm 0.26
Sulawesi Male (N = 18)	55.28 \pm 0.35	21.94 \pm 0.16	8.02 \pm 0.11
Buton Female (N = 5)	52.5 \pm 0.67	21.5 \pm 0.51	7.48 \pm 0.28
Buton Male (N = 9)	56.17 \pm 0.33	21.74 \pm 0.3	7.8 \pm 0.14
Kabaena Female (N = 14)	52.86 \pm 0.55	20.54 \pm 0.21	7.37 \pm 0.11
Kabaena Male (N = 18)	54.72 \pm 0.28	21.29 \pm 0.16	8.12 \pm 0.12
<i>Wangi-wangi Female (N = 12)</i>	49.92 \pm 0.16	19.83 \pm 0.16	7.0 \pm 0.19
<i>Wangi-wangi Male (N = 14)</i>	53.64 \pm 0.24	20.44 \pm 0.21	8.12 \pm 0.16
<i>Oroho Female (N = 7)</i>	50.86 \pm 0.46	19.94 \pm 0.21	7.34 \pm 0.3
<i>Oroho Male (N = 7)</i>	53.86 \pm 0.26	21.19 \pm 0.3	8.01 \pm 0.09
<i>Kaledupa Female (N = 12)</i>	52.83 \pm 0.36	20.11 \pm 0.18	7.45 \pm 0.16
<i>Kaledupa Male (N = 14)</i>	55.57 \pm 0.42	20.92 \pm 0.21	8.59 \pm 0.14
<i>Hoga Female (N = 13)</i>	50.81 \pm 0.24	20.08 \pm 0.14	7.42 \pm 0.13
<i>Hoga Male (N = 31)</i>	54.48 \pm 0.21	21.0 \pm 0.14	8.05 \pm 0.08
<i>Tomia Female (N = 7)</i>	51.29 \pm 0.29	20.23 \pm 0.22	6.91 \pm 0.16
<i>Tomia Male (N = 18)</i>	54.08 \pm 0.28	21.27 \pm 0.1	8.08 \pm 0.09
<i>Lintea Selatan Female (N = 5)</i>	50.6 \pm 0.68	20.32 \pm 0.22	7.48 \pm 0.33
<i>Lintea Selatan Male (N = 15)</i>	54.67 \pm 0.23	21.27 \pm 0.18	8.72 \pm 0.11
<i>Binongko Female (N = 10)</i>	50.8 \pm 0.39	20.22 \pm 0.19	6.94 \pm 0.19
<i>Binongko Male (N = 9)</i>	55.11 \pm 0.14	21.56 \pm 0.3	8.04 \pm 0.19

There was significantly less overlap in morphological niche on the Wakatobi Islands than in the mainland system (Welch t-test $t = 2.870$, $df = 5.784$, $P < 0.05$) (Figure 7.2, Figure S7.1 and Table S7.1). The morphological niche volume of female Olive-backed Sunbirds was significantly smaller on the Wakatobi Islands than in the mainland system (Welch t-test $t = 3.036$, $df = 3.887$, $P < 0.05$) (Figure 7.3). There was no difference in the morphological niche volume of male Olive-backed Sunbirds between the two areas (Welch t-test $t = 1.031$, $df = 7.7805$, $P = 0.334$).

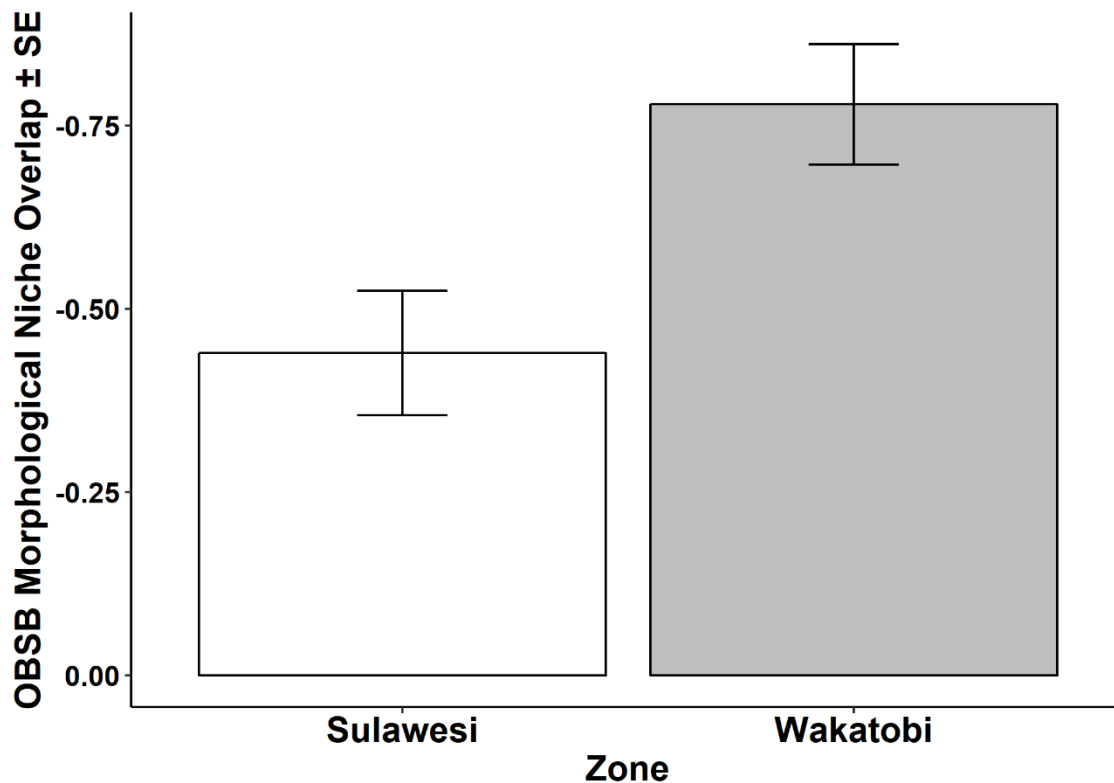


Figure 7.2: Barplot showing the mean (\pm standard error) proportion of morphological niche overlap between female and male Olive-backed Sunbirds (OBSB) on Sulawesi and the continental islands, and on the Wakatobi Islands. Note; values plotted are \log_{10} transformed and on a negative scale, so a larger volume (Wakatobi) indicates less niche overlap.

