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Source: Bulletin of the British Ornithologists' Club, 142(3) : 278-301

Published By: British Ornithologists' Club

URL: <https://doi.org/10.25226/bboc.v142i3.2022.a2>

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Breeding records of the birds of south-east Sulawesi, Indonesia: a collation of observations encompassing nearly 20 years of research in Wallacea

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Received 22 December 2021; revised 12 April 2022; published 6 September 2022

<http://zoobank.org/urn:lsid:zoobank.org:pub:F336FCA0-BBE8-4DF2-8C41-ED2894804A21>

SUMMARY.—The islands of the Wallacean biodiversity hotspot support diverse and highly endemic bird communities, yet remain ornithologically poorly studied. There is a particular paucity of data regarding breeding biology for the region's birds. Here, we help to address this research gap by collating observations of breeding evidence made during nearly 20 years of field work between 1999 and 2018 in south-east Sulawesi and its offshore islands. Data were collected between April and September, with a special focus on July and August, which is the dry season across the southern half of Sulawesi. In total, we summarise 1,064 observations of potential breeding in 66 species, of which 27 are Wallacean endemics (including the Critically Endangered Maleo *Macrocephalon maleo*), and 39 species of wider range (including the Endangered Milky Stork *Mycteria cinerea*). Records include species with little or no previously published information on their breeding biology, such as Pygmy Hanging Parrot *Loriculus exilis*, Sulawesi Pitta *Erythropitta celebensis* and an undescribed *Zosterops* species, provisionally referred to as Wangi-wangi White-eye.

The Wallacean biodiversity 'hotspot' (Myers *et al.* 2000) supports diverse bird communities with a high proportion of endemic species, although these remain poorly studied (Cannon *et al.* 2007, Eaton *et al.* 2021). Though some early studies provided significant insight into the avifauna of particular islands, such as the work of Verheijen (1964) on Flores and Noske (2003) on Timor, significant gaps in knowledge persisted for many years, as highlighted in the foundational compilations of regional ornithological knowledge (White & Bruce 1986, Coates & Bishop 1997). In recent years knowledge regarding the taxonomy, distribution and conservation status of the region's species has improved via significant new field and museum-based research (e.g. Indrawan *et al.* 2006, Martin *et al.* 2012, Reeve *et al.* 2015, Bashari & Arndt 2016, Verbelen *et al.* 2017, Monkhouse *et al.* 2018, Ng *et al.* 2018, O'Connell 2019, Irham *et al.* 2020, Rheindt *et al.* 2020) and efforts to organise citizen science data such as eBird (<https://ebird.org/home>). These advances have been compiled in a new regional field guide (Eaton *et al.* 2016, 2021) and informed the growing *Birds of the world* (<https://birdsoftheworld.org/bow/home>) online database of the world's avifauna.

However, basic information concerning the natural history of most Wallacean species is still lacking, hampering an understanding of how species within the region might respond to environmental challenges (Lees *et al.* 2020). Outside the detailed work of Verheijen (1964), who rigorously collected >1,000 records of breeding birds on Flores, the relatively sparse data on avian biology from Wallacea has largely come from opportunistic observations

by field workers. Accumulating and quantifying data this way is a slow process (Fierro-Calderón *et al.* 2021), which has been hampered by the fact that Wallacea is still relatively understudied, with numerous endemic bird species going unrecognised until recently (O'Connell *et al.* 2019c, Rheindt *et al.* 2020), highlighting the relatively low baseline scientific knowledge of the region's avifauna. This shortfall in natural history data was quantified by Noske (2017), who demonstrated that 57% of all Wallacean endemics possess no published data on their breeding biology and 72% no data regarding nest characteristics. As breeding by birds in Wallacea is strongly seasonal, being driven by changes in precipitation between the wet and dry seasons (Verheijen 1964, Noske 2003), filling knowledge gaps concerning breeding patterns in Wallacean birds provides vital information to understand how likely future changes in regional climate may affect species' ecologies. As movements by some Wallacean species are complex, with seasonal short-range breeding migrations noted for species such as Island Monarch *Monarcha cinerascens* and Elegant Pitta *Pitta elegans*, collecting data on breeding behaviour informs our understanding of key breeding sites for species with complex life histories (Eaton *et al.* 2021).

In this study, we respond to Noske's (2017) call for more published breeding data on Wallacean birds by summarising all information related to breeding biology obtained throughout a series of long-running bird surveys of south-east Sulawesi and its offshore islands, Indonesia. These surveys formed part of near-annual field seasons between 1999 and 2018, in a collaborative partnership between Operation Wallacea (www.opwall.com), Trinity College Dublin (TCD), Universitas Halu Oleo (UHO), Bogor Agricultural University (IPB) and University of Wollongong (UOW).

Study area and Methods

Data on the breeding biology of the birds of south-east Sulawesi were collected during two parallel ornithological research projects focusing on different aspects of the regional avifauna. Systematic research was conducted on Buton most years during the study period (2004–14 and 2018) by Operation Wallacea, IPB, UHO and UOW ornithologists, surveying set transect routes in forest and forest edge habitats in central and north Buton to monitor bird populations, along with limited mist-netting (see Martin *et al.* 2012 for detailed methods, survey periods and habitat descriptions). In addition, researchers from TCD and UHO undertook a long-term study of avian speciation and biogeography in south-east Sulawesi, collecting data from most islands in the region (including Buton) over a number of field seasons during 1999–2017 (Table 1); for detailed methods, survey periods and habitat descriptions see O'Connell *et al.* (2017, 2019d, 2020) and Monkhouse *et al.* (2018). Briefly, these surveys involved mist-netting and transects in edge habitats (scrub, mangrove, farmland, forest edge), moving regularly and covering a large variety of sites for short periods.

The goals of these surveys were not explicitly to obtain information on the breeding biology of Wallacean birds. Rather they were to address questions relating to ecological (Martin & Blackburn 2014), biogeographical (O'Connell *et al.* 2019a, Ó Marcaigh *et al.* 2021, Ó Marcaigh *et al.* 2022) and evolutionary (Kelly *et al.* 2014, O'Connell *et al.* 2019b,c) processes in the region. However, during the course of these surveys, numerous opportunistic observations were made of breeding biology, in the form of nests and juvenile birds, handling individuals in breeding condition during mist-netting work, and behavioural observations. Together, these efforts encompassed work on mainland south-east Sulawesi, the five large islands off the coast of south-east Sulawesi (Buton, Muna, Wawonii, Kabaena and Menui), the four major Wakatobi Islands (Wangi-wangi, Kaledupa, Tomia and Binongko, uplifted Quaternary coral limestone islands always separated from Sulawesi; Milsom *et al.* 1999,

