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An assessment of the avifauna of the Wakatobi Islands, South-east Sulawesi, Indonesia: species recorded and taxonomic considerations

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Abstract. The Wakatobi Islands are an archipelago of deep-sea islands lying off the south-east peninsula of Sulawesi. Despite being recognised as an Important Bird Area, the avifauna of these islands has long been neglected. While relatively extensive surveys have been carried out on nearby Buton Island (the largest satellite of South-east Sulawesi), the avifauna of the Wakatobi Islands went unstudied for nearly a century following the expedition of Heinrich Kühn in 1901–1902. Between 1999–2019 ornithologists visited nine of the archipelago's islands on eight expeditions, seeking to carry out a modern assessment of the islands' avifauna and re-evaluate the taxonomy of the avifauna. These expeditions combined transect surveys and mist netting. These formal surveys were targeted at small passerines, the focus of the taxonomic work, however all birds encountered were recorded allowing for a broad qualitative assessment of the avifaunal communities inhabiting the islands. In total, 100 bird species were recorded, of which 12 are Wallacean endemics, six are classified as Near Threatened and one as Critically Endangered. Here we present the species recorded during this study and review the historical literature to provide an inventory of the avifauna of the Wakatobi Islands. In addition, we review the taxonomy of Wakatobi populations including recent developments of note, highlighting potentially underappreciated endemism, and provide some information on relative abundance of bird species present.

Key words. Wallacea, taxonomy, biodiversity, birds, Indonesia, Tukangbesi

INTRODUCTION

The Wakatobi Islands are a chain of uplifted Quaternary coral limestone islands in the western Banda Sea (Milsom et al., 1999; Nugraha & Hall, 2018). They are located to the east of the much larger Buton Island, which itself lies off the south-eastern coast of Sulawesi, Indonesia (Fig. 1). The Wakatobi Islands sit atop a platform of Australasian origin and have never been connected to mainland Sulawesi (Milsom et al., 1999). The northern extremity of the chain lies approximately 27 km off the eastern coast of Buton, and from here extends 106 km in a south-easterly direction, following the orientation of the largely submerged continental fragment of the Tukangbesi platform (Smith & Silver, 1991). In historic biological accounts, these islands have been known as the Tukangbesi Islands, but most modern accounts refer to them as the Wakatobi Islands. "Wakatobi" is an acronym in which subsequent two-letter motifs refer to each of the four major islands running from north-west to south-east: Wangi-wangi (ca. 155 km^2), Kaledupa (ca. 64 km^2), Tomia (alternatively Tomea, ca. 53 km^2), and Binongko (ca. 100km^2). The major islands are surrounded by sixteen smaller attendant islands and atolls (Clifton, 2003). Some of the attendant islands lie very close to the major islands, while others are more isolated. The island of Runduma (ca. 5.5 km^2), for example, lies ca. 54 km to the north-east of Kaledupa, and the island of Moromaho (ca. 3 km^2) lies ca. 57 km to the south-east of Binongko.

The entire archipelago is low-lying, with a maximum elevation of 270 masl on Wangi-Wangi (Milsom et al., 1999). Politically the islands form their own regency within the province of South-east Sulawesi, the Wakatobi Regency (Kabupaten Wakatobi), which supports a population of approximately 100,000 people (Clifton & Unsworth, 2010). All islands lie within the 14,000 km^2 Wakatobi Marine Protected Area, the second-largest marine reserve in Indonesia, and the land area of each island is nominally designated as a 'Special Land Zone' (Clifton & Unsworth, 2010). In 2012 the islands were also designated a UNESCO Biosphere Reserve (UNESCO, 2019). Despite this protection, however, the relatively high population here, coupled with the islands' flat, accessible topography, have led to much of the

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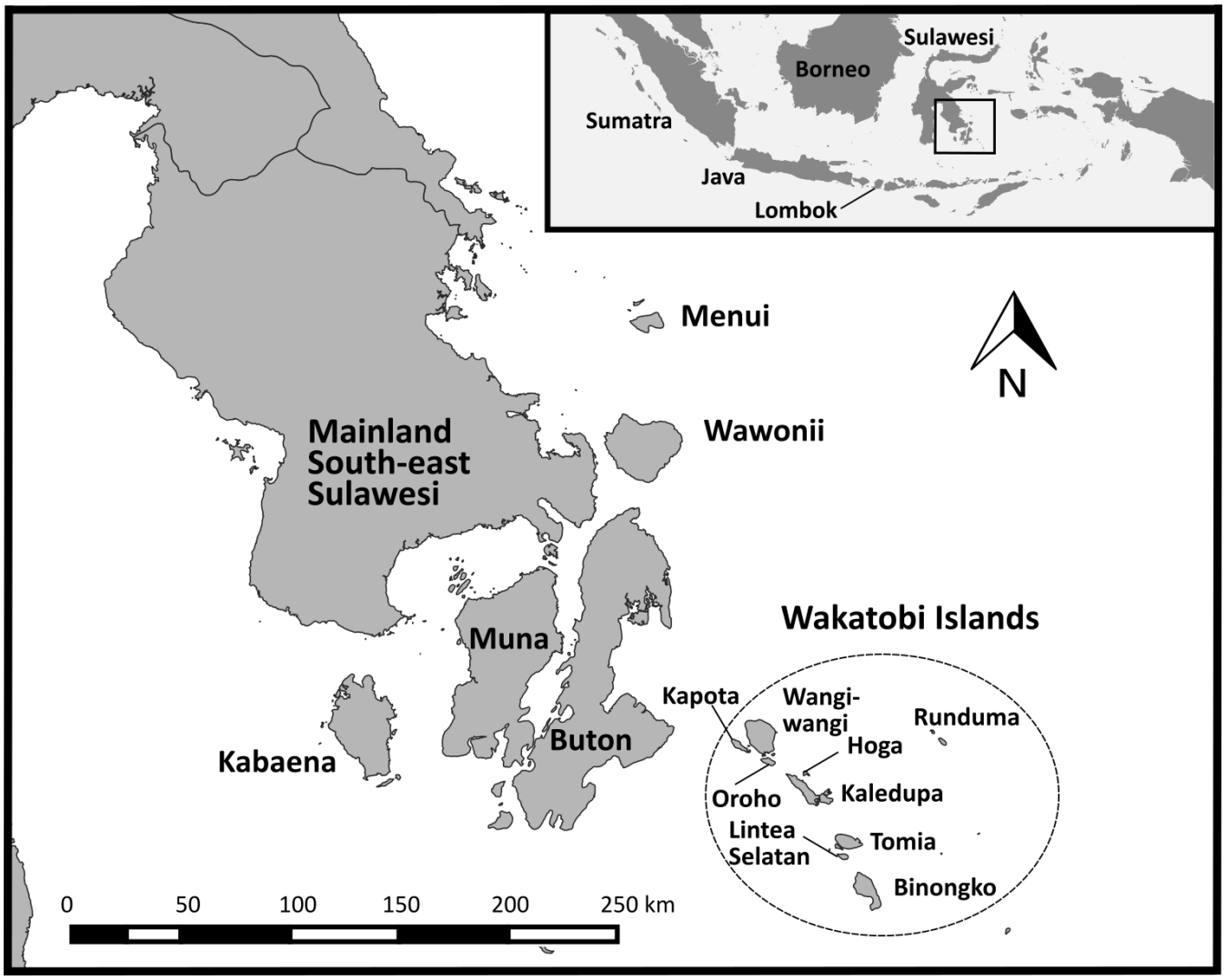

Fig. 1. Location of the Wakatobi Islands in relation to mainland South-east Sulawesi and its other offshore islands. The inset shows the location of the South-east Sulawesi region within Indonesia and the wider region.

archipelago's original vegetation being cleared, especially on the four main islands, where agricultural land and secondary scrub now predominate (Kelly, 2014; O'Connell, 2019). However, pockets of forest persist on all the main islands, and forest remains the dominant vegetation type on several smaller islands. High quality mangrove and fringing reef habitat can also still be found around the smaller islands and in some patches on the larger islands, although many littoral areas of the Wakatobi Islands have suffered similar degradation to terrestrial habitats.

