

Phylogeography of three endemic birds of Maratua Island, a potential archive of Bornean biogeography

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Abstract. Maratua is an oceanic island ca. 50 km off the east coast of Borneo and home to several endemic taxa of birds and mammals. To determine the phylogeographic relationships of three of Maratua’s most distinctive avian endemics—a shama *Copsychus stricklandii barbouri*, a bulbul *Pycnonotus atriceps hodiernus*, and a monarch *Hypothymis azurea aeria*—we compared their mitochondrial ND2 sequences with those of putatively closely related Southeast Asian populations. We found that Maratua’s shama and bulbul are substantially differentiated from populations on Borneo and elsewhere in Southeast Asia, whereas Maratua’s monarch is not. The shama’s phylogeographic tree indicates a sister relationship between *C. s. barbouri* and *C. s. stricklandii* of northeast Borneo, both of which have white crowns (ND2 distance ~2%). These two taxa, in turn, are >3% divergent from *C. malabaricus* populations, which have black crowns. The relative morphological and genetic similarity of *C. s. barbouri* and *C. s. stricklandii* suggests that *C. stricklandii* had a broader distribution in eastern Borneo in the mid-Pleistocene and that *C. s. stricklandii* has more recently moved or been restricted to its current position in northeast Borneo. Maratua has thus acted as a biogeographic “museum”, preserving evidence of *C. stricklandii*’s former distribution. The Maratuan *P. atriceps* is about equidistant genetically from other *P. atriceps* populations. It is distinguished by an overall grey body plumage, whereas *P. atriceps* elsewhere is mostly yellow (with grey morphs appearing only rarely). The universality of grey birds on Maratua is likely the result of a founder effect. The Maratuan monarch’s genetic similarity to the mainland Bornean population suggests either that it is a recent invader or that substantial gene flow occurs between Borneo and Maratua in this species. The genetic and morphological distinctiveness of the shama and bulbul are adequate to consider them both as full species.

Keywords. *Copsychus malabaricus*, *Copsychus stricklandii*, *Hypothymis azurea*, phylogeography, *Pycnonotus atriceps*, rare morphs

INTRODUCTION

Maratua is a small oceanic island ca. 50 km east of east Kalimantan, Indonesian Borneo (Fig. 1). It is home to only 35 resident land-bird species, one monkey, and two rats. Among its depauperate vertebrate fauna, however, are some endemic taxa with substantial potential to inform biogeographers about the history of species distributions and diversification on Borneo. Maratua is close enough to Borneo

to attract occasional terrestrial immigrants, but isolated enough to act as a “museum”, preserving the morphology and genetic character of faunas that inhabited eastern Borneo long ago (Fooden, 1995). In this respect Maratua resembles, on a smaller scale, the Mentawai Islands off southwestern Sumatra (see Fig. 2B), which have preserved a surprising array of early Sundaic vertebrates, including an endemic gibbon and a proboscis-like monkey (Wilting et al., 2012).

The first collector to visit Maratua was Harry Cusheir Raven in 1912–1913. He obtained specimens of all of the island’s terrestrial bird and mammal species for the US National Museum (Miller, 1913; Riley, 1930; Kellogg, 1944; Deignan, 1959). In 1926, E. P. Mjöberg made the second collection, this time for Harvard University (Bangs & Peters, 1927). The curators who handled these early specimens were impressed by the distinctiveness of Maratua’s birds and mammals, and they named several as new species (Miller, 1913; Bangs & Peters, 1927; Kellogg, 1944). Most of these names have survived to modern times as subspecific epithets: viz., *Macaca fascicularis tua* (Long-tailed Macaque) (Fooden, 1995), *Rattus tiomanicus mara* (Malayan Field Rat) (Musser & Califa, 1982), *Aerodramus salangana maratua* (Mossy-nest Swiftlet), *A. fuciphagus perplexus* (Edible-nest Swiftlet), *Pycnonotus atriceps hodiernus* (Black-headed

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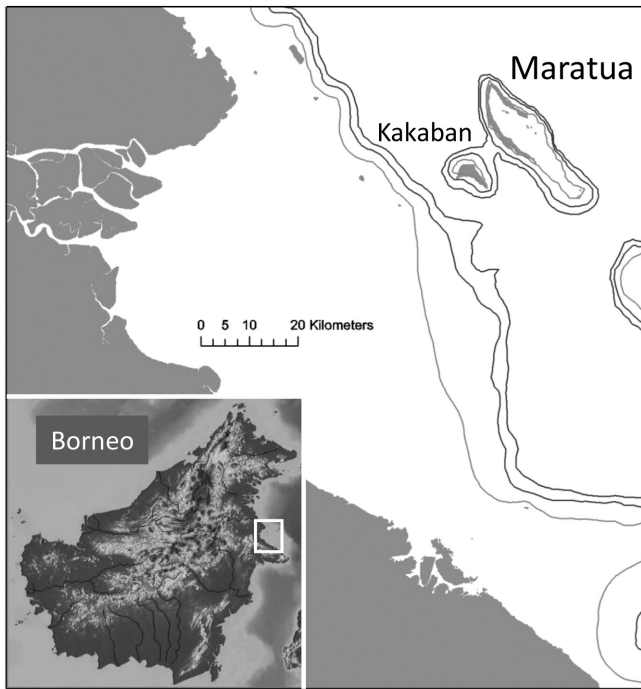