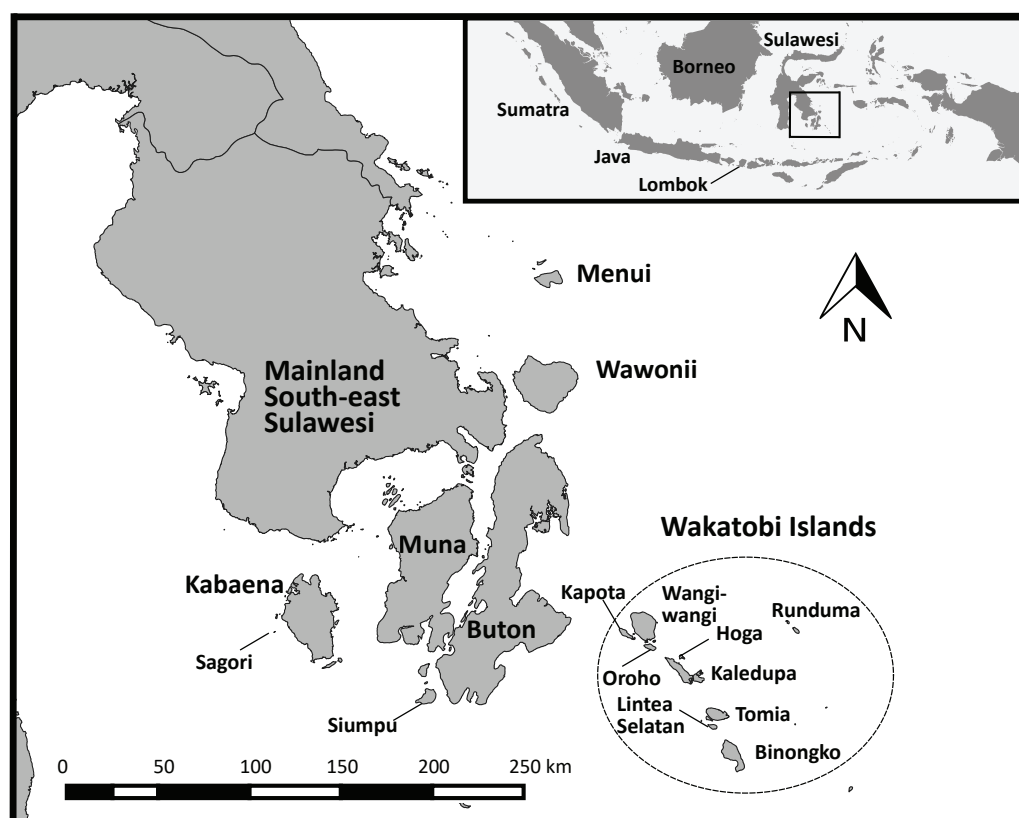


Figure 1. South-east Sulawesi and its offshore islands. The inset shows the location of the region within Indonesia and the wider area.

Nugraha & Hall 2018), a number of small islets off the coasts of these islands, and isolated Runduma Island (Fig. 1, Table 1). Breeding bird records were collected on 16 of these islands (Table 1). With the exception of a visit to the Wakatobi Islands in April/May 2013, all field work was conducted during July–September (Wakatobi Islands) and June–August (all other islands), with a particular concentration of effort in July and August. Comparable quantification of field work effort is impossible for the collection of breeding records, as many important observations were made outside structured surveys, and survey personnel, timing and focus varied significantly between years and islands. However, broadly, Buton has received the most consistent and detailed survey effort, followed by the islands of Kabaena, mainland Sulawesi, Hoga, Kaledupa, Wangi-wangi and Tomia (Table 1) (Martin *et al.* 2012, 2015, 2017a, O'Connell *et al.* 2017, 2019d, 2020, Monkhouse *et al.* 2018). Visits to other islands were generally brief or limited in scope.

In the Sulawesi region, precipitation follows a tropical monsoon climate, with a June–September dry season and November–April wet season (Whitten *et al.* 2002). Mean annual rainfall ranges between 1,500 and 2,000 mm, peaking in April–June. Mean annual temperatures range from 25°C to 27°C (Whitten *et al.* 2002). Birds have been noted to breed year-round in Wallacea (Noske *et al.* 2013), but generally display seasonal peaks related to rainfall. How precipitation patterns affect breeding in Sulawesi's bird species remains an open question. In the most detailed year-round breeding survey in Wallacea, Verheijen (1964) found that peak activity on Flores was at the start of the dry season, and Linsley *et al.* (1998) reported a similar result based on more fragmentary data from Sumba. However,

TABLE 1
Summary of islands visited in south-east Sulawesi, and the years in which breeding records were collected. Islands denoted ‘(W)’ form part of the Wakatobi chain. The total number of records of breeding evidence, with number of species in parentheses, across the full time period on each island is presented in the final column. Field work was heavily weighted towards July and August. ‘NA’ indicates periods where no field work was undertaken on that island.

Island name	Years with breeding records	No. of breeding records, with no. of species (in parentheses)						
		April	May	June	July	August	September	Total records (and no. of species)
Sulawesi mainland	2007, 2012, 2016, 2017	NA	NA	12 (4)	53 (18)	139 (20)	NA	204 (25)
Buton	1999, 2001–14, 2016–18	NA	NA	8 (8)	88 (26)	72 (23)	9 (4)	177 (42)
Muna	2017	NA	NA	30 (9)	19 (8)	NA	NA	49 (12)
Wawonii	2017	NA	NA	NA	8 (5)	NA	NA	8 (5)
Kabaena	1999, 2001, 2003, 2016	NA	NA	13 (7)	NA	122 (18)	42 (16)	177 (23)
Sagori	2016	NA	NA	1 (1)	NA	NA	NA	1 (1)
Siumpu	1999	NA	NA	NA	NA	NA	6 (3)	6 (3)
Menui	2017	NA	NA	NA	NA	64 (7)	NA	64 (7)
Wangi-wangi (W)	2003, 2005, 2010, 2012	NA	NA	NA	9 (4)	22 (6)	1 (1)	35 (6)
Oroho (W)	2003, 2012	NA	NA	NA	NA	1 (1)	4 (3)	5 (4)
Hoga (W)	1999, 2003, 2010, 2012	NA	NA	NA	15 (4)	18 (5)	16 (4)	49 (7)
Kaledupa (W)	1999, 2003, 2007, 2010, 2012	NA	NA	NA	19 (7)	NA	47 (7)	76 (10)
Tomia (W)	2005, 2010, 2012, 2013	NA	3 (3)	NA	68 (8)	24 (4)	11 (2)	106 (8)
Lintea Selatan (W)	2005	NA	NA	NA	NA	NA	27 (3)	27 (3)
Binongko (W)	2005, 2010	0	0	NA	NA	23 (5)	29 (4)	52 (7)
Runduma (W)	2005, 2013	4 (2)	NA	NA	NA	NA	21 (5)	25 (5)

Noske (2003) discovered a distinctly different pattern on Timor, with breeding largely ceasing in the dry season (June–September) and peaking twice in the wet season (March–April and November–December). Our survey (concentrated on July–August) is at the start of the dry season in south-east Sulawesi, so may also capture peak breeding activity if the pattern is similar to Flores (Verheijen 1964). On most islands surveyed, edge habitats were those most accessible for survey work; therefore much of our effort focused on scrub, forest edge, farmland and mangroves across all islands (Fig. 2B) (O’Connell *et al.* 2017, 2019d, 2020, Monkhouse *et al.* 2018). The exception to this was Buton, where large tracts of lowland rainforest with a canopy height of >25 m (Whitten *et al.* 2002) remain, and significant survey effort was focused on Lambusango Forest Reserve, a 650 km² expanse of tropical monsoon forest in central Buton, and Buton Utara Nature Reserve (920 km²) in northern Buton (Fig. 2A) (Martin *et al.* 2012). In addition, short surveys were undertaken of paddyfield areas on Buton, Wawonii and Sulawesi (Fig. 2C) (Martin *et al.* 2012, O’Connell *et al.* 2019d), the UHO urban forest in Kendari city (mainland Sulawesi), the small monsoonal dry forest on Menui (23.5 km²) (Fig. 2D) (Monkhouse *et al.* 2018) and the remaining lowland rainforest on Kabaena (fragmentary areas with a closed canopy at c.12 m) (Robinson-Dean *et al.* 2002).