Historically, scientific knowledge of the avifauna of the Wakatobi Islands largely dates from a single expedition by Heinrich Kühn, who spent three months collecting specimens there from November 1901 to January 1902, visiting the islands of Wangi-wangi, Kaledupa, Tomia, and Binongko (Hartert, 1903). Kühn recorded 57 species as present on the islands, and Hartert (1903) proposed three of these as endemic subspecies (*Oriolus chinensis oscillans*, *Otus magicus kalidupae*, and *Tanygnathus megalorynchos viridipennis*) and four as endemic species (*Zosterops flavissima*, *Dicaeum kuehni*, *Cinnuris infrenata*, and *Hypotaenidia kuehni*), all of which were later re-classified as subspecies. Kühn also reported that by the beginning of the 20th century the islands were densely populated and almost all forest had already been cleared (Hartert, 1903). In the current literature, multiple sources provide accounts of species that occur here (White & Bruce, 1986; Coates & Bishop, 1997; Eaton et al., 2016; Billerman et al., 2020), with much of this information originating from Hartert (1903). These sources have highlighted the conservation importance of the archipelago, and the Wakatobi Islands are already classified as an Important Bird Area (IBA), principally due to the occurrence here of the Critically Endangered Yellow-crested Cockatoo (*Cacatua sulphurea*) (BirdLife International, 2020b). However, despite its recognition as an IBA, the avifauna of the Wakatobi Islands has been neglected for nearly a century, with little information on the status of bird populations being published.

Beginning in the late 1990s, ornithologists began to take renewed interest in the South-east Sulawesi region. This has resulted in a series of detailed inventories of the avifauna of the major satellite islands off South-east Sulawesi, including Buton, Muna, Wawonii, Menui, and Kabaena Islands, with Buton Island receiving particularly detailed

coverage (Catterall, 1996; Martin et al., 2012, 2015, 2017; O'Connell et al., 2017, 2019d; Monkhouse et al., 2018). Modern assessments of the taxonomy of bird populations in the region have also highlighted the underappreciated endemism of the Wakatobi Islands, supporting some of the taxonomic splits originally proposed by Hartert (1903), which had not been accepted by subsequent taxonomists (Hartert, 1903; Collar & Marsden, 2014; O'Connell et al., 2019c), and drawing attention to other potentially unrecognised endemic populations (Kelly & Marples, 2010; Kelly et al., 2014; O'Connell et al., 2019b, c). These findings illustrate the need for a broader update on the status of the avifauna of the Wakatobi Islands as a whole. Here, we present what we believe to be the first modern re-evaluation of the avifauna of the Wakatobi Islands, based on data collected periodically over a 20-year period running between 1999 and 2019, as part of a long term study focusing on the taxonomy of the region's small passerine bird species, but taking into account wider avifaunal diversity. We provide here a full inventory of species documented as occurring on these islands during this time, highlight notable range extensions, assess populations in need of taxonomic re-evaluation and contribute information on bird population status.

MATERIAL AND METHODS

Bird records from the Wakatobi Islands were principally collected as part of a long-term project run by Trinity College Dublin, Halu Oleo University, and Operation Wallacea, investigating speciation and biogeography in the bird populations of these islands (Kelly & Marples, 2010; Kelly et al., 2014; O'Connell et al., 2019a–c). Research expeditions to the Wakatobi Islands associated with this project commenced in 1999, with subsequent visits in 2003, 2005, 2007, 2010, 2012, and 2013, totalling 28 weeks of survey work, largely undertaken during the months of July–September, with one four-week visit during April (see Supplementary Material Table S1). Together, these expeditions visited the four main islands of Wangi-wangi, Kaledupa, Tomia, and Binongko, as well as the island of Runduma ca. 54 km to the north-east of Kaledupa, and four smaller islands: Oroho (alternatively Kompone or Komponaone, ca. 12.7 km^2), Kapota (alternatively Kambode, ca. 18.3 km^2), Hoga (ca. 3.5 km^2), and Lintea Selatan (ca. 8.2 km^2). The latter four islands each lie ca. 2.5 km off the respective coasts of Wangi-wangi (Oroho and Kapota), Kaledupa (Hoga) and Tomia (Lintea Selatan) (Fig. 1).

Avifauna biodiversity records were generated by opportunistic observation recorded in a trip log, line transects, and mist netting. In 1999–2010 the primary focus was mist netting, in 2013 the focus was line transects, and in 2012 both activities were carried out (Table S1). Although the primary purpose of the line transects and mist netting was to gather behavioural data and biometric data, respectively, from a guild of small passerines (Nectariniidae, Dicaeidae, and Zosteropidae), this provided an opportunity for a general assessment of avifaunal biodiversity, and all bird species seen or heard were recorded. Road-based line transects were carried out by SBAK, AK, and TEM, primarily in agricultural land and rough scrub habitats. Transects were 1 km long, undertaken along roads, paths and tracks, with all bird species seen or heard recorded. No distance limits were placed on bird records as long as the species was clearly identifiable, however density information was not collected, so records of the wider avifauna were qualitative. Data were collected between 0600–0830 hours and 1515–1730 hours each day. A total of 89 transect surveys were carried out, each 30–45 minutes long; 18 on Wangi-wangi, 6 on Kapota, 18 on Kaledupa, 8 on Hoga, 25 on Tomia, 10 on Binongko, and 6 on Runduma. Mist netting was conducted by DJK and NMM, primarily in mangrove, forest edge, farmland, and scrub (habitats generally suitable for capturing small passerines) using a selection of 2.6-m × 9-m, 12-m or 18-m fine mesh mist nets. Mist nets were opened between approximately 0530–1000 hours and were checked every 15 minutes. A total of 84 mist netting sessions were carried out; 18 on Wangi-wangi, 4 on Oroho, 19 on Kaledupa, 13 on Hoga, 14 on Tomia, 3 on Lintea Selatan, 10 on Binongko, and 3 on Runduma.

In addition to these structured survey efforts, a summary trip log in 2003, and more detailed daily logs in 2010, 2012 and 2013, were used to compile all bird records from mist netting and transects, along with all birds detected by general opportunistic observations. These included sightings made when travelling to and from survey sites, and records made from casual exploration of the islands, including an additional birdwatching visit on 23–27 September 2019 by FER to Wangi-wangi and Oroho. These opportunistic records were made in a range of habitats, including forests, cultivated land, rough scrub, mangroves, beaches, and fringing reefs. Opportunistic records were also kept of pelagic species observed on boat trips between the islands. Where possible, sound recordings and record photos were taken. Sound recordings were made using a Zoom H2 Handy Recorder with a Sennheiser Me62 Omni-Directional Condenser Microphone Capsule and a K6 power supply, with a microphone mounted on a Telinga V2 Foldable Parabolic Reflector.

Species identification for birds detected by all methods was confirmed using Coates and Bishop (1997) and Eaton et al. (2016). Xeno-canto (2019) was used as a reference source for identifying sound recordings. Records from all surveys were compiled into an inventory of all species detected in the Wakatobi Islands, with further notation indicating which species were detected on each of the nine islands on which survey work was completed. As part of compiling this inventory, a thorough search of the literature was conducted to ensure that all historical records of the avifauna of the Wakatobi Islands were included in a final checklist for the islands. Taxonomy for this inventory followed Eaton et al. (2016), with the exception of species where recent strong primary evidence has suggested a different classification, as outlined in species specific accounts. The endemism and conservation status of each species within the inventory was noted, with Wallacean endemics being defined using Myers et al. (2000), Indonesian endemics identified using Eaton et al. (2016), and conservation status following IUCN (2019).

We also noted which species were seasonal migrants to the region and which are likely to have been anthropogenically introduced to the Wakatobi Islands, using information provided by White and Bruce (1986), Coates and Bishop (1997), Eaton et al. (2016), and Billerman et al. (2020).

For years with a daily log (2010, 2012, and 2013) relative abundances were estimated based on frequency of encounter per island for islands visited for at least five days; Rare – one record, Occasional – two to three records, Common – recorded most days (>60% of days), and Abundant – recorded every day. For mist netting sessions from 2010, when precise information on the number and length of nets, plus net opening and closing times, was available, capture rates in captures per metre hours was calculated. Metre hours (mh) of netting is the number of metres of net length used multiplied by hours of use, so a 12-m net used for three hours would be 36 mh of netting effort.

We then determined which of the records in our inventory constituted novel range extensions. A record was considered to be a range extension for that species if it had not previously been recorded for that island by White and Bruce (1986), Coates and Bishop (1997) or in the primary literature. Range maps from Eaton et al. (2016), IUCN (2019) or Billerman et al. (2020) do not claim to be of sufficient detail to be reliable indicators of individual island records within the Wakatobi Islands unless a species' occurrence on any particular island is stated explicitly in the text. Therefore, island occurrences of species were generally disregarded if solely based on maps from the latter three sources.