Fig. 1. Location of Maratua Island off the east coast of Borneo (inset). Bathymetric contours are, from shallowest to deepest, -40 m, -120 m, and -200 m. Water depth data are from **GEBCO One Minute Grid**—a global one arc-minute grid; data updated in 2008 (http://www.gebco.net/data_and_products/gridded_bathymetry_data/). Inset from www.maps-for-free.com.

Bulbul), *Copsychus stricklandii barbouri* (White-crowned Shama), *Hypothymis azurea aerea* (Black-naped Monarch), *Anthreptes malacensis mjobergi* (Brown-throated Sunbird), and *Aplonis panayensis alipodis* (Asian Glossy Starling) (Smythies, 1999; Gill & Donsker, 2014). Early investigators also recognised that endemism on Maratua is due to the island's permanent isolation beyond the "100 fathom" (180 m) mark of the Sunda continental shelf (Bangs & Peters, 1927; Riley, 1930; Kellogg, 1944). In fact, the island was probably never connected to mainland Borneo, not even during the lowest sea levels associated with glacial events (Voris, 2000; Bintanja et al., 2005).

The likely long-term isolation of Maratua raises the question of whether its endemic populations are differentiated genetically, as well as morphologically, from populations on "mainland" Borneo and elsewhere in Southeast Asia. To investigate this possibility, we compared mitochondrial gene sequences of three species or species groups with endemic representatives on Maratua: *Copsychus malabaricus*/*C. stricklandii*, *Pycnonotus atriceps*, and *Hypothymis azurea*. We selected these taxa because their Maratua populations are morphologically distinct from those on adjacent Borneo and because they were the only three taxa described as full species in the original descriptions of the island's birds (Bangs & Peters, 1927).

Background on Maratua Island. Maratua lies ca. 50 km east of east Borneo in the Derawan Islands, Berau Regency, East Kalimantan Province, Indonesia (Fig. 1). It is a raised volcanic atoll of thick coralline limestone, which supports

a relatively rich limestone-soil forest. The 2376 ha island is shaped like a thin horseshoe (0.3–1.4 km wide) surrounding a large lagoon (ca. 29.5 by 6.5 km), which is open on the southeastern side. The island reaches 110 m at its highest point (Kuenen, 1947; Tomascik et al., 1997; Becking et al., 2011). Kuenen (1947) believed the island developed as part of a barrier reef at the edge of the continental shelf. As the shelf gradually submerged and the coast of Borneo moved westward, the island became increasingly isolated. At a later stage, the atoll was raised by tectonic activity, which prevented all but the southern end from being eroded away. Most biological research on Maratua has focused on the rich marine life in the surrounding coral reefs, the lagoon, and some anchialine pools (Ng & Tomascik, 1994; Tomascik et al., 1997; de Voogd et al., 2009; Becking et al., 2011). Since the original collections of vertebrates 100 years ago, little work has been done on its terrestrial fauna.

When referring to Maratua, early writers put the island east of the 100 fathom (180 m) line (Bangs & Peters, 1927; Riley, 1930). This observation is important because 180 m is beyond the edge of the Sunda continental shelf when it is exposed by eustatic sea level drops during extreme Pleistocene glacial events (Voris, 2000; Bintanja et al., 2005). At this depth, Maratua is a permanently isolated oceanic island. However, the isolation of Maratua is not as extreme as implied by simple bathymetric measurement. As noted by Fooden (1995:90): "[Maratua] is separated from Borneo by a deep trench (>180 m) that is 17 km wide; the water gap is narrowed by the presence of a stepping-stone island, Kakaban (area ca. 5 km²), which intervenes in the middle of the trench." Indeed, as shown in Fig. 1, Kakaban Island almost connects Maratua to shallow water to the west. When sea level descended, for example, to 125 m below its current depth during the last glacial maximum (Bintanja et al., 2005), the distance from Maratua-Kakaban to Borneo was much reduced. This does not mean, however, that coastal habitats during periods of low sea level were appropriate for potentially dispersing forest inhabitants.

Review of the study taxa. Maratua's shama, bulbul, and monarch are each members of widespread Southeast Asian species or species groups (Fig. 2). Although originally described as full species (Bangs & Peters, 1927), all three were reduced from species to subspecies without comment by Chasen (1935) in his summary of Sundaic birds. However, Chasen apparently did not realise the degree of Maratua's isolation, because he described this oceanic island as part of Borneo along with continental islands, such as the Natunas, the Karimatas, Labuan, the Mantanani, Banggi, Balambangan, Malawali, and Pulau Laut (Chasen, 1935: xi). Nor had he likely seen specimens of the three taxa, which were in American museums (Phillipps & Phillipps, 2011: 348).