Evidence of breeding was provided by observations of: (1) active nests, (2) juveniles (with reference to Coates & Bishop 1997 and Eaton *et al.* 2016 for juvenile plumage features), (3) birds in breeding condition, i.e. females with clear brood patches or carrying eggs (gravid), and males with obvious cloacal protuberances, identified during mist-net surveys,

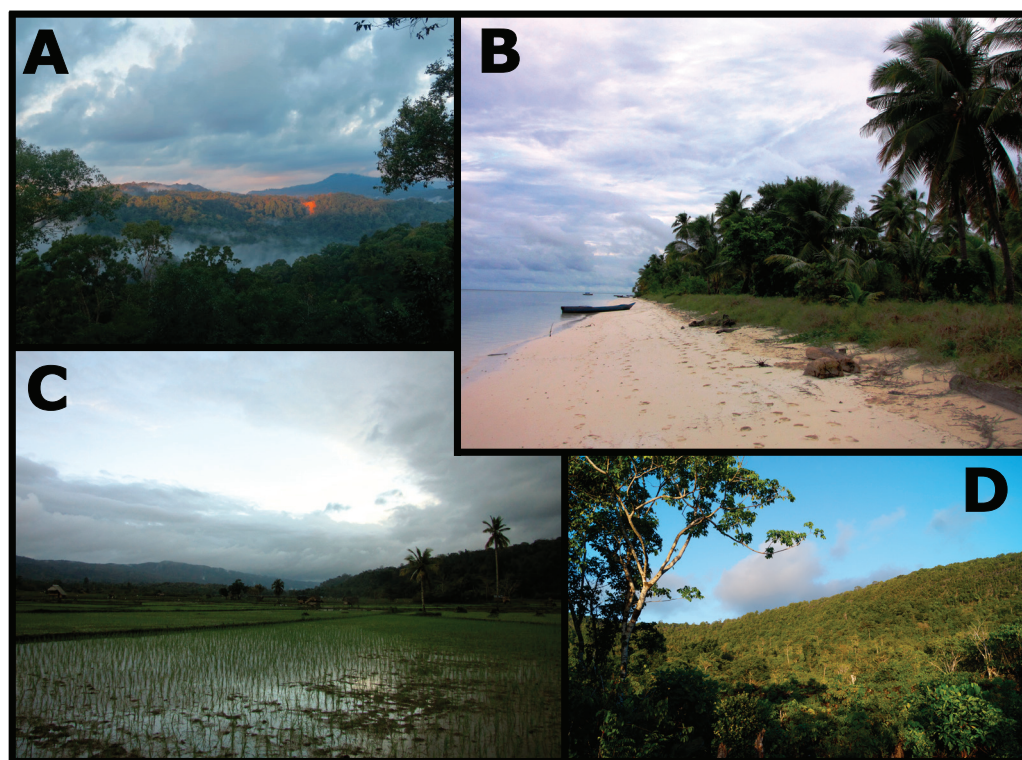


Figure 2. A range of habitats covered by the survey effort in south-east Sulawesi showing: (A) lowland rainforest on Buton (Thomas E. Martin), (B) beach and coastal scrub on Hoga in the Wakatobi Islands (Thomas E. Martin), (C) rice paddies on Buton and secondary forest transitioning into (D) mature dry forest on Menui (Joseph Monkhouse)

with reference to Rogers *et al.* (1986) and Svensson (1992) for identifying these, and (4) characteristic breeding behaviour such as nestbuilding, display flights or copulation. Active nests were considered the primary evidence of breeding as this constitutes irrefutable proof linked to a known location, followed by juveniles (confirmed breeding, location and timing not certain as the distance juveniles travel, and duration juvenile plumage persists, vary significantly between species), birds in breeding condition (indicative of breeding but not confirmed) and finally behaviour (more weakly indicative of breeding). Breeding records were aggregated by species and island, and arranged in taxonomic order following Gill *et al.* (2021). In addition, for Wallacean endemics (following Myers *et al.* 2000) and threatened species (IUCN 2021), we provide further details of our observations and assess how these add to the existing data on these species' breeding biology. Where available, photos of notable records were uploaded to the Macaulay Library (<https://www.macaulaylibrary.org/>) and photo codes are provided in the format ML #.

Results

Overall, we collected 1,064 observations of potential breeding evidence for 66 species, of which 27 were Wallacean endemics (including the Critically Endangered Maleo and Near Threatened Red-backed Thrush *Geokichla erythronota*), and 39 species with a wider range (including the Endangered Milky Stork and Near Threatened Rufous-bellied Eagle *Lophotriorchis kienerii*) (Table 2, Table S1). Active nests were considered the strongest evidence of breeding, followed by juveniles, adults in breeding condition and finally adults

TABLE 2

Summary of new breeding records of 66 bird species on the islands of south-east Sulawesi. Taxonomy follows Gill *et al.* (2021). Species in bold and denoted * are endemic to the Wallacean biodiversity hotspot as defined by Myers *et al.* (2000). After the common name, an (I) indicates species introduced to Wallacea; CR = Critically Endangered, EN = Endangered, NT = Near Threatened (IUCN 2021). Initials in the ‘Island’ column correspond to the following island names: Sul = south-east Sulawesi mainland, But = Buton, Siu = Siumpu, Mun = Muna, Waw = Wawonii, Kab = Kabaena, Sag = Sagori, Men = Menui, Wan = Wangi-wangi, Oro = Oroho, Hog = Hoga, Kal = Kaledupa, Tom = Tomia, Lin = Lintea Selatan, Bin = Binongko, Run = Runduma. Initials in the ‘Category’ column correspond to the following categories: BB = breeding behaviour, BC = breeding condition, J = Juvenile, N = active nest. Months are denoted: Apr = April, August = Aug and September = Sep. All individual records providing date, location details and additional notes are presented in Table S1. Field work effort was heavily focused on July and August.

Family	Common name	Scientific name	Island	Category	Months					
					Apr	May	June	July	Aug	Sep
Megapodiidae	Maleo* CR	<i>Macrocephalon maleo</i>	But	J					1	
Columbidae	Spotted Dove	<i>Spilopelia chinensis</i>	Tom	BB				1		
			Sul	J				1	1	
	Common Emerald Dove	<i>Chalcophaps indica</i>	But	J					1	
			Mun	J				1		
			Waw	J				1		
			Kab	J					2	
			Men	J					1	
			Wan	J					2	
			Kal	J						3
			Hog	J					1	
			Tom	J				1		
			Run	J						1
	Stephan’s Emerald Dove	<i>Chalcophaps stephani</i>	But	J				1		
	Black-naped Fruit Dove	<i>Ptilinopus melanospilus</i>	Kal	J					1	
			Hog	J						1
Apodidae	Glossy Swiftlet	<i>Collocalia esculenta</i>	But	N			1			
			Kab	BC					1	
Cuculidae	Lesser Coucal	<i>Centropus bengalensis</i>	Sul	J				1		
			But	J				2	2	
	Yellow-billed Malkoha*	<i>Rhamphococcyx calyorhynchus</i>	Mun	BC				1		
	Little Bronze Cuckoo	<i>Chrysococcyx minutillus</i>	Sul	J					1	
				BC				1		
	Plaintive Cuckoo	<i>Cacomantis merulinus</i>	But	BC					1	
Ciconiidae	Brush Cuckoo	<i>Cacomantis variolosus</i>	Sul	J				1		
	Milky Stork EN	<i>Mycteria cinerea</i>	Kab	N						1