Finally, following recommendations from Lees et al. (2014), we collated photographs and recordings of as many species detected in the Wakatobi Islands as possible, and placed them in an online depository embedded within the Macaulay Library (2020). The unique voucher numbers of each were then noted to provide visual or audio verifications for as many species on the inventory as possible.

RESULTS

A total of 100 bird species were recorded in the Wakatobi Islands between 1999–2019, including 12 (12%) which are endemic to the Wallacea biodiversity hotspot, and a further three (3%) which are endemic to Indonesia/East Timor. Six species are classified as Near Threatened and one as Critically Endangered (IUCN, 2019). Photographic or acoustical evidence of occurrence was obtained for 51 species (51% of all species detected) and uploaded onto Macaulay Library (Table 1). An additional eight species were recorded by Hartert (1903), but not by the present study, bringing the total number of bird species ever recorded on the Wakatobi Islands to 108. All species detected in the Wakatobi Islands are summarised in Table 1. Relative abundance estimates for 2010, 2012, and 2013 are given in Table S1. A total of 73 species was recorded for Wangi-wangi, 55 for Oroho, 33 for Kapota, 74 for Kaledupa, 50 for Hoga, 56 for Tomia, 16 for Lintea Selatan, 49 for Binongko, and 27 for Runduma, though survey effort was uneven between islands (Table 1, Table S1). The islands contain a mixture of widespread dispersive species, a subset of species found on nearby Sulawesi and its large satellite islands such as the Sahul Sunbird *Cinnyris clementiae* and Black-faced Munia *Lonchura molucca* (Martin et al., 2012; O'Connell et al., 2017, 2019d) and some small island specialists only found on small islands in the Moluccas or Lesser Sundas such as the Island Monarch *Monarcha cinerascens* and Pink-headed Imperial Pigeon *Ducula rosacea* (the latter only being recorded on remote Runduma) (Table 1). A summary of records by individual trip is available in Supplementary Information Table S1.

A total of 30 species and 1096 individuals were captured during mist netting (Table S2). Captures were dominated by the common small passerines the Wakatobi White-eye *Zosterops flavissimus* (511), Sahul Sunbird (205) and Island Monarch (115) (Table S2), which also had generally the highest capture rates (Table S3). Most species were only rarely captured, with 11/30 only caught once, though this contributed some notable records such as the Oriental Reed-warbler *Acrocephalus orientalis* and proved important for providing photographic confirmation of cryptic species such as the Red-backed Buttonquail *Turnix maculosus* (Table 1, Table S2).

Additional information concerning observations of particularly notable records is provided below. Records considered notable are major range extensions (i.e., the first record for the Wakatobi Islands) for Wallacean endemics, Critically Endangered species, and populations whose taxonomy has recently been controversial, or which may require re-assessment. Wallacean endemic species are marked with an asterisk (*), Critically Endangered populations are marked CR.

Sulawesi Brush Cuckoo *Cacomantis irescens.** A species whose taxonomy remains confused, it is often merged with the Sunda Brush Cuckoo *C. sepulcralis* (Billerman et al., 2020; Gill & Donsker, 2020). Eaton et al. (2016) split the Sulawesi Brush Cuckoo from the Sunda Brush Cuckoo based on plumage and song characteristics. A modern phylogenetic assessment would help clarify their taxonomy. The population on the Wakatobi Islands display the characteristic olive-tinged back and higher pitched call of the Sulawesi Brush Cuckoo. This species was heard calling Commonly on Wangi-wangi, Kaledupa and Tomia, and Occasionally on Bingonko in forest or scrub habitats (Table S1). Captured during mist netting on Wangi-wangi once and Hoga twice (Table S2).

Barred Rail *Hypotaenidia torquata kuehni*. Described by Hartert (1903) as an endemic species to the Wakatobi Islands, *Hypotaenidia kuehni*, although modern accounts after Hartert (1903) have generally recognised this population as a subspecies of the Barred Rail, *H. torquata kuehni* (e.g., Coates & Bishop, 1997; Eaton et al., 2016; Billerman et al., 2020). Modern genetic material would help to assess its true taxonomic distinctness. However, this shy and elusive species was not caught during this study. It was rarely observed but Commonly heard (Table S1), once its vocalisation was learnt,

in overgrown farmland, coastal habitat, and wetland areas across the larger Wakatobi Islands and on Oroho.

Moluccan Scops-owl *Otus magicus kalidupae.* The Wakatobi population of scops-owl was described as a subspecies of the Sulawesi Scops-owl *O. manadensis kalidupae* by Hartert (1903) from two specimens collected on Kaledupa. Most modern accounts now treat this population as a subspecies of the Moluccan Scops-owl *Otus magicus* (White & Bruce, 1986; Coates & Bishop, 1997; Eaton et al., 2016) or—with little evidence provided—as an independent species (König et al., 2008), although Billerman et al. (2020) have continued to follow Hartert's (1903) outdated treatment. FER saw two separate individuals of this scops-owl, and heard a total of ~4 individuals, at one remnant patch of old-growth forest near the airport on Wangi-Wangi. We confirm that the voice of *kalidupae* is a coarse, non-melodious gruff note that falls within the range of vocal variation of the Moluccan Scops-owl *O. magicus*, and is extremely different from the high-pitched, more melodious single note uttered by Sulawesi Scops-owl *O. manadensis*, adding further support to the categorisation of White and Bruce (1986), Coates and Bishop (1997), and Eaton et al. (2016). Its affinity with Moluccan rather than Sulawesi Scops-owl fits into a larger distributional pattern shared by such genera as *Aviceda* bazas, *Edolisoma* cicadabirds and others, in which populations on Wakatobi often belong to a more widespread small-island species rather than the closely-related congener from the large landmass of Sulawesi. Our searches for this scops-owl in poor secondary growth revealed no vocalisations throughout the archipelago, including on Wangi-Wangi, indicating that this subspecies may be restricted to better forest habitat, which is spatially limited and highly fragmented within the archipelago, and as such may, by now, be seriously endangered.

Yellow-crested Cockatoo *Cacatua sulphurea paulandrewi* CR. This Critically Endangered species is under serious threat throughout its range, primarily due to the cage-bird trade (Collar & Marsden, 2014; Eaton et al., 2015; Harris et al., 2017; IUCN, 2019). It was recorded across the main Wakatobi Islands by Hartert (1903), but by the time of the present survey it was only recorded sparsely on three smaller satellite islands (names withheld). Collar and Marsden (2014) have proposed that the Wakatobi population is a distinct endemic subspecies *C. s. paulandrewi*, a treatment adopted by Eaton et al. (2016), though this proposed split is solely based on morphological comparisons using the small number of specimens collected by Kühn (Hartert, 1903) and is not universally accepted (Billerman et al., 2020; Gill & Donsker, 2020). Targeted conservation efforts are likely required to ensure this population remains viable.

Great-billed Parrot *Tanygnathus megalorynchos megalorynchos.* The Wakatobi population of Great-billed Parrot was described by Hartert (1903) as an endemic subspecies, *T. m. viridipennis*, although it has subsequently been combined with several other Great-billed Parrot populations from the Lesser Sundas and satellite islands of New Guinea to form the wide-ranging *T. m. megalorynchos*. It likely suffers from trapping to feed the Indonesian pet trade (Harris et al., 2017), but was encountered either Commonly or Occasionally throughout the larger Wakatobi Islands (Table S1), usually flying between patches of forest.

Black-naped Oriole *Oriolus chinensis celebensis.* The Wakatobi population of Black-naped Oriole was described by Hartert (1903) as an endemic subspecies, *O. c. oscillans*. It has since been synonymised with other Sulawesi populations as the subspecies *O. c. celebensis* (Eaton et al., 2016; Gill & Donsker, 2020). However, the taxonomy of this species is in flux and this designation is likely to change (Jønsson et al., 2010; Eaton et al., 2016). The Black-naped Oriole was found to be Abundant in a variety of habitats throughout the Wakatobi Islands during our survey work (Table S1). Captured during mist netting nine times in total, on Runduma (4), Hoga (3), Binongko (1), and Kaledupa (1) (Table S2).