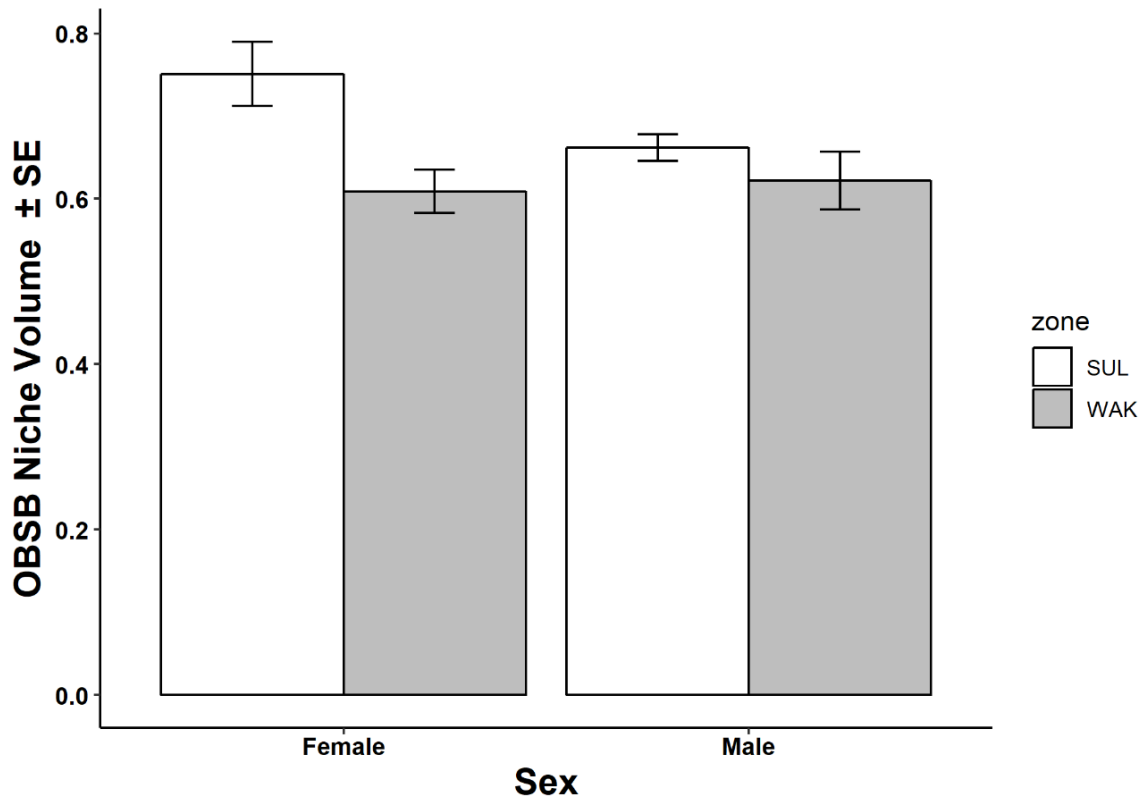


Figure 7.3: Barplot showing the mean niche volume (\pm standard error) of female and male Olive-backed Sunbirds (OBSB). Zone abbreviations; SUL - Sulawesi mainland and continental islands, WAK - Wakatobi Islands.

7.4.2. Transect abundance

A total of 116 transects were carried out; 67 across the three continental islands and 48 across five of the Wakatobi Islands (Wangi-wangi, Kaledupa, Hoga, Tomia and Binongko) (Table S7.2). There was a significant difference in the density of the Olive-backed Sunbird populations between islands (Poisson GLM: Pseudo $R^2 = 0.77$, $Z_{7106} = 50.277$, $P < 0.001$) (Figure 7.4 and Table S7.2). The Olive-backed Sunbird had a significantly higher density on all of the Wakatobi Islands, than in the mainland system (Tukey HSD: $P_{adj.} < 0.001$ for all comparisons) (Table S7.3). Within the Wakatobi Islands, Olive-backed Sunbirds had a significantly higher density on Tomia than Kaledupa (Tukey HSD: Estimate \pm SE = 0.309 ± 0.097 , $P_{adj.} < 0.05$), but there were no other significant differences. Within the mainland system, Kabaena had a significantly higher density of Olive-backed Sunbirds than Sulawesi (Tukey HSD: Estimate \pm SE = 0.600 ± 0.170 , $P_{adj.} < 0.01$) or Buton (Tukey HSD: Estimate \pm SE = 0.981 ± 0.219 , $P_{adj.} < 0.001$). Buton and Sulawesi did not differ (Table S7.3).

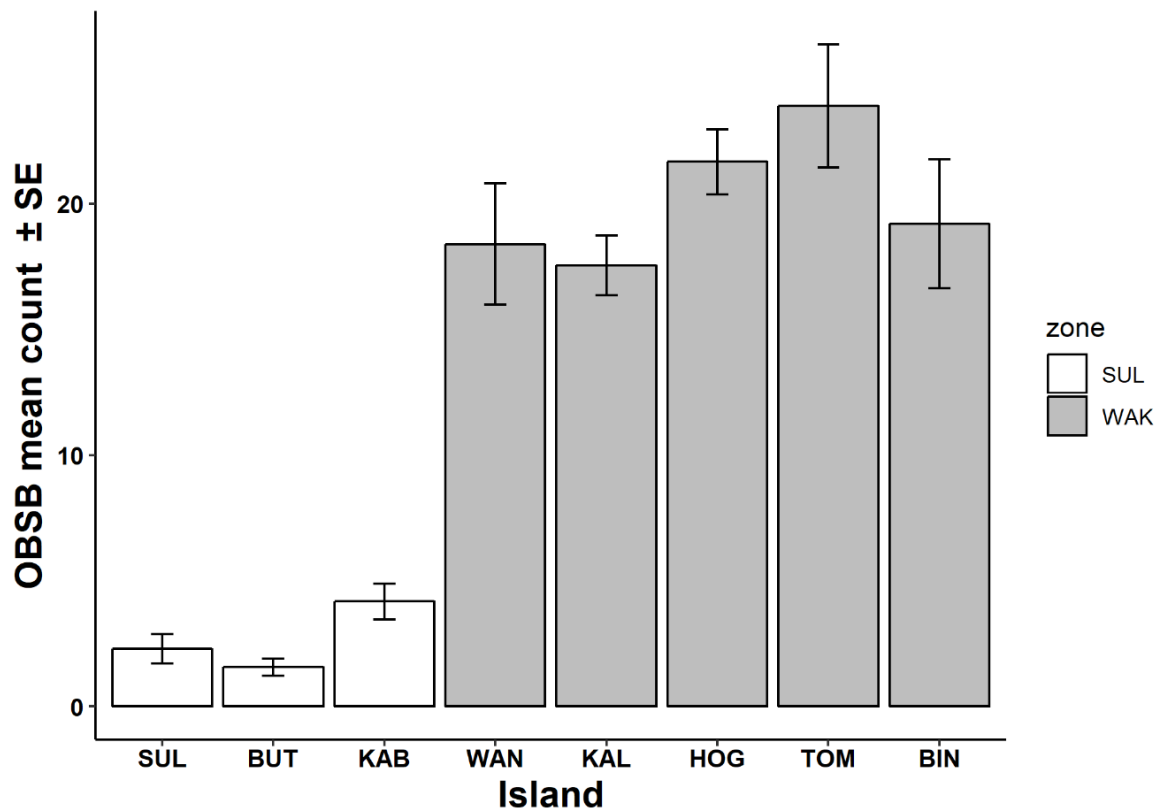


Figure 7.4: Barplot showing the mean transect count (\pm standard error) of Olive-backed Sunbirds (OBSB) across the study area. Zone abbreviations; SUL - Sulawesi mainland and continental islands, WAK - Wakatobi Islands. Island abbreviations; SUL- Sulawesi mainland, BUT - Buton, KAB - Kabaena, WAN - Wangi-wangi, KAL - Kaledupa, HOG - Hoga, TOM - Tomia and BIN - Binongko.

7.5. Discussion

This study investigated sexual dimorphism in an island colonising passerine bird, to assess whether it followed the expectation of increased sexual dimorphism in small island populations and what might be driving this. This was the first assessment of this pattern in the Nectariniidae. Our results showed increased sexual dimorphism in populations on small islands, demonstrated by a decrease in intersexual morphological niche overlap in populations on the small Wakatobi Islands, in comparison to the mainland system (Figure 7.2, Figure S7.1 and Table S7.1), supporting hypothesis 1. In addition we found that Olive-backed Sunbirds were significantly more abundant on the Wakatobi Islands (Figure 7.4), supporting hypothesis 3. However, we did not find any evidence for an expansion of morphological niche in the absence of mainland interspecific competitors, rather we found a decrease in the morphological niche volume for female Olive-backed Sunbirds, and no change for males (Figure 7.3). Therefore hypothesis 2 was not supported. Assessing these results together, we provide no indication of a direct effect of

interspecific competition on sexual dimorphism, but evidence that intersexual competition promotes niche divergence in high density populations.

The Olive-backed Sunbird populations assessed followed the expected pattern of increased sexual dimorphism in populations on small islands (Selander 1966; Butler *et al.* 2007) (Figure 7.2). This was associated with significantly higher abundance in the Wakatobi Island Olive-backed Sunbird populations (Figure 7.4). While there were some differences in abundance between islands within mainland system and Wakatobi Islands (Figure 7.4, Table S7.3), the strongest pattern was a consistently higher abundance on all of the small oceanic Wakatobi Islands, than on any of the larger continental islands. Increased population density in island colonist populations, on species depauperate islands, is known as density compensation (MacArthur *et al.* 1972). This phenomenon has been noted in a wide range of taxa, and has been associated with reduced species richness on islands, potentially leading to less interspecific competition for resources and lower predation pressure (Nilsson 1977; George 1987; McGrady-Steed and Morin 2000; Rodda and Dean-Bradley 2002; Buckley and Jetz 2007; Longino and Colwell 2011). The greater access to resources provided by freedom from interspecific competition can allow successful colonists of species depauperate islands to reach far higher densities than they do in mainland systems (Whittaker and Fernández-Palacios 2007). Intraspecific competition is at its most intense in these high density populations (Robinson-Wolrath and Owens 2003; Pafilis *et al.* 2009), and can drive selection for diversification within a population (Bolnick 2004; Svanbäck and Bolnick 2007), such as increased sexual dimorphism (Greenberg and Olsen 2010; Greenberg and Danner 2013).