Family	Common name	Scientific name	Island	Category	Months					
					Apr	May	June	July	Aug	Sep
Ardeidae	Striated Heron	<i>Butorides striata</i>	Sul	J					1	
			Waw	N				1		
Turnicidae	Barred Buttonquail	<i>Turnix suscitator</i>	But	J				1		
Tytonidae	Sulawesi Masked Owl*	<i>Tyto rosenbergii</i>	Kab	J						1
Strigidae	Speckled Boobook*	<i>Ninox punctulata</i>	But	J					1	
	Sulawesi Scops Owl*	<i>Otus manadensis</i>	But	BC					1	
Pandionidae	Eastern Osprey	<i>Pandion cristatus</i>	Oro	N					1	
Accipitridae	Barred Honey Buzzard*	<i>Pernis celebensis</i>	But	BB				1		
	Sulawesi Serpent Eagle*	<i>Spilornis rufipectus</i>	But	J				1		
	Rufous-bellied Eagle NT	<i>Lophotriorchis kienerii</i>	But	J				2		
	Black Eagle	<i>Ictinaetus malaiensis</i>	But	J				1		
	Spot-tailed Sparrowhawk*	<i>Accipiter trinotatus</i>	But	J				2		
	White-bellied Sea Eagle	<i>Haliaeetus leucogaster</i>	But	J				1		
			Sag	J			1			
	Brahminy Kite	<i>Haliastur indus</i>	But	J				1		
	Sulawesi Hawk-Eagle*	<i>Nisaetus lanceolatus</i>	But	J				2		
Alcedinidae	Sulawesi Dwarf Kingfisher*	<i>Ceyx fallax</i>	But	BC				1		
	Common Kingfisher	<i>Alcedo atthis</i>	Sul	J					1	
			Kab	J					1	2
	Ruddy Kingfisher	<i>Halcyon coromanda</i>	But	BC			1			
			Kab	J						1
	Green-backed Kingfisher*	<i>Actenoides monachus</i>	But	J				1		
	Collared Kingfisher	<i>Todiramphus chloris</i>	Sul	BC			1	2		
			But	J			1			
				BC				1		
			Hog	BC			2	1		
			Tom	BC			1			
			Bin	J				1		
				BC				2		
	Sacred Kingfisher	<i>Todiramphus sanctus</i>	Kal	J			3			
				BC			1			
			Hog	J				1	3	
				BC				1		
			Oro	J					1	

Family	Common name	Scientific name	Island	Category	Months					
					Apr	May	June	July	Aug	Sep
Picidae	Ashy Woodpecker*	<i>Mulleripicus fulvus</i>	But	N J				1	2	
Psittacidae	Pygmy Hanging Parrot*	<i>Loriculus exilis</i>	But	N			1			
Pittidae	Sulawesi Pitta*	<i>Erythropitta celebensis</i>	But	N			1			
Acanthizidae	Golden-bellied Gerygone	<i>Gerygone sulphurea</i>	Sul	J				3		
				BC				1	7	
			But	N					1	
				BC						1
Oriolidae	Black-naped Oriole	<i>Oriolus chinensis</i>	But	N			1			
			Mun	BC				1		
			Bin	J						1
			Run	BC						1
Campephagidae	White-shouldered Triller	<i>Lalage sueurii</i>	Kab	BC						1
	White-rumped Triller*	<i>Lalage leucopygialis</i>	Kal	J				1		
Artamidae	Ivory-backed Woodswallow*	<i>Artamus monachus</i>	But	N			1			
			Kab	BC					1	
Dicruridae	Hair-crested Drongo	<i>Dicrurus hottentottus</i>	Sul	BC					1	
			Kab	J						1
				BC					1	
Monarchidae	Island Monarch	<i>Monarcha cinerascens</i>	Men	N					1	
				J					5	
				BC					1	
			Wan	J				2	1	4
				BC				1	1	
			Oro	J						1
			Kal	J				2		2
				BC				3		
			Hog	J				3	1	
				BC					1	
			Tom	J		1		3		
				BC				1		
			Lin	J						6
				BC						1

Family	Common name	Scientific name	Island	Category	Months					
					Apr	May	June	July	Aug	Sep
	Pale blue Monarch *	<i>Hypothymis puella</i>	Bin	J						8
				BC						1
			Sul	J			2			
				BC				3		
			But	BC			1			
			Kab	BC				1		
Hirundinidae	Pacific Swallow	<i>Hirundo tahitica</i>	Sul	BC			1		2	
			But	N					1	
Pycnonotidae	Sooty-headed Bulbul (I)	<i>Pycnonotus aurigaster</i>	Sul	BC				1		
Zosteropidae	Lemon-bellied White-eye	<i>Zosterops chloris</i>	Sul	BC			6	8	24	
			But	N				1		
				BC				4	7	4
				BB					1	
			Mun	BC			7			
			Kab	J					1	3
				BC					10	6
			Run	BC						15
				BB	1					
			Wan	BC				3	6	
	Wakatobi White-eye *	<i>Zosterops flavissimus</i>		BB					1	
			Kal	J						2
				BC				9		28
				BB				1		
			Tom	J		1		1	1	
				BC				47	10	9
			Lin	BC						8
			Bin	J					1	
				BC					9	16
			Sul	BC				2	21	
	Pale-bellied White-eye *	<i>Zosterops consobrinorum</i>	But	BC				7	19	3
			Mun	J				2		
				BC			10	8		
			Kab	J			1			
				BC					17	3
			Wan	BC				2	8	
Pellorneidae	Sulawesi Babbler *	<i>Pellorneum celebense</i>	Sul	BC			1		9	
			But	J				9	1	

Family	Common name	Scientific name	Island	Category	Months					
					Apr	May	June	July	Aug	Sep
				BC				3	5	
				BB					1	
				Mun BC				2	1	
				Kab BC					3	3
Sturnidae	Metallic Starling	<i>Aplonis metallica</i>	Men	J					1	
	Moluccan Starling *	<i>Aplonis mysolensis</i>	Men	J					9	
	Short-tailed Starling	<i>Aplonis minor</i>	Mun	J			4			
			Bin	BC					1	
Turdidae	Red-backed Thrush * NT	<i>Geokichla erythronota</i>	Kab	J						1
				BC					2	
Muscicapidae	Pied Bush Chat	<i>Saxicola caprata</i>	Kab	BC						2
			Siu	BC						1
Dicaeidae	Yellow-sided Flowerpecker *	<i>Dicaeum aureolimbatum</i>	Sul	J			3		4	
				BC			1	3	12	
			But	N				1		
				J			1			
			Mun	BC					3	
				BC				1		
			Kab	J			2		2	
				BC					22	3
			Sul	BC				5	7	
				J				1	1	
	Grey-sided Flowerpecker *	<i>Dicaeum celebicum</i>	But	BC				7	3	
				BC			2	1		
			Mun	BC						
				J						2
			Siu	BC						1
				J						
			Kab	J			2		4	
				BC					4	
			Men	BC					3	
				J					1	
			Wan	BC				1	1	
				J						2
			Kal	J						1
				BC				1		1
			Hog	J						2
				BC				1		3
			Tom	J		1		1	2	

Family	Common name	Scientific name	Island	Category	Months					
					Apr	May	June	July	Aug	Sep
				BC					3	
Nectariniidae	Brown-throated Sunbird	<i>Anthreptes malacensis</i>	Sul	J					1	
				BC			1		7	
			But	N			1			
				J			5			
			BC	BC			9		1	
				BB			2			
			Mun	J			3			
				BC		1				
			Waw	J			4			
			Kab	J			4		1	
				BC					6	3
			Men	J					10	
				BC					14	
	Black Sunbird	<i>Leptocoma aspasia</i>	Sul	J			5		2	
				BC			3		11	
			But	BB			4			
				J			3		1	
			BC	BC			1		1	
				BB			3			
			Mun	J		1	1			
				Waw	J		1			
			Kab	BC					9	
				BB		1				
			Men	J					9	
				BC					6	
			BB	BB					2	
				J					2	
Olive-backed Sunbird	<i>Cinnyris jugularis</i>		Sul	BC			2		9	
				But	N		1	1		
			BC	J			2		1	
				BC			4		2	
			Siu	J						1
				BC						1
			Mun	BB		2				
				Waw	J		1			
			Kab	N		1				
				J		1		3		3
			BC	BC				9		5
				J					1	
			Men	BC					2	