Wallacean Cicadabird *Edolisoma amboinensis pererrata.** This population has previously been classified as a subspecies of Slender-billed Cicadabird *Edolisoma tenuirostre pererratum* endemic to the Wakatobi Islands (Hartert, 1916; White & Bruce, 1986; Coates & Bishop, 1997; Billerman et al., 2020). However, the recent detailed molecular assessment of the *Edolisoma tenuirostre*/*remotum* species complex by Pedersen et al. (2018) has shown the Wakatobi population to be a part of the Wallacean Cicadabird as in Eaton et al. (2016). An individual male was captured during mist netting and photographed by the authors (ML718272), supporting this assessment, showing the characteristic darker plumage of this species. The species was encountered in scrub or forest habitat, Commonly on Wangi-wangi and Hoga, Occasionally on Kaledupa and Tomia, and Rarely elsewhere (Table S1).

Sulawesi Triller *Lalage leucopygialis.** Trillers on the Wakatobi Islands were previously identified as belonging to the Lesueur's Triller *Lalage sueurii* (White & Bruce, 1986; Coates & Bishop, 1997; Eaton et al., 2016; Billerman et al., 2020). However, all individuals clearly identified on the Wakatobi Islands by the authors were Sulawesi Trillers. Both the Lesueur's Triller and Sulawesi Triller are found on nearby Buton (Martin et al., 2012), whereas on more isolated Menui Island only the Sulawesi Triller is found (Monkhouse et al., 2018), as was found to be the case on the Wakatobi Islands. Notes taken during field observations refer to individuals having a fairly broad supercilium, large white rump and a white wing panel definitely encompassing the tertials. In addition, their song was a chattering series consistent with the Sulawesi Triller, not a melodious series as in the Lesueur Triller. The species was encountered Occasionally–Abundantly in forest, scrub, and mangrove habitats throughout the main Wakatobi Islands (Table S1). A single individual was captured during mist netting on Kaledupa (Table S2).

Wakatobi White-eye *Zosterops flavissimus.** The Wakatobi population of Lemon-bellied White-eye was described by Hartert (1903) as a new species, *Zosterops flavissimus*, but later demoted to subspecies level within the Lemon-bellied White-eye as *Z. chloris flavissimus* by most modern sources (Eaton et al., 2016; Billerman et al., 2020). Recently

O'Connell et al. (2019c) combined genetic, morphological, bioacoustic, and plumage comparisons to find that *flavissimus* had been separate from the mainland Sulawesi population for 400–800,000 years, is smaller in body size, has a brighter yellow plumage with a unique orange forehead patch (Macaulay Library ML718273), and has diverged in song structure, singing at a higher frequency with more notes. These results confirmed the veracity of Hartert's (1903) original decision to describe this form at the species level. O'Connell et al. (2019c) proposed the common name Wakatobi White-eye for this species. This designation is already recognised by the IOC World Bird List Version 10.1 (Gill & Donsker, 2020). Intriguingly, the isolated Runduma Island population seems to represent a separate independent colonisation event of Lemon-bellied White-eyes *Z. chloris*, not Wakatobi White-eyes *Z. flavissimus*, from the closest 'mainland' population (*Z. c. intermedius*) on the larger island of Buton, within the last 10–20,000 years (O'Connell et al., 2019c). Buton Island is ca. 123 km from Runduma, as opposed to the ca. 54 km between the Kaledupa Island population of Wakatobi White-eye *Z. flavissimus* and Runduma (Fig. 1). The Runduma population is larger in body size than either *Z. c. intermedius* or the Wakatobi White-eye, and exhibits some modest mitochondrial divergence from both (O'Connell et al., 2019c). This isolated population may warrant further investigation of other potential ecological differences. Therefore, the Wakatobi archipelago hosts two *Zosterops* species from this lineage, the Wakatobi White-eye *Zosterops flavissimus* on the main chain of the Wakatobi Islands (Wangi-wangi, Kapota, Oroho, Kaledupa, Tomia, Lintea Selatan, and Binongko), and a Lemon-bellied White-eye *Zosterops chloris* population on remote Runduma Island. The Wakatobi White-eye is Abundant throughout the core Wakatobi Islands in large numbers (Table S1), except on Hoga Island, where it is curiously absent, despite only a ca. 2.5 km gap to the population on Kaledupa. Nearly half of all birds mist netted (511/1096) were Wakatobi White-eyes (Table S2), and their capture rate on Tomia (0.058 individuals per metre hour netting effort) was more than twice that of any other population's capture rate on the Wakatobi Islands (Table S3).

Wangi-wangi White-eye (undescribed *Zosterops*)*. A remarkable recent find for modern ornithology; a novel *Zosterops* species found only on densely populated Wangi-wangi Island. This population is a distinct species in morphology and genetics (O'Connell et al., 2019c). It quickly caught the attention of DJK and NMM during their first visit to Wangi-wangi in 2003 (Kelly & Marples, 2010), due to its distinctive large yellow bill (Macaulay Library ML718276), setting it apart from all other *Zosterops* species in the region. Unexpectedly, this species is even absent from Wangi-wangi's close satellite islands of Oroho and Kapota. The reason for this is unknown, particularly as the habitats of Wangi-wangi are generally highly degraded, so it is unlikely to relate to the presence of pristine habitat. This bird was likely overlooked by Kühn as he spent only a very short time on Wangi-wangi due to various bureaucratic hurdles (Hartert, 1903). The fact that no museum material exists for this species has delayed its description. Anecdotal reports already suggest that this new species is being traded at Indonesian bird markets, its novelty attracting buyers (P. Akbar, pers. comm.). This phenomenon has previously been noted in reptile species awaiting formal description (Losos, 2018). This species is at its most abundant in Wangi-wangi's remaining patches of relatively intact forest and was found to be strongly associated with the thick tangles, epiphytes and vines on emergent large trees. However, it also seems tolerant of degraded habitat, and was found to be Common in inland scrub, overgrown farmland and forest edge habitats (Table S1); in the 18 mist netting sessions conducted in those habitats, 20% of birds caught were 'Wangi-wangi White-eyes', with 48 individuals captured in total (Table S2). However, the fact that it is constrained to a single small island (155 km^2) makes it intensely vulnerable to persecution; a process that already appears to be happening. We highlight the formal taxonomic description and subsequent conservation status assessment of this species as an urgent conservation priority; an outcome that is likely to see this species listed as Endangered as it occupies an area of <500 km^2 (IUCN, 2012). Such recognition is a vital step towards ensuring legislation can be put in place to see the species effectively protected. We hope that this occurs before it is too late, the extinction of a species before it has been described not being an unprecedented occurrence (Lees & Pimm, 2015).

Grey-sided Flowerpecker *Dicaeum celebicum kuehni.** The Wakatobi population of Grey-sided Flowerpecker was described by Hartert (1903) as a new, endemic species, *Dicaeum kuehni*. This treatment was disregarded by modern accounts, most of which relegated it to subspecies level within the Grey-sided Flowerpecker *D. celebicum*. Kelly et al. (2014) proposed returning the Wakatobi population to full species rank (the Wakatobi Flowerpecker *Dicaeum kuehni*). This recommendation was made on the basis of genetic differences, the larger body size of the Wakatobi populations, its slightly blue-washed purplish upperparts, and greater extent of frontal red and paler grey flanks, in comparison with mainland Sulawesi *D. c. celebicum*. Most modern sources (e.g., Eaton et al., 2016; Billerman et al., 2020; Gill & Donsker, 2020) have yet to accept this designation, and bioacoustic analyses will likely be necessary to confirm the veracity of this split. It is present throughout the Wakatobi Islands and is generally Abundant (Table S1), apart from Runduma where it is absent. A total of 30 individuals were captured during mist netting across the islands (Table S2).