Unexpectedly, we found no expansion in morphological niche volume for either female or male Olive-backed Sunbirds on the Wakatobi Islands, in conditions with reduced interspecific competition. An expansion in niche in response to reduced interspecific competition on islands has been inferred as a major factor driving greater sexual dimorphism in insular populations (Selander 1966; Butler *et al.* 2007; Greenberg and Olsen 2010). However, no change was found in male Olive-backed Sunbird morphological niche between the Wakatobi and the mainland system, while female Olive-backed Sunbirds showed a decrease in morphological niche volume (Figure 7.3). The male Olive-backed Sunbird is heavier and is therefore likely to be the dominant forager (Francis *et al.* 2018), so in a population with increased intraspecific competition the female is likely to experience stronger selection to avoid intersexual competition (Peters and Grubb 1983; Desrochers 1989). Dayan and Simberloff (1994) found that an increase in sexual dimorphism in mustelids on a smaller, more species depauperate island was due to a niche shift

in females, not males. As in this study, male mustelids were the larger sex on both islands, and this sexual dimorphism was exaggerated on a smaller island by females showing reduced body size.

The lack of any expansion of morphological niche volume may indicate that the Olive-backed Sunbird's morphological niche was not being limited by interspecific competitors on Sulawesi mainland. While the increased abundance of Olive-backed Sunbird populations on the Wakatobi Islands indicated it probably has access to more resources than on the mainland (Grant 1966), resource partitioning with the additional competitors on the mainland may have been temporal or spatial rather than morphological (Schoener 1974; Albrecht and Gotelli 2001; Robertson *et al.* 2014). Additionally it is possible that resources are more limiting on the Wakatobi Islands preventing niche expansion. When investigating whether leaf-warblers in species depauperate areas of the Himalayas experienced character release, Ghosh-Harihar and Price (2014) actually found that they showed niche contraction, likely due to less diversity of prey in the species depauperate areas. The Wakatobi Islands exhibit little habitat diversity (Kelly and Marples 2010; O'Connell *et al.* 2018) and may lack the resource base for niche expansion. Further research into feeding and competitive behaviour in these Olive-backed Sunbird populations, and the resource availability on different islands, would give great insight into these results.

Another avenue of research that may shed light into these results would be to investigate the effect of predation pressure on our study populations. Predators can both depress populations and alter the foraging ecology of species (George 1987; Laundré *et al.* 2014), therefore predation pressure will likely affect both population size and niche. Two notable predators of small passerine birds present on the mainland, the Vinous-breasted Sparrowhawk *Accipiter rhodogaster* and Dwarf Sparrowhawk *Accipiter nanus*, are absent from the Wakatobi Islands (Eaton *et al.* 2016), as is the Little Bronze-cuckoo *Chalcites minutillus*, a known brood parasite of Olive-backed Sunbird nests (Payne *et al.* 2018; Cheke and Mann 2018e). This may contribute to the higher abundance of the Olive-backed Sunbird on the Wakatobi. However more study is required, as the distribution of these species is poorly known in the region (Eaton *et al.* 2016; Martin *et al.* 2018), and little is known about potential non-avian predators, particularly on the Wakatobi Islands.

This study highlighted the morphological shifts in an island radiation of a sexually dimorphic small passerine. Our results provide evidence of density compensation in small island

populations of the Olive-backed Sunbird and an association between population density and increased sexual dimorphism. Intersexual competition may therefore be the key driver in this process. We found no evidence of a direct effect of interspecific competition, but more research is needed to understand the relationship between species richness and sexual dimorphism. The sunbirds of the Indo-West Pacific provide an ideal group for further study into sexual dimorphism in island radiations, and the relative effect of intra- and inter-specific competition on niche. Gaining a greater understanding of how competition may drive adaptation provides further insight into how biodiversity is generated and maintained.

8. General Discussion

8.1. Biodiversity and speciation

8.1.1. Biodiversity monitoring and speciation research

Global biodiversity is poorly understood, despite its importance for humanity (Cardinale *et al.* 2012). Biodiversity can be measured at multiple levels (Proença *et al.* 2017), with increasing focus being directed towards trait diversity (Díaz and Cabido 2001; Ross *et al.* 2017; Legras *et al.* 2018) and phylogenetic diversity (Flynn *et al.* 2011; Chao *et al.* 2014; Veron *et al.* 2018). However despite not capturing the full picture of biodiversity, the species is still the primary unit used for setting conservation priorities (Katzner *et al.* 2011; Costello *et al.* 2015; IUCN 2018). There remain significant knowledge gaps both in terms of global species diversity, and species distributions (Pereira and Cooper 2006; May 2010; Mora *et al.* 2011). Efforts are being made to fill these gaps, aided by the use of relatively cheap and accessible modern molecular tools to uncover cryptic diversity (Costello *et al.* 2015; Costello 2015; Proença *et al.* 2017). The biodiversity of the Indo-Pacific and South-east Asia require particular attention, as they have been poorly studied until recently (Pereira *et al.* 2010; BirdLife International 2018b). This thesis makes an important addition to efforts to chart the biodiversity of the Indo-Pacific, focusing on South-east Sulawesi as our study system. We provide a greater understanding of the avifauna of South-east Sulawesi (Chapters 2 and 3), chart the diversification of the ‘great speciator’ taxa in the region (Chapters 4 and 5) and consider morphological adaptations associated with diversification (Chapters 4, 5, 6 and 7).

Biodiversity monitoring schemes have proved particularly valuable to conservation where they have been well structured and coordinated for long time periods (Schmeller *et al.* 2009), providing valuable datasets to analyse species trends and inform conservation planning (Gregory *et al.* 2007; Inger *et al.* 2015). In the tropics, coordinated schemes have had less time to develop (Sheil 2002) and there are still huge gaps in the baseline knowledge of species distributions. In Indonesia, Burung Indonesia are attempting to produce a bird atlas spanning the country (Taufiqurrahman *et al.* 2016), in order to promote and concentrate conservation efforts. While great strides have been made, their volunteer network is only in the process of building up and most records are still concentrated around Java (Burung Indonesia 2018). Chapters 2 and 3 filled in important gaps in the current understanding of avian species distributions in our study region in South-east Sulawesi. Of particular note are the records of the Endangered Milky Stork *Mycteria cinerea*. The South-east Sulawesi population of this species is poorly known, with the only known breeding population in Rawa Aopa National Park (Wardill *et al.*

al. 1998). This population is very isolated from the Milky Stork's core range on Sumatra (Elliott *et al.* 2018a), so identifying and protecting any further breeding populations on South-east Sulawesi would be key for this population's survival. The rice paddy areas to the north-west of Kendari city merit investigation to further understand their importance for feeding flocks of Milky Storks, and potentially as a breeding area. In addition they harbour populations of other threatened species such as Asian Woollynecks *Ciconia episcopus* and Knobbed Hornbills *Rhyticeros cassidix*. Highlighting the potential conservation value of Sulawesi comes at an important time, as Sulawesi and Papua become the new front of intensive forest clearance for plantations (Margono *et al.* 2014; Abood *et al.* 2015), unfortunately due to much of Sumatra and Borneo having already been cleared.