Family	Common name	Scientific name	Island	Category	Months					
					Apr	May	June	July	Aug	Sep
	Crimson Sunbird	<i>Aethopyga siparaja</i>	Wan	BB					2	
				BC					1	
			Kal	J				1		1
				BC				3		7
			Hog	BB				3		
				J				2	2	3
				BC				7	10	4
			Tom	J				5	2	
				BC				3	5	2
			Lin	BC						12
			Bin	BC					8	3
			Run	J	3					1
				BC						1
			Sul	J					3	
				BC				6		
			But	J					2	
				BC				3		
			Kab	BC					3	
Estrildidae	Black-faced Munia*	<i>Lonchura molucca</i>	Sul	J				3	2	
				BC				1		
			But	J					4	
			Kab	J					5	1
				BC				1		
			Kal	J				1		
			Tom	J				4		
				BC				1		
				BB					1	
			Bin	J					1	
			Sul	J				2		
				J					3	1
			But	J						
	Chestnut Munia	<i>Lonchura atricapilla</i>	Sul	BC					2	
	Pale-headed Munia*	<i>Lonchura pallida</i>	But	J				1		
Passeridae	Eurasian Tree Sparrow	<i>Passer montanus</i>	Sul	J				1		
				J				1	1	
			Kab	BC					2	
				N			1			
			Kal	J					10	1
				BC					3	1
				BC						1

exhibiting breeding behaviour. For the 66 species recorded as proven or potentially breeding, evidence of breeding came from active nests for 17 species (19 records in total, providing strongest evidence of breeding for 17 species), from juveniles for 48 species (313 records in total, providing strongest evidence of breeding for 38 species), from observations of birds in breeding condition for 35 species (705 records in total, providing strongest evidence of breeding for nine species) and observations of birds displaying breeding behaviour for nine species (27 records in total, providing primary evidence of breeding for two species). Therefore, breeding was confirmed for 55 species (active nests and juveniles) with evidence of potential breeding (breeding condition and behaviour) for an additional 11 species. The 66 species with breeding records represent 32 families, but 73% of all records are from three families of small passerines common in the region: white-eyes (33%), sunbirds (28%) and flowerpeckers (11.5%) (Table 2). The majority of breeding records, and the greatest diversity of breeding birds, were recorded on the larger islands that were visited more regularly (mainland Sulawesi, Buton and Kabaena), likely reflecting greater habitat diversity, although a significant number of records were also collected on the Wakatobi Islands of Kaledupa and Tomia where field work was undertaken in multiple years (Table 1). Buton had the greatest species diversity of breeding records (Table 1), particularly of active nests (Table 2), doubtless reflecting the greater effort (Table 1) at intensively surveyed forest sites.

Individual accounts for Wallacean endemics (denoted *), Critically Endangered (CR) and Endangered species (EN) are presented below, covering 28 species in detail, with the remaining 38 species covered in Table 2 and Table S1.

MALEO *Macrocephalon maleo* * CR

Known to lay year-round, with a peak breeding season October–April in northern Sulawesi (Elliott & Kirwan 2020). Eggs have been reported from October in Lore Lindu National Park (NP), central Sulawesi (van den Berg & Bosman 1986), and May–July and November–January in Rawa Aopa Watumohai NP, south-east Sulawesi, with freshly dug burrows also seen in September (Wardill *et al.* 1998, Elliott & Kirwan 2020). Nests communally on beaches or volcanically heated soil, with many nesting sites now abandoned due to over-collection of eggs (Coates & Bishop 1997, Eaton *et al.* 2021). All known Buton breeding sites have experienced severe habitat degradation (Froese & Mustari 2019), and this species has recently been upgraded from Endangered to Critically Endangered due to ongoing degradation of its nesting sites (IUCN 2021). A juvenile male was recorded in agricultural land abutting Kakenauwe Natural Reserve in central Buton on 1 August 2014 by TEM & JN (Martin *et al.* 2017a) (Table 2, Table S1, ML 709329).

YELLOW-BILLED MALKOHA *Rhamphococcyx calyphorhynchus* *

Thought to breed mainly November–December (Payne 2020a). Nest undescribed. Although this species is not considered to be a brood parasite, a juvenile has been described as being fed by a Crimson Sunbird *Aethopyga siparaja* (Rozendaal & Dekker 1989). A single female in breeding condition was mist-netted in scrub habitat in south-east Muna on 29 June 2017 by DJK & NMM (Table 2, Table S1).

MILKY STORK *Mycteria cinerea* EN

Fragmented distribution in Cambodia, Malaysia, Sumatra, Java and south and south-east Sulawesi (Elliott *et al.* 2020). Peak breeding appears to be in the dry season, July–August, both on Sumatra and Java, although on Java there is some evidence of nesting in March and November. Its colonies suffer heavily from human predation (Eaton *et al.* 2021). Little is known about the small breeding population on mainland south-east Sulawesi (Wardill *et al.*

1998). On Kabaena there is one record, a pair seen at a nest near Sikeli in early September 1999 by DJK, at the edge of an urban area near mangrove fragments, and a larger area of intensive coconut plantations, although further evidence of breeding (incubation or feeding) was not confirmed (O'Connell *et al.* 2017) (Table 2, Table S1).

SULAWESI MASKED OWL *Tyto rosenbergii* *

Very little information on breeding (Bruce & Marks 2020); three single records from north Sulawesi seem to indicate a late year (September–December) nesting period (Fletcher 1998, Mauro & Drijvers 2000, Fitzsimons 2010). Juvenile plumage is undescribed. A pair was observed feeding a chick on the crossbar of a soccer goal frame in west Kabaena on 9 September 1999 by DJK (O'Connell *et al.* 2017) (Table 2, Table S1).

SPECKLED BOOBOOK *Ninox punctulata* *

Breeding undescribed, nestlings reported in September (Olsen *et al.* 2020). A single juvenile was observed on Buton on 8 August 2013 (Table 2, Table S1, ML 709319). It was found by locals abandoned at the base of a large tree in lowland tropical forest near Labundobundo village (having possibly fallen from its nest). It was brought to the village (where it was observed by TEM; Fig. 3A), and returned to the same location later the same day.

SULAWESI SCOPS OWL *Otus manadensis* *

Almost no information on breeding, with some indication that it may commence just before the start of the monsoon (Holt *et al.* 2020). A single male with a cloacal protuberance was mist-netted in central Buton in forest edge habitat on 26 August 1999 by DJK & NMM (Table 2, Table S1).

BARRED HONEY BUZZARD *Pernis celebensis* *

Breeding biology almost unknown. Single records of breeding in May and September (Coates & Bishop 1997, Clark *et al.* 2020b), with a lone clutch of two eggs known. The display flight involves talon-grappling and high circling flights. An individual was observed over a village in central Buton in July 2009 by NTK, in undulating display flight, holding its wings upwards at the highest point of each undulation, before dropping, then climbing again (Table 2, Table S1).

SULAWESI SERPENT EAGLE *Spilornis rufipectus* *

Few breeding data available. Fledged young have been reported in May, with laying estimated to occur in January–February (Clark & Kirwan 2020a). Its juvenile plumage is visually distinctive from the adult by a white rather than dark grey head (Eaton *et al.* 2021). A juvenile was recorded in lowland forest in Lambusango Forest Reserve, Buton, on 11 July 2009 by NTK (Table 2, Table S1).

SPOT-TAILED SPARROWHAWK *Accipiter trinitatus* *

No breeding data available (Clark *et al.* 2020a). Individual juveniles were recorded in central Buton in July 2003 by DJK & NMM, and Lambusango Forest Reserve, Buton, on 10 July 2009 (Fig. 3B, Table 2, Table S1). The latter was caught in a mist-net set for bats shortly after dusk and observed by TEM.