Sahul Sunbird *Cinnyris clementiae infrenatus.* The Wakatobi population of the Sahul Sunbird was described by Hartert (1903) as an endemic species, *Cinnyris infrenatus*, but most modern accounts reclassified it as a subspecies either of the Olive-backed Sunbird *Cinnyris jugularis infrenatus* (Billerman et al., 2020; Gill & Donsker, 2020) or of the geographically more limited Sahul Sunbird *C. clementiae infrenatus* (Eaton et al., 2016). The later treatment seems likely to be widely adopted in the coming years due to the distinct differences in genetics and phenotype between the Sahul Sunbird and other populations of the "Olive-backed Sunbird" umbrella species (Eaton et al., 2016). *Cinnyris clementiae infrenatus* shows distinct plumage differences

from the mainland Sulawesi form *C. c. plateni*, with male *C. c. infrenatus* lacking the moustachial and superciliary stripe of *C. c. plateni*, and females having reduced superciliary stripes (Macaulay Library ML718266) (Kelly & Marples, 2011; Kelly, 2014; Billerman et al., 2020). In addition, *C. c. infrenatus* is smaller, and shows greater sexual dimorphism in morphology than *C. c. plateni* (O'Connell et al., 2019a). The taxonomy of the Sahul Sunbird as a whole is in flux, and several populations will likely be split from it in the coming years (Eaton et al., 2016; Billerman et al., 2020), potentially including the Wakatobi population. In contrast to the Lemon-bellied White-eye population, the Sahul Sunbird population on Runduma seems to have originated from the main Wakatobi Islands, rather than the Sulawesi mainland, based on plumage comparisons and preliminary genetic work (Kelly & Marples, 2010; Kelly, 2014). This species is ubiquitous throughout the Wakatobi Islands and is generally Abundant (Table S1), with 205 individuals captured during mist netting (Table S2).

DISCUSSION

Despite the Sulawesi region being a hotspot of endemism (Myers et al., 2000), knowledge of the avifauna of the area has long been fragmentary. The results we present here provide the most detailed summary of the avifauna of the Wakatobi Islands published to date, and represent a continuation of a series of papers by the authors seeking to address this knowledge deficit by describing the avifauna of Sulawesi and its offshore islands (Rheindt et al., 2010, 2014, 2020; Martin et al., 2012, 2015, 2017; O'Connell et al., 2017, 2019d; Monkhouse et al., 2018). Our results summarise an extensive series of surveys undertaken over a 20-year period, covering nine of the islands in the archipelago and recording 100 bird species, 12 of which are Wallacean endemics. Of these bird populations several are of taxonomic interest and two (Yellow-crested Cockatoo and Wangi-wangi White-eye) are of critical conservation concern.

As well as providing a timely update on the biodiversity of the Wakatobi Islands, this contribution serves as testament to the rigor of Heinrich Kühn's initial work on the islands, and of Ernst Hartert's subsequent assessment of his specimens. With much more limited time and resources, Kühn recorded 49 out of the 100 species we record here, plus an additional eight species we did not record (Hartert, 1903). Of the eight species not recorded by our fieldwork (Table 1), Gray's Grasshopper-warbler *Locustella fasciolata*, Grey Wagtail *Motacilla cinerea*, Pechora Pipit *Anthus gustavi*, and Pintail Snipe *Gallinago stenura* are all migrants that would be expected to be present during the northern hemisphere winter period, so would have been missed by the present study. Increasing habitat loss may have meant that the Sulawesi Masked-owl *Tyto rosenbergii* could no longer persist on the Wakatobi Islands, although it is more likely that this cryptic, nocturnal species was simply missed, a not unlikely outcome given that few dedicated nocturnal surveys were completed by the authors. The Black Bittern *Ixobrychus flavicollis* is extremely shy and could easily be missed. Of the two remaining species recorded by Kühn, but not in modern times, the Golden-headed Cisticola *Cisticola exilis* and the Barred Dove *Geopelia maugeus* would be expected to be more easily recorded, but may have very localised populations. Kühn visited the islands between November and January (Hartert, 1903), during the wet season, when the Golden-headed Cisticola is much more vocal. Modern visits took place between April and September, during the dry season. Hartert (1903) noted that the Barred Dove populations on the Wakatobi Islands were a recent addition to the Sulawesi fauna. This population has since been considered to have been introduced to the region from the Lesser Sundas (Eaton et al., 2016; Billerman et al., 2020). In addition, recent work is providing evidence for the taxonomic distinctions made by Kühn and Hartert, supporting their initial splitting of the Wakatobi *Zosterops* as a separate species from its mainland relatives (Hartert, 1903; O'Connell et al., 2019c). Equivalent reassessment of the other populations previously designated as endemic by Hartert (1903) may yield similar results.

While the inventory we present here (Table 1) adds a large number of new records, it is important to note it is unlikely to be an exhaustive account of the avian community of the Wakatobi Islands. Our formal surveys were not designed to record general avian biodiversity, but to target small passerines, as part of research into biogeographic patterns in South-east Sulawesi. As a result, pelagic species and nocturnal species may have been under-recorded or overlooked entirely. Furthermore, in order to assess the migratory species that utilise this region, surveys at different times of year would be required to survey northern hemisphere winter visitors, Australian dry season visitors and to capture local movements by species such as the Elegant Pitta *Pitta elegans*. In addition, remote Moromaho Island (ca. 57 km south-east of Binongko), remains a significant knowledge gap. It was once known to be a key breeding location for the region's seabirds (de Korte, 1984, 1989, 1991; Kelly & Marples, 2010), but is thought to have been converted to intensive coconut cultivation. de Korte (1991) provided the last assessment of the Moromaho seabird colony, estimating it contained 1,000 to 2,000 pairs of Red-footed Boobies *Sula sula* and no more than 100 pairs of Greater Frigatebirds *Fregata minor* breeding on the island in 1987. Despite such caveats, our data make an important contribution to filling knowledge gaps about the biodiversity of Sulawesi.

In particular, it is hoped that this paper will draw attention to the still neglected fauna of the Wakatobi Islands. Although the islands fall within the 'Special Land Zone' of the Wakatobi Marine Protected Area (Clifton & Unsworth, 2010), they receive little effective protection and most terrestrial habitats are heavily degraded. Of particular concern is the risk posed by trappers for the cage-bird trade to the remaining populations of Yellow-crested Cockatoo and the novel single island endemic Wangi-wangi White-eye (Collar & Marsden, 2014; Eaton et al., 2015; Harris et al., 2017). Continued hunting pressure could seriously threaten either of these sensitive populations. It is hoped that recognition of the Wangi-wangi White-eye, coupled with the Wakatobi White-eye (O'Connell et al., 2019c; Gill & Donsker, 2020),

will allow these islands to be classified as an Endemic Bird Area (Stattersfield et al., 1998; BirdLife International, 2020a). Further endemism is likely to be confirmed by closer investigation of other highlighted bird populations on these islands (Hartert, 1903; Collar & Marsden, 2014; Kelly et al., 2014; O'Connell et al., 2019b). This work is given impetus by the looming biodiversity crisis that threatens not just Southeast Asia (Sodhi et al., 2004; Wilcove et al., 2013; Symes et al., 2018), but the whole world (WWF, 2018). Much biodiversity, and the evolutionary lessons it can teach us, faces extinction if we do not recognise and protect it.

AUTHOR CONTRIBUTIONS

DOC, DJK, SBAK, KA, AK, NMM, FER, and TEM conceived this study. DJK, SBAK, AK, NMM, FER, and TEM carried out field work. DOC and TEM led the writing and searched the literature for historical records. All authors contributed to revising and improving the manuscript.

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LITERATURE CITED

Billerman SM, Keeney BK, Rodewald PG & Schulenberg TS (2020) Birds of the World. Cornell Laboratory of Ornithology, Ithaca, New York, USA. https://birdsoftheworld.org/bow/home (Accessed 01 June 2020).

BirdLife International (2020a) Endemic Bird Area (EBA) summary. http://datazone.birdlife.org/eba (Accessed 18 February 2020).

BirdLife International (2020b) Important Bird Areas factsheet: Wakatobi. http://datazone.birdlife.org/site/factsheet/wakatobi-iba-indonesia (Accessed 07 February 2020).

Catterall M (1996) Bird survey on Buton island. Unpublished Operation Wallacea Report, 144 pp.

Clifton J (2003) Prospects for co-management in Indonesia's marine protected areas. Marine Policy, 27: 389–395.

Clifton J & Unsworth RKF (2010) Introduction. In: Clifton J, Unsworth RKF & Smith DJ (eds.) Marine Research and Conservation in the Coral Triangle: The Wakatobi National Park. Nova, New York. Pp. 10–18.

Coates BJ & Bishop KD (1997) A guide to the birds of Wallacea: Sulawesi, the Moluccas, and Lesser Sunda Islands, Indonesia. Dove Publications, Queensland, 536 pp., 64 colour pls., 5 figs., 1 map.