Recent research has demonstrated that the Indo-Pacific region is home to a huge amount of unrecognised biodiversity (Lohman *et al.* 2010; Murray *et al.* 2012; Cibois *et al.* 2014), particularly in the 'great speciator' lineages (Andersen *et al.* 2013; Andersen *et al.* 2014; Andersen *et al.* 2015b). In Chapters 4 and 5 we investigated these lineages in South-east Sulawesi, uncovering further cryptic diversity. Chapter 5 outlines the presence of two unrecognised white-eye species on the Wakatobi Islands. As well as providing support for the recognition of a completely novel white-eye species, Chapter 5 also illustrates the utility of an integrative approach to taxonomy, utilising multiple measures to recognise cryptic species like *Z. c. flavissimus* (Tobias *et al.* 2010; Padial *et al.* 2010; Fišer *et al.* 2018; Alström *et al.* 2018). We hope these findings will result in the recognition of the species status of the *Z. c. flavissimus* population on the Wakatobi Islands by avian taxonomic authorities, such as del Hoya *et al.* (2018) and Gill and Donsker (2018), and propose the name Wakatobi White-eye. In order to be recognised as a BirdLife International Endemic Bird Area, a region needs to be home to two species entirely restricted to that area (Stattersfield *et al.* 1998; BirdLife International 2018a). We believe that a strong argument could be made that the Wakatobi Islands deserve this status, as the region would fulfil this criterion and additionally be home to five endemic subspecies (after the promotion of *Z. c. flavissimus* to full species status) (Kelly and Marples 2010; Collar and Marsden 2014). Chapter 4 also highlights that the Wakatobi Collared Kingfisher population may represent an endemic subspecies, subject to assessing vocal and plumage traits. Recognition as an Endemic Bird Area would highlight the need for greater conservation efforts in the Wakatobi Islands.

Most terrestrial habitats in the Wakatobi Islands are highly degraded and they receive no protection. *Zosterops c. flavissimus* is a highly adaptable colonist of edge habitats (van Balen

2018b), so is unlikely to be negatively affected by any further anthropogenic influences on the Wakatobi Islands. However the 'Wangi-wangi White-eye' population may be vulnerable as it is restricted to one small (155 km²) island. This species needs urgent recognition and assessment of its conservation status. Highlighting the conservation relevance of the Wakatobi Islands would also benefit other populations in need of protection, particularly the Wakatobi endemic subspecies of the Yellow-crested Cockatoo *Cacatua sulphurea djampeana*, one of the few remaining populations of this Critically Endangered species (Collar and Marsden 2014; Rowley *et al.* 2018).

8.1.2. Integrative avian taxonomy considered

Modern molecular tools have allowed for rapid discovery of a huge amount of unrecognised species diversity (Hebert *et al.* 2004a; Barrowclough *et al.* 2016; Hebert *et al.* 2016), proving both a boon and a challenge to taxonomists (Fišer *et al.* 2018). While useful for highlighting divergent taxa (Hebert and Gregory 2005), molecular tools suffer from some of the same problems of other methods for delimiting species, particularly when splitting closely related taxa (Rubinoff and Holland 2005; Brower 2006). The amount of genetic divergence required to split a species, and how you measure that, is difficult to define as species differ greatly in the amount of within-species genetic variability (Hebert *et al.* 2004b; Shearer and Coffroth 2008; Toews *et al.* 2016). This has led to increased implementation of an integrative taxonomic approach, requiring multiple measures of both genetic and phenotypic data to split species (Will *et al.* 2005; Padial *et al.* 2010; Schlick-Steiner *et al.* 2010; Alström *et al.* 2018).

A recent focus on integrative taxonomy has been particularly evident in avian taxonomy. While much of the work in pioneering DNA barcoding approaches to species delimitation was carried out with birds (Hebert *et al.* 2004b; Kerr *et al.* 2007; Kerr *et al.* 2009), this approach appears to have lost favour amongst taxonomic authorities. Avian species identified solely using a barcoding approach are unlikely to be accepted (del Hoyo *et al.* 2018d). Some studies have used deeper genomic sampling (Toews *et al.* 2016; Ng *et al.* 2018), but the resources for this are not widely available and the question still remains, what level of genetic divergence is worthy of species recognition? The primary resource for avian taxonomic information, the Handbook of the Birds of the World Alive (HBW Alive), produced in concert with BirdLife International, has taken a step back from using molecular methods, particularly for delimiting closely related species (del Hoyo *et al.* 2018d). They are now using the Tobias criteria scoring system following Tobias *et al.* (2010) (Appendices - Section 5.1). This system focuses on plumage, song, morphological and behavioural traits for separating species. In many ways it represents a return

to favour of the phenetic species concept (de Queiroz 2007). This approach has drawn strong criticism from some fronts (Remsen 2016), particularly due to its disregard of phylogenetic data. A strength of this system which has been championed is its speed, allowing for the huge quantity of taxonomic revisions carried out during the publishing of the Handbook of the Birds of the World (Collar *et al.* 2016; del Hoya *et al.* 2018). However the ‘great speciator’ radiations of the Indo-Pacific have highlighted the issue of exclusion of phylogenetic data. Widespread phylogenies of the Collared Kingfisher (Andersen *et al.* 2015b) and Golden Whistler *Pachycephala pectoralis* (Andersen *et al.* 2014; Jønsson *et al.* 2014) showed that these species, were in fact species complexes, made up of multiple well differentiated species. However, the lack of natural history data from much of the Indo-Pacific has stalled any official recognitions of these species by HBW Alive and BirdLife International (Woodall 2018a; Boles *et al.* 2018). It seems unlikely that detailed phenotypic and song data will be collected for these populations across the Indo-Pacific in the immediate future, leaving their status in limbo. The International Ornithological Congress, has acted faster and now recognises 10 species from the Collared Kingfisher species complex (Gill and Donsker 2018), but there is no indication that HBW Alive will follow suit.

This thesis has provided an opportunity to work with the Tobias criteria and consider its applicability on a small scale, in taxa with little baseline information. In general the Tobias criteria must be viewed in a positive light, as clear guidelines are given, providing an excellent framework to build a body of evidence towards drawing taxonomic boundaries. The insistence on using song and plumage data can prove challenging, as some species do not lend themselves to being recorded. However this places all species splits on a much sounder footing as it provides a good basis for assuming reproductive isolation (Uy *et al.* 2009). The lack of song recordings prevented a proposal that the Wakatobi Collared Kingfisher be recognised as a subspecies in Chapter 4. However, this informed the work carried out in Chapter 5, which was ultimately greatly strengthened by the inclusion of song analyses. This additionally allows for future considerations of song evolution (section 8.3 Future directions). In this way, collecting further phenotypic data can allow for greater insight into the speciation process and what is likely required for population isolation (Bickford *et al.* 2007; Angulo and Icochea 2010; Fišer *et al.* 2018).

The work carried out by del Hoya *et al.* (2018) for HBW Alive must be lauded for its scope, and for providing a benchmark by which to judge taxonomic research going forward. However a number of issues remain. The Tobias criteria lack guidelines on what is required of a

subspecies. The requirement of a robust sample size for all phenotypic measures used in a Tobias scoring is often impractical in under-studied parts of the world. This has been shown by two species recently proposed for the Sulawesi region which have been yet to be recognised. Populations from which it is difficult to collect song data, such as flowerpeckers (Kelly *et al.* 2014), or that are simply difficult to catch and measure such as flycatchers (Harris *et al.* 2014), can be stuck just below the Tobias score for species status (Clement and Bonan 2018; Cheke and Mann 2018d), despite being phylogenetically distinct. Ultimately, no one measure is ever likely to provide a panacea to the frequently vexing question of how to define a species (de Queiroz 2007). Rigorous integrative approaches provide our best answer. Therefore the exclusion of genetic data from the Tobias criteria can only be to its detriment. Since the bulk of outdated avian taxonomy has been revised in the volumes of HBW, perhaps now is the time to reincorporate phylogeny into integrative taxonomy?

8.2. Adaptations to island life and potential drivers of diversification

Island colonisation is associated with a suite of adaptations to what is typically a more ecologically constrained, species depauperate environment (Whittaker and Fernández-Palacios 2007). Understanding how populations adapt to island colonisation and isolation gives great insight into the speciation process, and how biodiversity is generated and maintained (Mayr and Diamond 2001; Nosil *et al.* 2009; Orsini *et al.* 2013). Our study system provided an opportunity to investigate how isolation, competition and novel environments can play a role in diversification, and consider the adaptations species make in island environments.