SULAWESI HAWK-EAGLE *Nisaetus lanceolatus* *

Few breeding data available (Clark & Kirwan 2020b). One nest recorded in August on Sulawesi (White & Bruce 1986), and season thought to be May–August, based on fledged

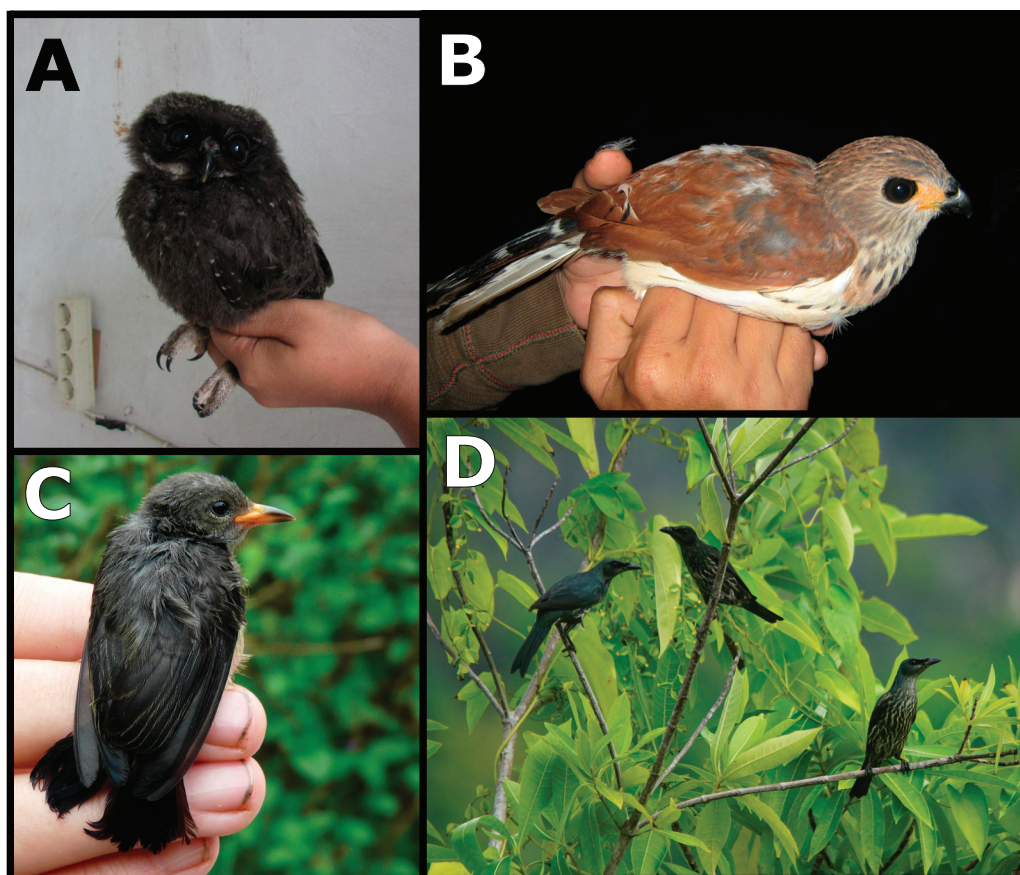


Figure 3. Juveniles of: (A) Speckled Boobook *Ninox punctulata*, Buton, August 2013 (Thomas E. Martin), (B) Spot-tailed Sparrowhawk *Accipiter trinotatus*, Buton, July 2009 (Thomas E. Martin), (C) Grey-sided Flowerpecker *Dicaeum celebicum*, Kabaena, August 2003 (David J. Kelly and Nicola M. Marples) and (D) Moluccan Starling *Aplonis mysolensis*, Menui, August 2017 (Joseph Monkhouse)

young also seen in the latter month (Ferguson-Lees & Christie 2001). Two juveniles observed during our study; one in Labundobundo village (central Buton) on 22 July 2014 by TEM, and one in Buton Utara Reserve (north Buton) on 12 July 2018 by PGA (Table 2, Table S1, ML 204689311).

SULAWESI DWARF KINGFISHER *Ceyx fallax**

Breeding biology poorly known (Kirwan *et al.* 2021). Reported to lay in August–November (Watling 1983, van den Berg & Bosman 1986, White & Bruce 1986) at Lore Lindu NP, with an active nest confirmed in October (Watling 1983). A pair (including a gravid female) was mist-netted together in Kakenauwe Natural Reserve, Buton, on 6 July 2014 by JN (Table 2, Table S1).

GREEN-BACKED KINGFISHER *Actenoides monachus**

Few breeding data available. Probably lays in February–March, with a recently fledged young in April (Kirwan *et al.* 2020). A single juvenile was recorded on 8 August 2016 in Buton Utara Nature Reserve by Lupi Yulian Sumanto (Martin *et al.* 2017a) (Table 2, Table S1, ML 709818).

ASHY WOODPECKER *Mulleripicus fulvus* *

Limited observations indicate nesting in March–August (Winkler & Christie 2020) and a fledgling was seen in December in Lore Lindu NP in December (D. D. Putra unpubl. data). Two juveniles were recorded on 5 August 2007 in central Buton by DJK & NMM. Additionally, on 12 July 2018 a male and female were observed together by PGA at a large hollow in a tree on the edge of Kakenauwe Natural Reserve, Buton (Fig. 4A). The cavity entrance was c.10 cm in circumference. This was probably an active nest, although the birds were flushed by a passing car before this could be confirmed (Table 2, Table S1).

PYGMY HANGING PARROT *Loriculus exilis* *

Few breeding data available. Known to breed in February and August and to nest in holes in dead palms (White & Bruce 1986, Collar *et al.* 2020), with reports of breeding from Lore Lindu NP in October–November (D. D. Putra unpubl. data). Possible nesting behaviour in this species (and a possible active nest) was observed in Kakenauwe village, Buton, on 10 July 2018 by PGA. A pair was seen on this date repeatedly entering a cavity atop a derelict wooden-cored concrete utility pillar in the village (Fig. 4C). The cavity entrance was c.25 cm in circumference and broadly round in shape. This behaviour was subsequently noted several further times over the next three weeks, although by late July only the male was