Collar NJ & Marsden SJ (2014) The subspecies of Yellow-crested Cockatoo *Cacatua sulphurea*. Forktail, 30: 23–27.

de Korte J (1984) Status and conservation of seabird colonies in Indonesia. In: Croxall JP, Evans PGH & Schreiber RW (eds.) Status and conservation of the world's seabirds. ICPB, Cambridge. Pp. 527–546.

de Korte J (1989) Threats to Indonesian seabird colonies. Conservation Biology, 3(4): 336–340.

de Korte J (1991) Status and conservation of Indonesia's seabird colonies. In: Croxall JP (ed.) Seabird status and conservation: a supplement. ICBP, Cambridge. Pp. 225–247.

Eaton JA, Shepherd CR, Rheindt FE, Harris JBC, Van Balen S, Wilcove DS & Collar NJ (2015) Trade-driven extinctions and near-extinctions of avian taxa in Sundaic Indonesia. Forktail, 31: 1–12.

Eaton JA, van Balen B, Brickle NW & Rheindt FE (2016) Birds of the Indonesian Archipelago: Greater Sundas and Wallacea. Lynx Edicions, Barcelona, 496 pp.

Gill F & Donsker D (eds.) (2020) IOC World Bird List. Version 10.1. https://www.worldbirdnames.org/ioc-lists/master-list-2/ (Accessed 18 February 2020).

Harris JBC, Tingley MW, Hua F, Yong DL, Adeney JM, Lee TM, Marthy W, Prawiradilaga DM, Sekercioglu CH & Winarni N (2017) Measuring the impact of the pet trade on Indonesian birds. Conservation Biology, 31(2): 394–405.

Hartert E (1903) On the birds collected on the Tukang-Besi Islands and Buton, south-east of Celebes, by Mr. Heinrich Kuhn. Novitates Zoologicae, 10: 18–38.

Hartert E (1916) A new form of *Coracina*. Bulletin of the British Ornithologists' Club, 36: 65.

IUCN [International Union for Conservation of Nature] (2012) IUCN Red List Categories and Criteria: Version 3.1. Second Edition. https://www.iucnredlist.org/resources/categories-and-criteria (Accessed 08 April 2020).

IUCN [International Union for Conservation of Nature] (2019) The IUCN Red List of Threatened Species, Version 2019.3. https://www.iucnredlist.org/ (Accessed 17 December 2019).

Jønsson KA, Bowie RCK, Moyle RG, Irestedt M, Christidis L, Norman JA & Fjeldså J (2010) Phylogeny and biogeography of Oriolidae (Aves: Passeriformes). Ecography, 33(2): 232–241.

Kelly DJ & Marples NM (2010) Bird populations of the Wakatobi. In: Clifton J, Unsworth RKF & Smith DJ (eds.) Marine research and conservation in the Coral Triangle: the Wakatobi National Park. Nova, New York. Pp. 149–170.

Kelly DJ & Marples NM (2011) Olive-backed Sunbird *Cinnyris jugularis* in southeast Sulawesi. BirdingASIA, 15: 15–16.

Kelly SBA (2014) Integrative avian taxonomy and the role of competition in the diversification of passerine birds. PhD Thesis, Trinity College Dublin, Ireland, 114 pp.

Kelly SBA, Kelly DJ, Cooper N, Bahrun A, Analuddin K & Marples NM (2014) Molecular and phenotypic data support the recognition of the Wakatobi Flowerpecker (*Dicaeum*

kuehni) from the unique and understudied Sulawesi region. PLoS ONE, 9: e98694.

König C, Weick F & Becking J-H (2008) Owls of the World. Christopher Helm, London, 528 pp.

Lees AC, Naka LN, Aleixo A, Cohn-Haft M, Piacentini V de Q, Santos MPD & Silveira LF (2014) Conducting rigorous avian inventories: Amazonian case studies and a roadmap for improvement. Revista Brasileira de Ornitologia, 22: 107–120.

Lees AC & Pimm SL (2015) Species, extinct before we know them? Current Biology, 25(5): R177–R180.

Losos JB (2018) Newly Described Cuban Anole Already for Sale in Europe. Anole Annals. http://www.anoleannals.org/2018/12/04/newly-described-cuban-anole-already-for-sale-in-europe/ (Accessed 19 February 2020).

Macaulay Library (2020) The Cornell Lab of Ornithology Macaulay Library. https://www.macaulaylibrary.org/ (Accessed 01 June 2020).

Martin TE, Kelly DJ, Keogh NT, Heriyadi D, Singer HA & Blackburn GA (2012) The avifauna of Lambusango Forest Reserve, Buton Island, south-east Sulawesi, with additional sightings from southern Buton. Forktail, 28: 107–112.

Martin TE, Kelly SBA, Froese G, Brodie J, Mulyani Y & Kelly DJ (2015) New records from Buton Island, Sulawesi, Indonesia. BirdingASIA, 23: 128.

Martin TE, Monkhouse J, Akbar PG, Halliday, Baddams J, Mulyani Y, Kaban A, Sumanto LY, Keogh NT & Nightingale J (2017) Notes on the distribution, status and natural history of ten species on Buton island, Southeast Sulawesi, Indonesia. BirdingASIA, 28: 74–77.

Milsom J, Ali J & Sudarwono (1999) Structure and collision history of the Buton continental fragment, eastern Indonesia. AAPG Bulletin, 83(10): 1666–1689.

Monkhouse J, O'Connell DP, Karya A, Analuddin K, Kelly DJ, Marples NM & Martin TE (2018) The avifauna of Menui Island, south-east Sulawesi, Indonesia. Forktail, 34: 42–17.

Myers N, Mittermeier RA, Mittermeier CG, Da Fonseca GAB & Kent J (2000) Biodiversity hotspots for conservation priorities. Nature, 403: 853–858.

Nugraha AMS & Hall R (2018) Late Cenozoic palaeogeography of Sulawesi, Indonesia. Palaeogeography, Palaeoclimatology, Palaeoecology, 490: 191–209.

O'Connell DP (2019) Avian speciation and biodiversity in South-east Sulawesi, Indonesia: drivers of diversification. PhD Thesis, Trinity College Dublin, Ireland, xiii + 198 pp. http://www.tara.tcd.ie/bitstream/handle/2262/86105/Darren%20O%27Connell_PhD_Thesis_main_body2019.pdf?sequence=4&isAllowed=y

O'Connell DP, Kelly DJ, Kelly SBA, Sealy S, Karya A, Analuddin K & Marples NM (2019a) Increased sexual dimorphism in dense populations of Olive-backed Sunbirds on small islands: morphological niche contraction in females but not males. Emu - Austral Ornithology, 119(3): 296–307.

O'Connell DP, Kelly DJ, Lawless N, Karya A, Analuddin K & Marples NM (2019b) Diversification of a 'great speciator' in the Wallacea region: differing responses of closely related resident and migratory kingfisher species (Aves: Alcedinidae: *Todiramphus*). Ibis, 161: 806–823.

O'Connell DP, Kelly DJ, Lawless N, O'Brien K, Ó Marcaigh F, Karya A, Analuddin K & Marples NM (2019c) A sympatric pair of undescribed white-eye species (Aves: Zosteropidae: *Zosterops*) with different origins. Zoological Journal of the Linnean Society, 186(3): 701–724.

O'Connell DP, Ó Marcaigh F, O'Neill A, Griffen R, Karya A, Analuddin K, Kelly DJ & Marples NM (2019d) The avifauna of Muna and Wawonii Islands, with additional records from mainland South-east Sulawesi, Indonesia. Forktail, 35: 50–56.

O'Connell DP, Sealy S, Ó Marcaigh F, Karya A, Bahrun A, Analuddin K, Kelly DJ & Marples NM (2017) The avifauna of Kabaena Island, south-east Sulawesi, Indonesia. Forktail, 33: 14–19.

Pedersen MP, Irestedt M, Joseph L, Rahbek C & Jønsson KA (2018) Phylogeography of a 'great speciator' (Aves: *Edolisoma tenuirostre*) reveals complex dispersal and diversification dynamics across the Indo-Pacific. Journal of Biogeography, 45(4): 826–837.

Rheindt FE, Prawiradilaga DM, Ashari H, Suparno, Gwee CY, Lee GWX, Wu MY & Ng NSR (2020) A lost world in Wallacea: Description of a montane archipelagic avifauna. Science, 367(6474): 167–170.

Rheindt FE, Prawiradilaga DM, Suparno S, Ashari H & Wilton PR (2014) New and significant island records, range extensions and elevational extensions of birds in eastern Sulawesi, its nearby satellites, and Ternate. Treubia, 41: 61–90.