8.2.1. Population isolation and dispersal

The ‘great speciators’ prove a particularly intriguing group, as these lineages contain both widespread island colonisers and a high proportion of single island endemics (Mayr and Diamond 2001). This raises the question, “How do populations from lineages with such excellent dispersal abilities become isolated?”. Diamond *et al.* (1976) referred to this as the paradox of the ‘great speciators’ and proposed that rapid shifts in dispersal ability must have occurred in these populations. Recent research into ‘great speciator’ lineages has found evidence of shifts in dispersal ability in isolated populations of ‘great speciator’ lineages (Jønsson *et al.* 2014; Pedersen *et al.* 2018), in line with the proposal by Diamond *et al.* (1976). In Chapter 5 we inferred the dispersal capacity of different white-eye populations using their wing length and weight. We found that the population of Lemon-bellied White-eyes that recently colonised Runduma Island showed greater inferred dispersal capacity than the mainland source population, as would be expected of a recent colonist (0.08-0.22 Myr ago, Figure 5.7) (Ricklefs and Cox 1972; Mayr and

Diamond 2001). In contrast the Wakatobi *Z. c. flavissimus* population showed significantly less inferred dispersal capacity than its mainland relatives, perhaps showing the loss of dispersal capacity that has been found in many island-colonising taxa (Bellemain and Ricklefs 2008; Losos and Ricklefs 2009). This is likely due to selection for traits other than dispersal capacity in older island lineages which have had longer to adapt to the local environment (Gillespie *et al.* 2012). The Wakatobi *Z. c. flavissimus* population diverged from the mainland Lemon-bellied White-eye population 0.38-0.8 Myr ago (Figure 5.7). A genus wide test in white-eyes, relating population dispersal capacity to its divergence time from its closest relative, following Pedersen *et al.* (2018), would allow for an analysis of the ubiquity of this phenomenon in ‘great speciators’.

8.2.2. The island rule considered

This thesis has provided the opportunity to investigate how a number of factors may affect morphological adaptation to island life. Within this context it is interesting to consider the ‘island rule’, which has often been invoked to explain body size evolution in island populations. The ‘island rule’ predicts evolution towards a medium body size, by both small and large species, due to less predation pressure, a more constrained resource base and the increased likelihood of a more generalist diet (Foster 1964; Van Valen 1973; Clegg and Owens 2002; Lomolino 2005; Price and Phillimore 2007; Lomolino *et al.* 2013). However, recent research has called into question the generality of the ‘island rule’ and proposed body size evolution depended on the characteristics of the islands and species involved (Meiri *et al.* 2006; Meiri *et al.* 2008; Meiri *et al.* 2011; Itescu *et al.* 2014). Though this thesis only considers a limited number of island populations, evidence from Chapters 4 and 5 does not support a general ‘island rule’. While the Wakatobi Collared Kingfisher and Runduma Lemon-bellied White-eye populations increased in body size, in comparison to the mainland populations, the Wakatobi *Z. c. flavissimus* populations decreased in body size in comparison to mainland Lemon-bellied White-eye. The decrease in body size of the *Z. c. flavissimus* populations runs counter to the assumption of the ‘island rule’ for a small species. Assessment of how widely the ‘island rule’ applies to birds has been limited (Clegg and Owens 2002) and a wider analysis would provide greater insight.

8.2.3. Competition as a driver of diversification

As well as population isolation, inter- and intra-specific competition can play a major role in shaping a species’ evolution (Gause 1934; Hardin 1960; MacArthur and Levins 1967; Grant 1972). Competition is thought to play a role in diversification and speciation, as populations of a species exposed to a highly competitive environment will experience different selection pressures than those not exposed to the same competition (Pfennig and Pfennig 2012). Closely

related competitors are likely to be of greatest importance (Reif *et al.* 2018). Closely related species usually share a similar niche, due to phylogenetic niche conservatism, which refers to the tendency for species to retain ancestral traits (Lee-Yaw and Irwin 2015). In Chapter 4 we suggest ecological character displacement as a possible mode of diversification in the early stages of speciation in Collared Kingfishers, as this population may be forced to partition its niche morphologically with the Sacred Kingfisher on the Wakatobi islands, rather than by habitat partitioning as on the mainland (Brown and Wilson 1956; Dayan and Simberloff 2005; Stuart and Losos 2013). In Chapter 6 we investigated interspecific competition in another pair of congeneric competitors, the Lemon-bellied White-eye and the Pale-bellied White-eye. At sites where the Lemon-bellied White-eye was in allopatry (urban areas and a small island) from the Pale-bellied White-eye, it showed an expansion in morphological niche and a large increase in density. The decrease in interspecific competitive pressure may be allowing Lemon-bellied White-eyes in allopatry to experience character release (Grant 1972; Arthur 1982; Bolnick *et al.* 2010). The increase in population density is likely to have led to higher intraspecific competition (Robinson-Wolrath and Owens 2003), which may have driven the niche expansion (Svårdson 1949; Roughgarden 1974; Svanbäck and Bolnick 2007). Competitively mediated selection has been shown to be important in the morphological adaptation of other white-eyes (Robinson-Wolrath and Owens 2003; Wijesundara and Freed 2018). Along with the proposed case of character displacement in *Z. c. flavissimus* in the presence of the 'Wangi-wangi White-eye', identified by Kelly (2014), these results demonstrate that competitively mediated selection may also be an important factor in shaping the evolution of the white-eyes of South-east Sulawesi.

While the patterns observed in our study species in South-east Sulawesi appear to match the description of competitively mediated selection, the assumptions underlying this concept require deeper consideration. Since being proposed by Brown and Wilson (1956) ecological character displacement has proved a popular and often cited concept, providing an intuitive explanation of patterns of diversification in competing species. Grant (1972) provided a more detailed framework for character displacement and character release, coining the term competitively mediated selection. Schluter and McPhail (1992) shaped the modern criteria for demonstrating the occurrence of ecological character displacement; 1. The pattern should not occur by chance, 2. Sites of sympatry and allopatry should not differ greatly in food, climate, or other environmental features affecting the phenotype, 3. Morphological differences should reflect differences in resource use, 4. There must be independent evidence for competition, 5. Enhanced differences should result from actual evolutionary shifts, not from the biased colonisation and extinction of similar-sized individuals and 6. Phenotypic differences should

have a genetic basis. Though competitively mediated selection has been widely inferred subsequent to this (Dayan and Simberloff 1994; Simberloff *et al.* 2000; Robinson *et al.* 2000; Reifová *et al.* 2011; Norberg and Norberg 2015; Wijesundara and Freed 2018), <5% of studies have met the criteria of Schluter and McPhail (1992), with many failing to meet several criteria (Dayan and Simberloff 2005; Stuart and Losos 2013). The unique long term study of Darwin's finches in the Galapagos is a notable exception which illustrated all six criteria (Grant and Grant 2006; Lamichhane *et al.* 2015; Lamichhane *et al.* 2016). The most recent review of the subject suggested that the Schluter and McPhail (1992) criteria are too stringent and that studies that match four of the six criteria are doing very well (Stuart and Losos 2013). However, even if a more relaxed interpretation of competitively mediated selection is employed, without demonstrating genetic change, phenotypic plasticity cannot be ruled out as an alternative explanation to competitively mediated selection (Pfennig *et al.* 2006).

Phenotypic plasticity can produce a rapid adaptive response to different environmental conditions, without genetic change (Turcotte and Levine 2016). Plastic responses are likely to facilitate species' survival when faced with novel habitats (McNew *et al.* 2017), food resources (Charmantier *et al.* 2008) and species interactions (Agrawal 2001). However recent research has suggested that phenotypic plasticity and competitively mediated selection may not be mutually exclusive. Phenotypic plasticity might play a key role in the early stages of character release and displacement, producing an adaptive response which may become fixed as the plastic trait is exposed to selection (Pfennig and Pfennig 2010). If plastic change in a trait is adaptive it can be stabilised by the evolution of genetic differences through genetic assimilation (West-Eberhard 2003; Crispo 2007; Pfennig and Martin 2010). Levis *et al.* (2017) provided evidence of this process in an experimental system where the Plains Spadefoot Toad *Spea bombifrons* lost diet-induced gene expression plasticity when in sympatry with the New Mexico Spadefoot Toad *Spea multiplicata*. In sympatry with New Mexico Spadefoot Toads, Plains Spadefoot Toads specialised as carnivores, to avoid interspecific competition, while in allopatry they were omnivorous.