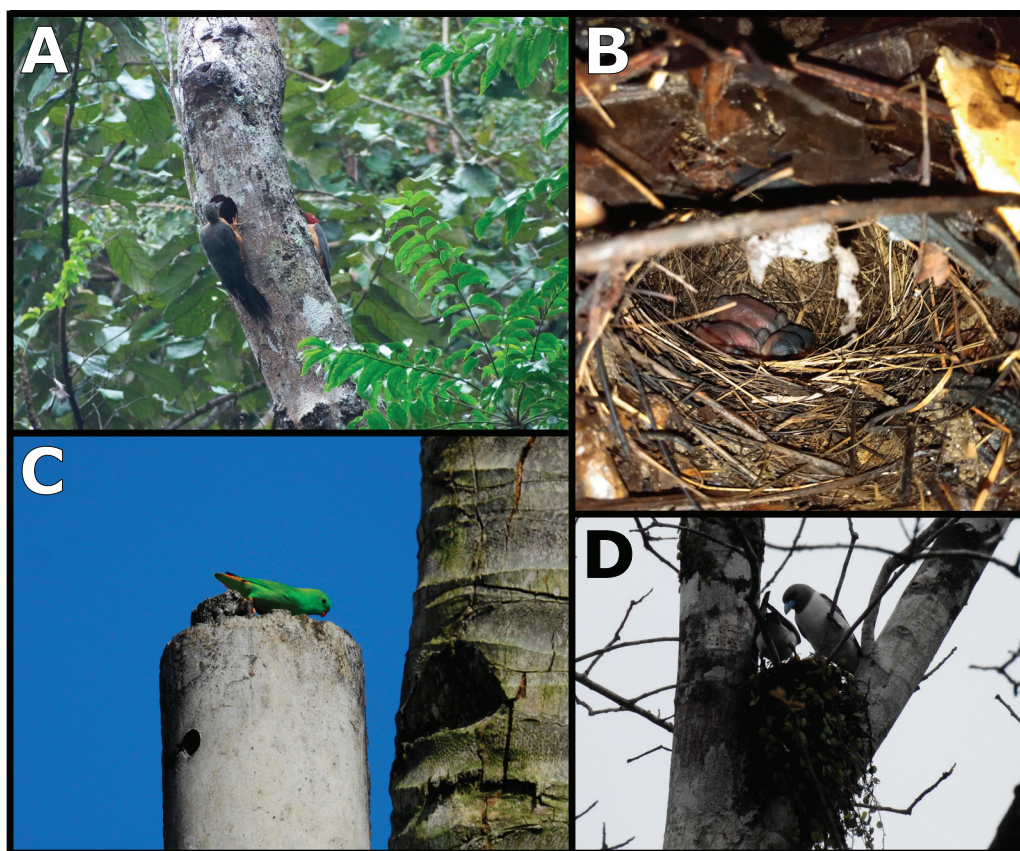


Figure 4. Photos of observed/assumed nesting attempts by: (A) Ashy Woodpecker *Mulleripicus fulvus*, Buton, July 2018 (Panji G. Akbar), (B) Sulawesi Pitta *Erythropitta celebensis*, Buton, June 2016 (Arini Wijayanti), (C) Pygmy Hanging Parrot *Loriculus exilis*, Buton, July 2018 (Panji G. Akbar) and (D) Ivory-backed Woodswallow *Artamus monachus*, Buton, June 2018 (Panji G. Akbar)

seen entering and exiting the cavity, with another bird (presumably the female) calling from inside it. During these observations, an all-male flock of five Pygmy Hanging Parrots was also seen regularly in a coconut tree near the pillar, which the (presumably nesting) pair appeared to tolerate (Table 2, Table S1). These observations demonstrate the species can probably breed in anthropogenically modified habitats, and artificial wood-core pillars may offer alternative nesting sites to the palms previously noted as being used by the species.

SULAWESI PITTA *Erythropitta celebensis* *

Few breeding data available. Singing males on territory in January–March, with the breeding season probably stretching to at least October, nestlings recorded in early March (White & Bruce 1986), and juveniles in September, late November and early January (del Hoyo *et al.* 2020b). One nest was described as sited in a hole dug in the slope of a riverbank, constructed of twigs and leaves, and bound with cotton or hairy plant materials, and held a clutch of two eggs. An active nest was recorded during this study in lowland rainforest at Buton Utara Nature Reserve, Buton, on 26 June 2016 by AW (Fig. 4B, Table 2, Table S1). An adult was unintentionally flushed off the nest, which held two chicks and was a cup-like structure constructed of entwined grasses and other vegetation.

WHITE-RUMPED TRILLER *Lalage leucopygialis* *

Few breeding data available. Thought to breed in May and construct an open-cup nest (Taylor 2020). A juvenile male was seen on Kaledupa on 17 July 2010 by DJK & NMM (Table 2, Table S1).

IVORY-BACKED WOODSWALLOW *Artamus monachus* *

Very few breeding data available. Two active nests previously reported, both in late July (Rowley *et al.* 2020). A single female in breeding condition was mist-netted in central Kabaena on 21 August 2003 by DJK & NMM. Additionally, a pair was seen building a nest (with 3–4 additional birds perched in a nearby tree) in agricultural land in north Buton on 30 June 2018 by PGA. This nest was c.15 m above ground, in a forked branch of a *Spondias dulcis* tree, using nesting material that appeared to be leaves of a *Pyrrosia* fern (Fig. 4D). The nest was c.15 cm in diameter. Regular visits indicated the female was on the nest on 1 July, and continued to be observed there until 15 July (Table 2, Table S1).

PALE BLUE MONARCH *Hypothymis puella* *

Recently split from the widespread Black-naped Monarch *H. azurea* based on deep genetic divergence (Fabre *et al.* 2012, Gill *et al.* 2021), with limited breeding data available. Season possibly June–September (del Hoyo *et al.* 2020a), with a neat cup nest constructed of twigs, plastered with spider webs and other fine material. Nest usually located several metres above ground in a tree fork. During mist-netting surveys by DJK & NMM, individuals in breeding condition were recorded on 22 August 2003 in central Kabaena and 6 July 2012 in north Buton, with three in breeding condition at the south-eastern tip of mainland Sulawesi in late August 2007, in scrub and farmland. In addition, two juveniles were seen during transect surveys at the south-eastern tip of mainland Sulawesi on 10 July 2016 by DOC (Table 2, Table S1).

PALE-BELLIED WHITE-EYE *Zosterops consobrinorum* *

Few breeding data available, with a single nest found in early August and an adult feeding a juvenile in October (van Balen 2020). Numerous individuals in breeding condition and juveniles were recorded in scrub and farmland during mist-netting surveys in July–

September throughout the study period on Sulawesi, Buton, Muna and Kabaena by DJK & NMM (Table 2, Table S1).

WAKATOBI WHITE-EYE *Zosterops flavissimus* *

Recently split from the widespread Lemon-bellied White-eye *Z. chloris* based on divergence in plumage, genetics, morphology and song (O'Connell *et al.* 2019c), but no published breeding data (van Balen 2021). Numerous individuals in breeding condition, exhibiting breeding behaviour and juveniles were recorded on the main Wakatobi Islands by DJK, NMM & SBK, during mist-netting and transects in July–September, throughout the study period, in scrub, mangrove and farmland. In addition, a juvenile was observed on 5 May 2013 on Tomia (Table 2, Table S1).

WANGI-WANGI WHITE-EYE undescribed *Zosterops* *

A single-island endemic whose formal description has not been completed (O'Connell *et al.* 2020, 2021) with no published breeding data. A total of ten in breeding condition was mist-netted in scrub and farmland during July–August on Wangi-wangi, mainly in 2003, 2005, 2010 and 2012 by DJK & NMM (Table 2, Table S1).

SULAWESI BABBLER *Pellorneum celebense* *

Breeds April–December (White & Bruce 1986), with a clutch of two eggs in a cup of dead leaves (Collar & Robson 2020). Numerous individuals in breeding condition, exhibiting breeding behaviour and juveniles were recorded during mist-netting surveys in July–September, throughout the study period, in scrub, forest, forest edge and farmland on Sulawesi, Buton, Muna and Kabaena, by DJK, NMM & WS (Table 2, Table S1).

MOLUCCAN STARLING *Aplonis mysolensis* *

No published data on season, but observed nesting colonially in tree holes with usually 15–50 individuals per colony (Coates & Bishop 1997, Craig & Feare 2020). The Menui population is an outlier to the species' core range in the Moluccas (Iqbal & Tepu 2014, Monkhouse *et al.* 2018). A total of nine juveniles was recorded in areas of scrub on Menui in early August 2017 by DJK, JM, DOC & NMM (Fig. 3D, Table 2, Table S1, ML 204689311).

RED-BACKED THRUSH *Geokichla erythronota* * NT

No published breeding data (Collar 2020). Two individuals in breeding condition were mist-netted in central Kabaena in mid-August 2003, whilst a single juvenile was mist-netted there in forest edge habitat on 14 September 1999, all by DJK & NMM (Table 2, Table S1).