Rheindt FE, Verbelen F, Putra DD, Rahman A & Indrawan M (2010) New biogeographic records in the avifauna of Peleng Island (Sulawesi, Indonesia), with taxonomic notes on some endemic taxa. Bulletin of the British Ornithologists' Club, 130: 181–207.

Smith RB & Silver ELIA (1991) Geology of a Miocene collision complex, Buton, eastern Indonesia. Geological Society of America Bulletin, 103(5): 660–678.

Sodhi NS, Koh LP, Brook BW & Ng PKL (2004) Southeast Asian biodiversity: an impending disaster. Trends in Ecology & Evolution, 19: 654–660.

Stattersfield AJ, Crosby MJ, Long AJ & Wege DC (1998) Endemic bird areas of the world. BirdLife International, Cambridge, 846 pp.

Symes WS, Edwards DP, Miettinen J, Rheindt FE & Carrasco LR (2018) Combined impacts of deforestation and wildlife trade on tropical biodiversity are severely underestimated. Nature Communications, 9(1): 4052.

UNESCO (2019) Wakatobi Biosphere Reserve, Indonesia. United Nations Education, Scientific and Cultural Organization. https://en.unesco.org/biosphere/aspac/wakatobi (Accessed 07 April 2020).

White CMN & Bruce MD (1986) The birds of Wallacea (Sulawesi, the Moluccas and Lesser Sunda Islands, Indonesia): an annotated check-list. BOU Check-list No. 7. British Ornithologists' Union, London, 524 pp.

Wilcove DS, Giam X, Edwards DP, Fisher B & Koh LP (2013) Navjot's nightmare revisited: logging, agriculture, and biodiversity in Southeast Asia. Trends in Ecology & Evolution, 28(9): 531–540.

WWF (2018) Living Planet Report - 2018: Aiming Higher. Grooten M & Almond REA (eds.) World Wildlife Fund, Gland, Switzerland, 144 pp.

Xeno-canto Foundation (2019) xeno-canto. Powered by the Xeno-canto Foundation and Naturalis Biodiversity Center. https://www.xeno-canto.org/ (Accessed 04 December 2019).

APPENDIX

Table 1. Summary of bird species recorded in the Wakatobi Islands, with species recorded by the present study (1999–2019) above the black line, and species recorded solely recorded by Hartert (1903) below the black line. Taxonomy generally follows Eaton et al. (2016), with the exception of species marked # where recent strong primary evidence has suggested a different classification, as outlined in species specific accounts. Denotations (✓) in the columns Wa, Or, Kap, Ho, Ka, To, LS, Bi, and Ru indicate records of species occurring on the islands of Wangi-wangi, Oroho, Kapota, Hoga, Kaledupa, Tomia, Lintea Selatan, Binongko, and Runduma, respectively. Records followed by a † are thought to be new records for that island. Denotations (X) indicate where a species in this list was previously recorded for an island by Hartert (1903) but was not recorded there during the current study. Species listed by the IUCN (2019) as Near Threatened or Critically Endangered are indicated by NT and CR, respectively, after the scientific name. Species marked * are regionally endemic to the Wallacean biodiversity hotspot as defined by Myers et al. (2000). Species marked ‡ are endemic to Indonesia and/or East Timor (Eaton et al., 2016). Species marked (I) are introduced to the study area. Species marked as 'undescribed' are awaiting formal taxonomic description. Species marked <M> indicate that the species is a seasonal migrant to the Wakatobi Islands. Macaulay Library (ML) codes correspond to voucher numbers for species photographs or sound recordings uploaded to the Macaulay Library (2020). Individual islands records are withheld for the Yellow-crested Cockatoo due to its vulnerability to the caged bird trade.

Family	Common name	Scientific name	Wa	Or	Kap	Ho	Ka	To	LS	Bi	Ru	ML voucher #
Megapodiidae	Orange-footed Scrubfowl	*Megapodius reinwardt*	✓†	✓†		✓†	✓		✓†		✓†	ML718338
Phasianidae	Blue-breasted Quail	*Synoicus chinensis*	✓†									
Columbidae	Rock Dove	*Columba livia* (I)	✓†				✓†	✓†				
	Spotted Dove	*Spilopelia chinensis* (I)	✓	✓†	✓†	✓†	✓	✓		✓		ML718202
	Sulawesi Cuckoo-dove	*Macropygia albicapilla* *	✓	✓†		✓†	✓	✓†		✓		ML718355
	Asian Emerald Dove	*Chalcophaps indica*	✓		✓†	✓†	✓†	✓†		✓	✓†	ML718258
	Pink-necked Green-pigeon	*Treron vernans*	✓†			✓†				✓†		
	Grey-cheeked Green-pigeon	*Treron griseicauda* ‡	✓†	✓†		✓†	✓	✓	✓†	✓	✓†	ML718212
	Elegant Imperial Pigeon	*Ducula concinna* ‡	✓†	✓†	✓†	✓†	✓	✓	✓†	✓		ML718204
	Pink-headed Imperial Pigeon	*Ducula rosacea* NT									✓†	
	Pied Imperial Pigeon	*Ducula bicolor*					✓†	✓†				
	Black-naped Fruit-dove	*Ptilinopus melanospilus*	✓	✓†	✓†	✓†	✓	✓		✓	✓†	ML718252
Caprimulgidae	Great Eared-nightjar	*Lyncornis macrotis*	✓†	✓†	✓†	✓†	✓†					ML718197
Hemiprocnidae	Grey-rumped Treeswift	*Hemiprocne longipennis*					✓†					
Apodidae	Glossy Swiftlet	*Collocalia esculenta*	✓†	✓†	✓†	✓†	✓†	✓†	✓†	✓†	✓†	ML718259
	Uniform Swiftlet	*Aerodramus vanikorensis*								✓†		
	Asian Palm Swift	*Cypsiurus balasiensis*					✓†	✓†		✓†		
Cuculidae	Lesser Coucal	*Centropus bengalensis*	✓				✓	✓		✓		ML718265
	Channel-billed Cuckoo	*Scythrops novaehollandiae* <M>	✓	✓†	✓†		✓					ML700636
	Plaintive Cuckoo	*Cacomantis merulinus*	✓†	✓†		✓†	✓†			✓†		
	Sulawesi Brush Cuckoo	*Cacomantis variolosus* *	✓†	✓†		✓†	✓	✓	✓†			ML718254
	Drongo Cuckoo	*Surniculus lugubris*					✓†	✓†				
Rallidae	Barred Rail	*Hypotaenidia torquata*	✓	✓†		✓†	✓	✓	✓†	✓		
	Buff-banded Rail	*Hypotaenidia philippensis*					✓†					ML718255
	White-breasted Waterhen	*Amaurornis phoenicurus*					✓	✓		✓	✓†	