Competitively mediated selection as a concept is experiencing renewed interest, with calls for research into this phenomenon to be less character focused and to look at wider aspects of species' interactions (Germain *et al.* 2018). Recent studies have begun to shed light on how species segregate microhabitat as well as morphology, revealing complex patterns of syntopy and allotopy within sympatric zones (Yousefi *et al.* 2017; Reif *et al.* 2018; Sottas *et al.* 2018). Within our own study species our observations of patterns consistent with competitively mediated selection must be considered a starting point for further research. Investigation of

microhabitat segregation would likely prove fruitful, as our white-eye and kingfisher species appear to partition habitat on many islands. As this field of research continues to develop ‘great speciators’ may prove useful study groups in which to test the assumptions of competitively mediated selection, due to their wide range, the frequency with which they are found in secondary sympatry with close relatives and their rapid pace of diversification.

Competition not only happens between species, as with character displacement, but within them. Strongly sexually dimorphic species provide a particularly interesting group in which to study adaptations to island life, as each sex occupies a slightly different niche within the total species niche. Changes in selection pressure can lead to changes in the level of sexual dimorphism in a population (Butler *et al.* 2007; Sacchi *et al.* 2015). In Chapter 7 we found that sexual dimorphism and abundance increased in Olive-backed Sunbird populations, on small islands, as has been observed in a variety of other taxa (Selander 1966; Ebenman and Nilsson 1982; Dayan and Simberloff 1994; Pearson *et al.* 2002). This is typically explained by an increase of niche size by both sexes in circumstances where there are fewer interspecific competitors (Selander 1966; Greenberg and Olsen 2010). However we found no evidence of niche expansion in either sex, rather we found that there was a decrease in morphological niche in females and no change in males. Male Olive-backed Sunbirds are the larger sex (Cheke and Mann 2018e), so would likely be the dominant forager (Francis *et al.* 2018) and may exclude the females from their niche space in high density populations. Dayan and Simberloff (1994) found a similar result when looking at increased sexual dimorphism in mustelids on a smaller island. They found it was explained by a decrease in body size in females only, with no change in the larger male. In these cases females may have had to shift morphological niche in order to avoid intersexual competition with the larger male (Doebeli 2011; Meiri *et al.* 2014). This finding illustrates the importance of considering sexual dimorphism when studying island radiations, as sexually dimorphic species are likely to be constrained in their morphological diversification in ways that monomorphic species are not (Bolnick and Doebeli 2003).

8.2.4. Urban areas as ecological islands

Chapter 6 provided intriguing evidence that urban areas may act as ecological islands for edge-adapted, urban-colonising species, such as the Lemon-bellied White-eye. Urban populations of Lemon-bellied White-eyes showed an expansion of morphological niche and an increase in density relative to those found in coastal habitats on the mainland. This was also true of a small island population on Runduma. Island-like processes are typically only noted in areas with strong geographical boundaries isolating them, such as islands in bodies of water (MacArthur and

Wilson 1967; Whittaker and Fernández-Palacios 2007), ponds or lakes separated by land (Keddy 1976; Gotoh *et al.* 2011) or mountains separated by lowlands (Johansson *et al.* 2007; Husemann *et al.* 2015). Island-like effects in mainland habitats without a strong geographical boundary have only been noted on a few occasions in species-depauperate, ecologically-constrained, saltmarshes and mangroves (Greenberg and Olsen 2010; Luther and Greenberg 2011). Greenberg and Olsen (2010) and Luther and Greenberg (2011) showed evidence of density compensation and niche expansion in sparrow populations in these coastal environments, which were only separated by their harsh ecologies. This relationship has not been previously noted for urban areas, and they lack the typical features which define isolated systems, such as the strong barrier to dispersal which we find with true geographic islands (Whittaker and Fernández-Palacios 2007), or the filtering effect of elevational gradients found in mountain systems (Kluge and Kessler 2011). However urban areas do show many of the features which may select for island colonising species.

While food in urban areas is often abundant, it is frequently patchy, subject to turnover as land use changes and requires the adoption of novel foraging techniques (Shochat *et al.* 2006). This selects for adaptable species which are not sensitive to disturbance (Shochat *et al.* 2006; Alberti *et al.* 2017b). Plentiful food, and fewer interspecific competitors, means that successful urban colonists can achieve much higher densities than in natural habitats, but therefore experience much higher intraspecific competition (Shochat *et al.* 2004). The relatively open spaces of urban areas are likely to select for speed and performance in locomotion, rather than the ability to navigate a complex environment, such as a forest (Winchell *et al.* 2016; Winchell *et al.* 2018). Møller (2009) found that urban colonising birds in the Western Palearctic are characterised by adaptable foraging habits, high fecundity, wide ranges and excellent dispersal ability. They are typically edge species who can take advantage of fragmented habitats (McKinney 2006; Ries and Sisk 2010). All of these characteristics listed are associated with the island colonising taxa of the Indo-Pacific (Mayr and Diamond 2001), particularly the 'great speciators', which are known for their wide ranges, adaptability and dispersal ability. This may make them ideal urban-colonising species. Thus far the potential of Indo-Pacific island colonisers to colonise human altered landscapes has not received much attention. There are only a handful of anecdotal observations of widespread kingfisher edge species displacing local endemic kingfishers in disturbed habitats (Ward 1968; Diamond and Marshall 1977; Andersen *et al.* 2017). However, it seems likely that widespread edge species will benefit from an increase in human impact throughout the Indo-Pacific, while local endemics may suffer. This phenomenon

merits further study to understand how release from interspecific competition and access to novel resources may play a role in the evolution of urban colonising species.

8.3. Future directions

Each chapter of this thesis has attempted to provide insight into biodiversity and speciation in South-east Sulawesi. They in turn have raised many more questions. The wide geographic range, relatively poorly studied flora and fauna, and diversity of island environments, means the Indo-Pacific provides a unique opportunity for research. Further research in this region is vital for taxonomic assessment and cataloguing of biodiversity in a rapidly developing region and analysing evolutionary processes in island systems. The widespread island-colonising taxa of the Indo-Pacific such as the ‘great speciator’ lineages, are a valuable study group to gain understanding of evolution and island biogeography. They are found in a wide variety of island environments, under different degrees of geographic isolation, and regularly in secondary sympatry with close relatives. This allows researchers to test the effects of selection under a variety of different pressures, and investigate how habitat type, isolation and competition may influence evolution.

Where logistically possible, it would be desirable to adopt the intensive study designs used with a number of fairy-wren species in Australia, tit species in Europe and the Heron Island (Australia) Silvereye *Zosterops lateralis* population. Adaptations to differing resource bases on islands are likely to be important drivers of diversification in island radiations (Newton 2003), but such adaptations are often only inferred from morphological difference. Tagging (with colour rings or radio frequency identification tags) of measured individuals would allow monitoring of feeding behaviours. This could tie morphological traits to ecological niches. Such studies could be carried out on competing species in areas of sympatry and allopatry, to provide a greater understanding of the influence of inter- and intra-specific competitive interactions. Alternatively, sampling target populations and potential food resources at multiple time points through the year would allow for the use of stable isotopes as a proxy of diet.

A number of specific questions directly utilising either the data or ideas generated in this thesis are outlined below

8.3.1. Biodiversity and taxonomic assessment

8.3.1.1 Biodiversity monitoring in South-east Sulawesi

Chapters 2 and 3, along with Martin *et al.* (2015), (2017), (2018) and (2019) demonstrated that there is much unrecorded biodiversity present in South-east Sulawesi. Further manuscripts are

being prepared, documenting the biodiversity of the region. These manuscripts will provide a first checklist of the avifauna of Menui Island, an updated assessment of the avifauna of the Wakatobi Islands, and further records for sites on mainland Sulawesi.

8.3.1.2 Wider assessment of Lemon-bellied White-eye and Collared Kingfisher radiations

In Chapter 5 we brought greater resolution to Lemon-bellied White-eye taxonomy, demonstrating that *Z. c. flavissimus* deserves to be recognised as a separate species, the ‘Wakatobi White-eye’. However the Lemon-bellied White-eye complex is still poorly understood, with widespread, disjunct, populations spread across Indonesia. They require taxonomic revision utilising the integrated methodology we have employed. Chapter 4 highlighted a potential new subspecies of Collared Kingfisher on the Wakatobi Islands. A more in-depth assessment of this population involving vocal and plumage characters would bring greater definition to this group. A wider sampling of populations in the Sunda Islands and across Sulawesi would place the Wakatobi population in an appropriate context and allow for broader revision of the taxonomy of these species. In a wider setting, the work of Andersen *et al.* (2015b) has led to much taxonomic revision of the Collared Kingfisher species complex to the east of Sulawesi (Gill and Donsker 2018). Collared Kingfisher populations from Indonesia westwards, as far as the Red Sea, have received much less attention and may contain much cryptic diversity.