YELLOW-SIDED FLOWERPECKER *Dicaeum aureolimbatus* *

Active nests were previously reported on Togian Island in June and August, and fledglings in November; juveniles were reported in late August to early September on Sangihe (Cheke & Mann 2020a). Numerous individuals in breeding condition and juveniles were recorded during mist-netting surveys in July–September, throughout the study period, in scrub and farmland on Sulawesi, Buton, Muna and Kabaena by DJK & NMM (Table 2, Table S1). An active nest was found at a beach near Labundobundo village, Buton, on 9 July 2014 by JN. It was suspended from a branch in a tall dead tree, set apart from the mangrove vegetation that otherwise predominated along the relevant stretch of coast.

GREY-SIDED FLOWERPECKER *Dicaeum celebicum* *

No published data on breeding season (Cheke & Mann 2020b). Numerous individuals in breeding condition and juveniles (Fig. 3B) were recorded in scrub and farmland during mist-netting surveys by DJK & NMM in July–September, throughout the study period, on Sulawesi, Buton, Muna, Kabaena, Menui and on all of the Wakatobi Islands (except Binongko, where the species is rare, and Runduma, where it is absent; O'Connell *et al.* 2020). In addition, a juvenile was seen on Tomia on 9 May 2013 by SBAK (Table 2, Table S1).

BLACK-FACED MUNIA *Lonchura molucca* *

Said to breed at the end of the rainy season and early dry season. Breeding was observed in July–September and January at Lore Lindu in central Sulawesi (Watling 1983), with nests in March–June on Flores. Juveniles seen in May–July on Sumba and in June on Timor (Noske 2003, Payne 2020b). Numerous individuals in breeding condition, exhibiting breeding behaviour and juveniles were recorded in scrub and farmland during mist-netting and transects by DJK, SBAK & NMM in July–September, throughout the study period, on Sulawesi, Buton, Kabaena, Kaledupa, Tomia and Binongko (Table 2, Table S1).

PALE-HEADED MUNIA *Lonchura pallida* *

Reported to breed year-round in central Sulawesi (Watling 1983, Payne 2020c). A juvenile was recorded in farmland in central Buton on 14 July 2012 by DJK & NMM (Table 2, Table S1).

Discussion

Our results provide an extensive summary of breeding data for bird species in south-east Sulawesi based on nearly 20 years of field work. The data we present improve understanding of the basic natural history of Wallacean species. This paper provides extensive observations of breeding by 66 bird species. These include rare observations of breeding behaviour and nest structure for several poorly studied endemics, including Pygmy Hanging Parrot, Sulawesi Pitta and Ivory-backed Woodswallow. In addition, we present important evidence of breeding activity by one Critically Endangered and one Endangered species. The Milky Stork nesting attempt recorded on Kabaena sheds light on potential breeding areas for the poorly understood Sulawesi population of this widespread but rare species. The record of a juvenile Maleo confirms that this species is both extant and breeding on Buton (as of 2014). Our observations of breeding condition in Wangi-wangi White-eye provide the first data regarding life history parameters in this single-island endemic, which could be classified as Endangered due to its restricted range (O'Connell *et al.* 2019c, 2021).

Our recording period was focused on the start of the dry season on Sulawesi, which is the peak breeding period on nearby Flores (Verheijen 1964). Breeding of birds in Wallacea is strongly seasonal and influenced by precipitation, but how this affects the timing of breeding varies on different islands (Verheijen 1964, Linsley *et al.* 1998, Noske 2003). As the impacts of climate change progress, the region is likely to experience more extreme seasonality, with wetter wet seasons and drier dry seasons (Chou *et al.* 2013). Therefore, filling gaps in our knowledge of avian breeding biology on Sulawesi is vital to provide baseline data on timing of breeding, informing how these species might respond to anthropogenic habitat and climate change in this part of Wallacea (Lees *et al.* 2020).

Our assessment of avian breeding biology in south-east Sulawesi has several clear limitations. First, our survey methods were not designed to maximise the recording of breeding behaviour, with the focus instead being on biodiversity (Buton) and speciation

(all other islands covered by TCD & UHO). Therefore, nest searches and behavioural observations were not prioritised, and our data are very much opportunistic in nature. The majority of our records of breeding behaviour involve common small passerines that are easily trapped using mist-nets (Table 2, Table S1), but this contribution should be considered a descriptive account of breeding behaviour, rather than a strict quantification of such activity at each field site. Second, field work was largely concentrated in late June–August and consequently provides only a snapshot of potential seasonality. These limitations make it difficult to infer phenological trends for the species in our dataset. Additionally, tropical birds tend to have longer breeding seasons than those in temperate regions, and timing of breeding can vary significantly between trophic guilds (Stutchbury & Morton 2001). Our study region is also geologically and ecologically complex (Whitten *et al.* 2002, Nugraha & Hall 2018), and this may cause the breeding biology of bird species to differ even on neighbouring islands. For example, the islands of Kabaena and Wawonii have distinctly different underlying geology (ultramafic) and associated plant communities (Galey *et al.* 2017, Trethowan *et al.* 2020, Ó Marcaigh *et al.* 2021). The entire study area is also strongly influenced by El Niño–Southern Oscillation cycles, which exert influence on breeding probability and phenology (Duursma *et al.* 2018, Smart *et al.* 2021). Thus, breeding patterns on different islands, and in extreme El Niño/La Niña years, may produce distinctive patterns that our data are unable to reveal.

It is also interesting to note which species are missing from our dataset, particularly in the mature lowland rainforest of Buton Island. Many species considered relatively common by Martin *et al.* (2012), e.g. Green Imperial Pigeon *Ducula aenea*, Knobbed Hornbill *Rhyticeros cassidix* and Sulawesi Hornbill *Rhabdotorrhinus exarhatus*, lack a single observation of breeding behaviour despite nearly 20 years of field work. It is acknowledged that surveying the demographics of tropical birds is often difficult (Robinson *et al.* 2018), but the absence of many common species from our dataset highlights that obtaining breeding data for tropical birds is also problematic unless targeted methods (see Fierro-Calderón *et al.* 2021) are employed. Even these may be inhibited in ‘canopy-heavy’ ecosystems such as on Buton, where many species rarely come close to ground level (Martin *et al.* 2017b). Indeed, the many conspicuous gaps in our dataset indicate that difficulties in data acquisition may be an important contributing factor to the dearth of information for Wallacean birds (Noske 2017). However, the lack of experienced observers in the region certainly is also a key limitation, although initiatives such as Atlas Burung Indonesia are beginning to remedy this shortfall (Taufiqurrahman *et al.* 2016).

Overall, however, this paper fills a number of knowledge gaps, particularly with respect to the breeding biology of 27 Wallacean endemics, many of which have few or no previous nesting data. This study also highlights the importance of collating opportunistic natural history data in poorly studied areas, even when assembling such data is not the primary focus. Like Noske (2017), we encourage other researchers in Wallacea (and other under-studied regions) to publish summaries of their breeding data, to further knowledge of avian breeding biology in this unique biodiversity hotspot.

Acknowledgements

We are grateful to Kementerian Riset Teknologi Dan Pendidikan Tinggi (RISTEKDIKTI) and the Indonesian Institute of Science (LIPI) for providing the necessary permits and approvals for this study throughout the field work period. We also thank Operation Wallacea for providing us with logistical support while working in Indonesia. We thank the many Operation Wallacea staff and volunteers who assisted with survey work, and members of the local communities in south-east Sulawesi for their hospitality. Finally, we thank Richard Noske, Colin Trainor, and BINCO for helpful comments on an earlier draft of the manuscript. DOC & TEM collated records and led the writing. All authors provided records and contributed to revising and improving the manuscript.

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Supplementary Information

Table S1. All individual records of bird breeding activity collected in south-east Sulawesi, providing date, location details, and additional notes.