Family	Common name	Scientific name	Wa	Or	Kap	Ho	Ka	To	LS	Bi	Ru	ML voucher #
Oceanitidae	Wilson's Storm-petrel	*Oceanites oceanicus*						✓†				
Ardeidae	Rufous Night Heron	*Nycticorax caledonicus*	✓†					✓†				
	Striated Heron	*Butorides striata*	✓	✓†		✓†	✓	✓†		✓		ML718261
	Great-billed Heron	*Ardea sumatrana*	✓	✓†	✓†	✓†	✓†	✓		✓		ML718337
	Purple Heron	*Ardea purpurea*	✓†	✓†		✓†				✓†		
	Eastern Great Egret	*Ardea modesta*	✓				✓				✓†	
	Little Egret	*Egretta garzetta*	✓†	✓†	✓†	✓†	✓†	✓†				
	Pacific Reef Egret	Egretta sacra					✓	✓		✓	✓†	
Pelecanidae	Australian Pelican	*Pelecanus conspicillatus* <M>								✓†		
Fregatidae	Great Frigatebird	*Fregata minor*	✓	✓†		✓†	✓	✓		✓	✓†	ML718260
Sulidae	Red-footed Booby	*Sula sula*	✓	✓†			✓	✓		✓	✓†	ML718340
Phalacrocoracidae	Little Pied Cormorant	*Microcarbo melanoleucos*		✓†	✓†		✓†					ML718356
	Little Black Cormorant	*Phalacrocorax sulcirostris*			✓†			✓†			✓†	
Burhinidae	Beach Thick-knee	*Esacus magnirostris* NT		✓†		✓†			✓†			ML718205
Recurvirostridae	Black-winged Stilt	*Himantopus himantopus*					✓†	✓†				
Charadriidae	Grey Plover	*Pluvialis squatarola* <M>		✓†								
	Pacific Golden Plover	*Pluvialis fulva* <M>	✓			✓†	✓					
	Malaysian Plover	*Anarhynchus peronii* NT				✓†	✓†					
	Siberian Plover	*Anarhynchus mongolus* <M>				✓†						
	Greater Sandplover	*Charadrius leschenaultia* <M>		✓†			✓		✓†			
Scolopacidae	Eastern Whimbrel	*Numenius phaeopus* <M>	✓	✓†	✓†	✓†	✓†		✓†	✓		ML718274
	Bar-tailed Godwit	*Limosa lapponica* NT <M>		✓†	✓†							
	Ruddy Turnstone	*Arenaria interpres* <M>		✓†		✓†						
	Red Knot	*Calidris canutus* NT <M>	✓†		✓†							
	Common Sandpiper	*Actitis hypoleucos* <M>	✓	✓†	✓†	✓†	✓	✓		✓	✓†	ML718257
	Wood Sandpiper	*Tringa glareola* <M>					✓†					
	Grey-tailed Tattler	*Tringa brevipes* NT <M>	✓	✓†		✓†	✓					ML718339
	Common Greenshank	*Tringa nebularia* <M>		✓†		✓†	✓†					
	Common Redshank	*Tringa totanus* <M>	✓	✓†		✓†	✓					
Turnicidae	Red-backed Buttonquail	*Turnix maculosus*	✓†					✓			✓†	ML718270
Glareolidae	Australian Pratincole	*Stiltia isabella* <M>	✓†					✓†				
Laridae	Gull-billed Tern	*Gelochelidon nilotica* <M>		✓†	✓†							
	Black-naped Tern	*Sterna sumatrana* <M>	✓†	✓†		✓†	X				✓†	
	Great Crested Tern	*Thalasseus bergii*		✓†	✓†						✓†	

Family	Common name	Scientific name	Wa	Or	Kap	Ho	Ka	To	LS	Bi	Ru	ML voucher #
Strigidae	Moluccan Scops-owl	*Otus magicus* *	✓†				X					ML205789251
Pandionidae	Osprey	*Pandion haliaetus*	✓	✓†	✓†	✓†	✓	✓†		✓		ML718330
Accipitridae	Pacific Baza	*Aviceda subcristata*	✓	✓†		✓†	✓					ML718331
	Spotted Harrier	*Circus assimilis*	✓†					✓†		✓†		
	Brown Goshawk	*Tachyspiza fasciatus*	✓	✓†			✓	✓		✓		
	Vinous-breasted Sparrowhawk	*Tachyspiza rhodogaster*	✓†				✓†					
	White-bellied Sea-eagle	*Icthyophaga leucogaster*	✓†		✓†		✓†			✓†	✓†	
	Brahminy Kite	*Haliastur indus*	✓	✓†								
	Rufous-winged Buzzard	*Butastur liventer*					✓†					
Meropidae	Rainbow Bee-eater	*Merops ornatus* <M>	✓†	✓†		✓†	✓†	✓†		✓†	✓†	ML718269
Coraciidae	Common Dollarbird	Eurystomus orientalis	✓	✓†			✓			✓	✓†	
Alcedinidae	Common Kingfisher	*Alcedo atthis*					✓					ML718256
	Collared Kingfisher	*Todiramphus chloris*	✓	✓†	✓†	✓	✓	✓	✓	✓	✓†	ML718264
	Sacred Kingfisher	*Todiramphus sanctus* <M>	✓	✓†	✓†	✓	✓	✓		✓	✓	ML718201
Falconidae	Indonesian Kestrel	*Falco moluccensis*	✓†				✓	✓		✓		
	Oriental Hobby	*Falco severus*						✓†				
Cacatuidae	Yellow-crested Cockatoo	*Cacatua sulphurea* CR										
Psittacidae	Ornate Lorikeet	*Trichoglossus ornatus* *					✓					
	Great-billed Parrot	*Tanygnathus megalorynchos*	✓	✓†		✓†	✓	✓				ML718211
Pittidae	Elegant Pitta	*Pitta elegans* *	✓			✓†	X					ML718196
Oriolidae	Black-naped Oriole	*Oriolus chinensis*	✓	✓†	✓†	✓†	✓	✓	✓†	✓	✓†	ML718253
Artamidae	White-breasted Woodswallow	*Artamus leucorynchus*	✓	✓†	✓†	✓†	✓	✓		✓		ML718203
Campephagidae	Wallacean Cicadabird	*Edolisoma amboinensis* *	✓		✓†	✓†	✓			✓		ML718272
	Sulawesi Triller	*Lalage leucopygialis* *	✓	✓†			✓	✓		✓		ML718218
Dicruridae	White-eyed Spangled Drongo	*Dicrurus leucops* *	✓	✓†	✓†	✓†	✓	✓		✓		ML718263
Monarchidae	Island Monarch	*Monarcha cinerascens*	✓	✓†	✓†	✓†	✓	✓	✓†	✓	✓†	ML718198
Corvidae	Sulawesi Crow	*Corvus celebensis* *	✓	✓†	✓†	✓†	✓	✓	✓†	✓	✓†	ML700637
Cisticolidae	Zitting Cisticola	*Cisticola juncidis*	✓†					✓				ML240795771
Acrocephalidae	Oriental Reed-warbler	*Acrocephalus orientalis* <M>									✓†	ML718267
Hirundinidae	Pacific Swallow	*Hirundo tahitica*	✓	✓†	✓†	✓†	✓	✓		✓		ML718200

Family	Common name	Scientific name	Wa	Or	Kap	Ho	Ka	To	LS	Bi	Ru	ML voucher #
Zosteropidae	Lemon-bellied White-eye	*Zosterops chloris*									✓	ML240794511
	Wakatobi White-eye	*Zosterops flavissimus* * #	✓	✓	✓†		✓	✓	✓	✓		ML718273
	Wangi-wangi White-eye	*Zosterops* undescribed *	✓									ML718276
Sturnidae	Short-tailed Starling	*Aplonis minor*	✓	✓†	✓†	✓†	✓	✓		✓		ML718271
Muscicapidae	Grey-streaked Flycatcher	*Muscicapa griseisticta* <M>	✓									
	Pied Bushchat	*Saxicola caprata*	✓†	✓†			✓†	✓†		✓†		ML718268
Dicaeidae	Grey-sided Flowerpecker	*Dicaeum celebicum* *	✓	✓	✓†	✓	✓	✓		✓		ML718262
Nectariniidae	Sahul Sunbird	*Cinnyris clementiaei*	✓	✓	✓†	✓	✓	✓	✓	✓	✓†	ML718266
Estrildidae	Black-faced Munia	*Lonchura molucca* ‡	✓	✓†		✓	✓	✓	✓†	✓		ML718206
Passeridae	Eurasian Tree Sparrow	*Passer montanus*	✓†		✓†		✓†	✓†		✓†	✓†	ML718357
Motacillidae	Eastern Yellow Wagtail	*Motacilla tschutschensis* <M>	✓									
Columbidae	Barred Dove	*Geopelia maugeus* (I)						X				
Ardeidae	Black Bittern	*Ixobrychus flavicollis*					X					
Scolopacidae	Pintail Snipe	*Gallinago stenura* <M>								X		
Tytonidae	Sulawesi Masked Owl	*Tyto rosenbergii* *					X					
Cisticolidae	Golden-headed Cisticola	*Cisticola exilis*					X					
Locustellidae	Gray's Grasshopper Warbler	*Locustella fasciolata* <M>	X				X	X		X		
Motacillidae	Grey Wagtail	*Motacilla cinerea* <M>					X	X				
	Pechora Pipit	*Anthus gustavi* <M>					X					

SUPPLEMENTARY MATERIAL

Table S1. Full list of species recorded, broken down by island and by expedition, with Relative Abundance estimates provided for islands visited for ≥5 days in 2010, 2012, and 2013. https://doi.org/10.6084/m9.figshare.12555248.v1

Table S2. All mist netting capture records from the Wakatobi Islands. https://doi.org/10.6084/m9.figshare.12555269.v1

Table S3. Netting effort and number of individuals captured per netting metre hour (mh) during the 2010 expedition. https://doi.org/10.6084/m9.figshare.12555281.v1