8.3.1.3 Assessment of sunbird radiations in the Indo-Pacific

The sunbird species of South-east Sulawesi, the Olive-backed Sunbird, Brown-throated Sunbird *Anthreptes malacensis*, Black Sunbird *Leptocoma aspasia* and Crimson Sunbird *Aethopyga siparaja*, all have wide ranges across many islands in the Indo-Pacific (Cheke and Mann 2018e; Cheke and Mann 2018a; Cheke and Mann 2018b; Cheke and Mann 2018c). Lohman *et al.* (2010) suggested that the Olive-backed Sunbird populations of the Philippines contained much cryptic diversity, but apart from that, the Nectariniidae populations of the Indo-Pacific have received little attention (though see Carstensen *et al.* 2009). Kelly (2014) demonstrated moderate differentiation in the Wakatobi Olive-backed Sunbird population from the mainland, labelling them as an ‘incipient species’. Preliminary work during the course of this thesis showed some differentiation in Black Sunbird populations (in morphology and the ND3 gene) on the island of Menui, which merits further investigation. The moderate differentiation evident within South-east Sulawesi suggests that a wider revision, assessing sunbird populations across their full ranges, would uncover much unrecognised diversity. In light of the results of Chapter 7, assessing the radiation of other widespread, sexually dimorphic species, such as other sunbird species, may provide insight into how strongly dimorphic species undergo speciation. Do all

sunbirds show increased sexual dimorphism on small islands, and is this associated with niche expansion, or decreased niche volume in the smaller sex?

8.3.2. Evolutionary questions

8.3.2.1 *Island colonisers in urban habitats - competitive advantage and niche effects*

Chapter 6 suggests an intriguing relationship between island-colonising ability and urban-colonising ability in Lemon-bellied White-eyes. However, there are few cities in South-east Sulawesi. Expanding sampling across the island of Sulawesi would give a greater insight into this phenomenon. South and North Sulawesi are much more urbanised than South-east Sulawesi (Biro Pusat Statistik 2010), so they are obvious choices of areas in which to expand. Sampling could also be expanded to other edge habitats. Lemon-bellied White-eyes were found in sympatry with Pale-bellied White-eyes c. 40 km inland, at the Lasada site on mainland Sulawesi (Figures 3.1 and 5.1) (Daft Logic 2018b), around flooded areas of a large paddy field and some adjacent fish ponds. Lemon-bellied White-eyes were absent from the surrounding countryside, where Pale-bellied White-eyes were found. Areas with a strong aquatic influence may provide enough of an edge habitat that Lemon-bellied White-eyes can survive in sympatry with Pale-bellied White-eyes, as they do in coastal areas. White-eyes were in low density and difficult to catch in the Lasada area, so were not sampled in sufficient numbers to be included in Chapter 6. Further sampling would allow investigation of Lemon-bellied White-eye adaption to different habitats and wide dispersal between suitable habitats.

Expanding sampling to the other peninsulas of Sulawesi would also allow an investigation of a wider range of competitors, such as the Black-crowned White-eye *Zosterops atrifrons* (North Sulawesi) or Black-ringed White-eye *Zosterops anomalus* (South Sulawesi). Viewing the Lemon-bellied White-eye's interactions with multiple potential congeneric competitors would allow for a deeper assessment of the role interspecific competition plays in limiting niche space. This could be carried out in tandem with a wider taxonomic revision of Lemon-bellied White-eye and Collared Kingfisher radiations. Understanding urban adaptation will provide insight into the likely winners and losers of increasing human influence in the Indo-Pacific.

8.3.2.2 *Niche partitioning in *Todiramphus* kingfishers.*

Chapter 4 described how ecologically similar *Todiramphus* kingfishers may partition their niches in different ways depending on the ecological circumstances of the island. Coupling further sampling of *Todiramphus* kingfishers in other island groups (8.3.1.2) with structured surveys

assessing the density and distribution of *Todiramphus* kingfishers would shed light on these interactions.

8.3.2.3 Dispersal constraints in an island archipelago

The data collected in South-east Sulawesi since 1999 by Dr David Kelly and Prof Nicola Marples, provides a relatively rare overview of the morphology of the small passerine community across an island archipelago. Utilising the method used in Chapter 5, a proxy for dispersal capacity was calculated for all the small passerines in the region (birds of <30 g), likely to be the group which suffers most from dispersal constraints. A preliminary cross-species analysis has suggested that dispersal capacity, inferred from their morphology, had a positive relationship with island distance from the mainland and island distance from the nearest neighbouring island, but a negative relationship with island area. Effectively, more poorly dispersing species do not reach smaller, more isolated islands. Further model refinement is needed to complete this analysis.

8.3.2.4 Supertramps - uniform island colonisers or cryptic genetic differentiation?

Diamond (1974) described 'supertramps' as species absent from larger islands, or restricted to their coastal fringes. They are typically specialised for overwater dispersal, life on small islands, and edge habitats (Mayr and Diamond 2001). They have been typically considered to show minimal differentiation between populations, due to their dispersal abilities. In their investigation of the archetypal 'supertramp', the Louisiade White-eye, Linck *et al.* (2016) found much more genetic differentiation between populations of a 'supertramp' than would have been previously expected, with more distant populations showing evidence of isolation. In Chapter 5 we showed that there was distinct genetic and phenotypic differentiation in isolated populations of Lemon-bellied White-eyes, another species designated a 'supertramp' (Eaton *et al.* 2016). These results call into question the usual assumptions made about 'supertramp' species. 'Supertramp' species may contain more cryptic diversity than previously appreciated.

Within our South-east Sulawesi study system, the Island Monarch *Monarcha cinerascens* is even more deserving of the 'supertramp' designation. It is only found on the small Wakatobi Islands, Runduma and Menui (Eaton *et al.* 2016). They are absent from mainland Sulawesi and the continental islands, where the Pale-blue Monarch *Hypothymis puella* is found. Outside of Sulawesi, Island Monarchs are only found on small islands in the Maluku Islands, Bismarck Archipelago and Solomon Islands. This species provides a rare opportunity to test the isolation of populations of an Indo-Pacific 'supertramp', and how this is affected by dispersal capacity. Following Linck *et al.* (2016), the genetic structure of the Island Monarch

populations of South-east Sulawesi could be investigated, to assess whether there is greater differentiation between the more isolated islands of Runduma and Menui, than between the geographically close Wakatobi Islands. Andersen *et al.* (2015a) provide Island Monarch sequence information from the Bismarck Archipelago and Solomon Islands, which would allow for this comparison to be extended outside of the Sulawesi region. To build on the methods used by Linck *et al.* (2016), similar comparisons could be carried out with the morphological data collected from the South-east Sulawesi populations, to assess whether more isolated populations were more morphologically distinct, with a focus on dispersal capacity (see Chapter 5).

Divergence dating (utilising the methods from Chapter 5) of the monarchs of South-east Sulawesi may give greater insight into the evolutionary history of a ‘supertramp’ species and their relationships with mainland equivalents. Were Island Monarchs the first to colonise Sulawesi, and subsequently pushed out of richer mainland habitats by a later colonisation by the Pale-blue Monarch? Or was the Pale-blue Monarch present first, and the Island Monarch dispersed into the region later, via edge habitats and long-distance open water dispersals?

8.3.2.5 Influence of resource availability on the abundance and body mass of a guild of small passerines

Transect surveys carried out in 2015, 2016 and 2017 collected detailed data on the abundance of small passerines in our study area known to feed on fruit, nectar and insects. This guild included all white-eyes, sunbirds, flowerpeckers, gerygones, monarchs, trillers and chats, totalling 11 species, with a focus on the first three groups (totalling eight species). As part of these transects, the number of fruiting and flowering plants were counted, insect abundance was surveyed using sticky traps and beating trays and the habitats encountered on the transects were broadly classified. Focal samples of target species during the transects allowed potential food resources to be categorised based on observations of feeding behaviour. These data could be used to gain greater understanding of the results of Chapter 6, assessing what resource and habitat characteristics are associated with increased density and morphological niche volume in populations. These data would also allow for analysis of other patterns in the distribution, abundance and morphology of the small passerine study guild, and how that relates to abundance of resources and of competitor species. The strongest pattern from preliminary analyses of the data was a significant positive relationship between abundance of coconut flowers and the density of Brown-throated Sunbird populations. Coconuts were one of the most common crops in our study area, being planted as an intensive monocrop in many locations. In

areas where the habitat was dominated by coconut plantation, and there was less secondary forest, the small passerine guild was also less species rich. The Brown-throated Sunbird is the largest and most aggressive competitor of the small nectivore/frugivore guild in our study system (pers. obs.). Decreased habitat diversity in coconut-dominated landscapes may be compounded by increased competition with the Brown-throated Sunbird for all other small passerine species. These data may give further insight into how more generalist species may benefit from human modification of the environment in this region. Further model selection and refinement is needed to investigate these questions.

8.3.2.6 *The drivers of song evolution in island lineages*

Bird song is of great interest in the study of speciation, as it is a key pre-mating isolation mechanism in birds, and so can be of great importance as a barrier to gene flow in diverging populations (Uy *et al.* 2009). Song is a complex cultural trait which can be affected by cultural drift and sexual selection (Podos *et al.* 2004; Potvin and Clegg 2015). Recent research suggests that avian morphology, particularly bill and body size, may have a strong effect on song in bird populations (Huber and Podos 2006; Potvin 2013; Derryberry *et al.* 2018). This may be of great importance in speciation in birds, and may explain how groups like white-eyes show such a rapid rate of diversification (Moyle *et al.* 2009). If a population develops morphological adaptations to a new environment, and there is a corresponding change in song, this may lead to rapid isolation between populations (Diamond 1998). Even if there is still some mixing between populations, an individual singing a different song may be recognised as a sub-optimal mate (Uy *et al.* 2009). It is for this reason that bird song is considered a ‘magic trait’; a trait involved in both reproductive isolation and ecological divergence (Servedio *et al.* 2011; Servedio and Kopp 2012).

The dataset of white-eye song built for Chapter 5 provides the opportunity to test how morphological change and habitat features may affect birdsong. Initial examination suggests body size may play an important role, as *Z. c. flavissimus* on the Wakatobi Islands is smaller than the mainland Lemon-bellied White-eyes and sings songs with both a higher frequency (pitch) and greater number of notes in each discrete burst of song; a result similar to that found by Potvin (2013) in an island white-eye population. One element missing from the study by Potvin (2013) was a detailed assessment of the effect of habitat structure on song. As much of our song data were collected along the transects described in 8.3.2.6, we could use the habitat categorisations collected on these transects, along with environmental data from BioClim, following Derryberry *et al.* (2018), to characterise the habitats for each site. This would allow a

site-specific comparison, investigating the effect of different morphological and environmental characteristics on bird song. Individual vocal traits would be assessed, rather than using a PCA as in Chapter 5, as spectral and temporal traits are likely to be affected differently, and there may be trade-offs between different aspects of vocal performance (Derryberry *et al.* 2018).

This analysis would provide insight into what drives the process of song evolution at the early stages of population separation, and allow us to contrast a lineage that is speciating (Lemon-bellied White-eye) with one which is not (Pale-bellied White-eye). Expanding this analysis to calls as well as songs would be informative. Calls should be less strongly influenced by sexual selection and so provide a better signature of the effect of the environment or morphology on bird vocalisations (Potvin 2013). In addition to work on white-eyes, assessing the drivers of song evolution in Sulawesi Babblers *Trichastoma celebense* (for which a large amount of song data has been collected) would allow for an analysis of how environmental factors might have a different effect in a species that is usually found in the undergrowth in closed habitats (Collar and Robson 2018), in contrast to our white-eye species, which spend much more time in open areas (van Balen 2018c; van Balen 2018b).

8.4. Conclusions

The different strands of research in this thesis allowed for an assessment of the avian diversity of South-east Sulawesi at multiple levels; surveying total species richness, revising the taxonomy of unrecognised populations and gaining understanding of the morphological adaptations associated with island colonisation. In Chapters 2 and 3 we filled in gaps in the knowledge of the avifauna of South-east Sulawesi, identifying potentially important populations, e.g. Milky Stork. Chapters 4 and 5 evaluated the diversification of the ‘great speciator’ taxa of South-east Sulawesi, proposing two new white-eye species and uncovering underappreciated diversity. This was particularly true of the supposed ‘supertramp’ the Lemon-bellied White-eye, calling into question the assumption of panmixia in ‘supertramps’. The ‘Wangi-wangi White-eye’ is a particularly intriguing new species. Its status as a single island endemic in an oceanic archipelago, and the huge distance to its closest relatives, begs the question of how it got there. As more and more white-eye species are sequenced we may gain greater insight into its evolutionary origin. Chapters 4 and 5 also flag up other populations for further taxonomic refinement, the Wakatobi Collared Kingfisher population and Runduma Lemon-bellied White-eye populations may represent endemic subspecies for South-east Sulawesi, dependent on collection of voucher specimens and analysis of song and plumage data. Outside South-east

Sulawesi, the under-studied Lemon-bellied White-eye clearly needs a reassessment of the taxonomic limits between its widely spread populations.

Chapters 4-7 allowed us to investigate different morphological adaptations that are associated with island colonisation and the early stages of speciation. Chapter 5 suggested that a reduced dispersal ability, in comparison to source populations, may be a feature of populations of widespread island colonisers which become isolated. In Chapter 4 we discussed how potential differences in habitat, and associated increases in interspecific competition, may have driven a niche shift in Collared Kingfishers on the Wakatobi Islands. These ideas were investigated further in Chapters 6 and 7. Chapter 6 outlined how Lemon-bellied White-eyes had a larger morphological niche volume and greater population density in allopatry from the Pale-bellied White-eye, on both a small island and in urban areas. These Lemon-bellied White-eye populations may have been experiencing density compensation due to greater access to resources in a species depauperate environment. Reduced interspecific competition, and greater intraspecific competition in high density populations, likely led to the increase in niche volume seen in the Lemon-bellied White-eye populations. The potential for urban areas to act as ecological islands for island colonising edge species across the Indo-Pacific merits further study, as other observations of this phenomenon have been mostly anecdotal (Ward 1968; Diamond and Marshall 1977; Andersen *et al.* 2017). Local endemic species are likely to lose out in human altered landscapes dominated by edge species. Chapter 7 looked at some of the effects of island colonisation on sexual dimorphism. As expected, populations of Olive-backed Sunbirds on the small oceanic Wakatobi Islands showed greater sexual dimorphism and higher population density than those on the mainland and continental islands. However, this was not associated with an increase in morphological niche volume, in either sex, in the absence of mainland competitors, as is typically assumed to be the case. There was no difference in the niche volume of males from Wakatobi and mainland populations, but females from the Wakatobi Islands had a smaller niche volume than those from the mainland. Potentially, because females experience greater intraspecific competition in the high density populations of the Wakatobi Islands, their niche volume has contracted to reduce intersexual competition. Intersexual competition of this nature is likely an important factor shaping the evolution of island radiations of sexually dimorphic species.

This thesis illustrates how studying the populations of Indo-Pacific island colonisers, particularly the 'great speciator' lineages, provides the opportunity to contribute both taxonomic revision and insight into the early stages of speciation. Their rapid speed of

evolutionary change, ability to colonise islands and the frequency with which they are found in secondary sympatry makes 'great speciators' ideal groups in which to study speciation. The diversity of species within 'great speciator' lineages; single island endemics, widespread colonisers and small island 'supertramps', provides opportunities to analyse how taxa with very different life ecologies adapt to island colonisation and isolation. This work is given impetus by the looming biodiversity crisis that threatens not just Southeast Asia (Sodhi *et al.* 2004; Wilcove *et al.* 2013), but the whole world (WWF 2018). Much biodiversity, and the evolutionary lessons it can teach us, faces extinction before being formally recognised.

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