Until recently, White-rumped Shama (*Copsychus malabaricus*) was a polytypic species comprising 12 subspecies extending from India, across Indochina to Hainan, and throughout Sundaland (Collar, 2005). Recently, however, two of its subspecies, Andaman Shama (*C. m. albiventris*) and White-

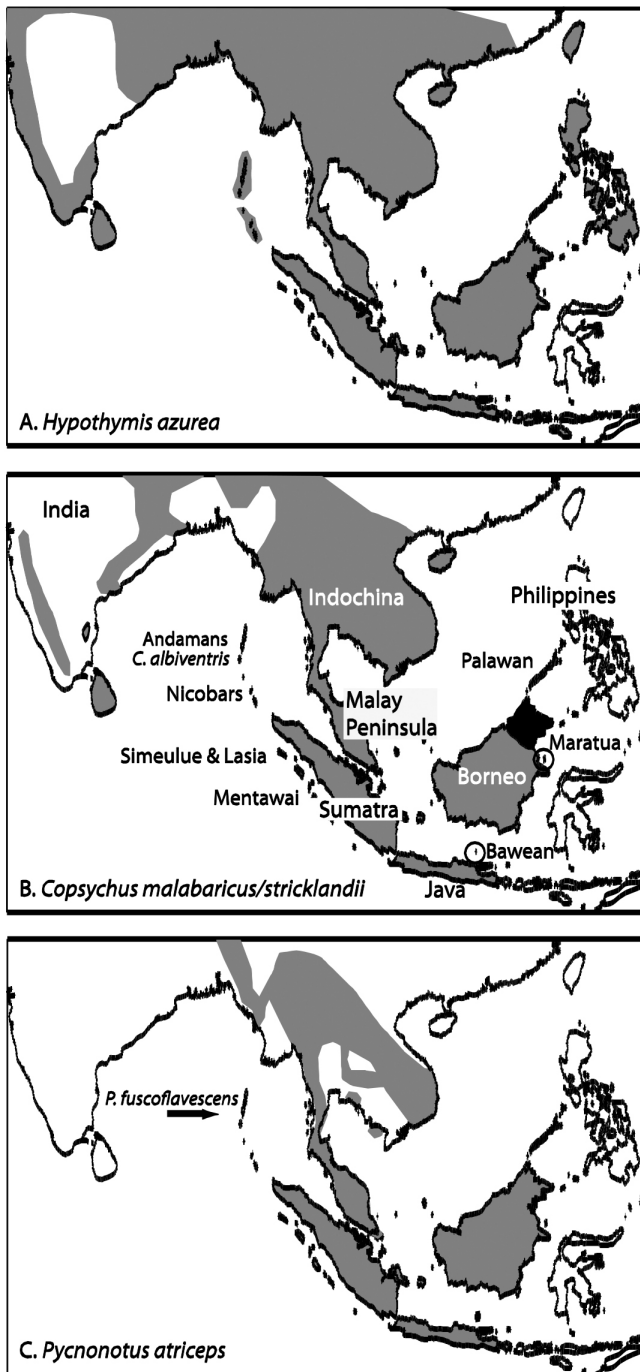


Fig. 2. Distribution (dark areas) of the three species or species groups whose Maratua populations were examined in this study (Collar, 2005; Fishpool & Tobias, 2005; Coates et al., 2006). In (B), the distribution of *Copsychus stricklandii stricklandii* in northeast Borneo is indicated in black.

crowned Shama (*C. m. stricklandii*), were raised to full species, with *C. stricklandii* comprising subspecies *C. s. stricklandii* of northeastern Borneo and *C. s. barbouri* of Maratua (Gill & Donsker, 2014). On Borneo, *C. malabaricus* occupies most of the island, but is replaced in the northeast (essentially Sabah) and on Maratua by *Copsychus stricklandii* (Fig. 3). Because of their similarity and parapatric distribution (Collar, 2004; Gawin, 2014), we refer to *C. malabaricus* and *C. stricklandii* as a “species group” in this paper. The two taxa differ most noticeably in crown feathering; *C. stricklandii* has white crown feathers, whereas *C. malabaricus*

has black crown feathers. The white-crowned *C. s. barbouri* is larger than *C. s. stricklandii*, and its tail is entirely black (Bangs & Peters, 1927; Collar, 2004). In phylogeographic comparisons of *C. malabaricus/stricklandii* populations in this paper, we used the closely related *C. niger* of Palawan as outgroup (Lim et al., 2010).

Black-headed Bulbul (*Pycnonotus atriceps*) ranges from eastern India through Indochina and across all of Sundaland to Palawan and Bali. It is divided into four subspecies. *P. a. atriceps* occurs on the Asian mainland and large continental islands, whereas the other subspecies are restricted to smaller islands: *P. a. hyperemnus* on Simeulue, Nias, and Mentawai of western Sumatra, *P. a. baweanus* on Bawean Island in the Java Sea, and *P. a. hodiernus* on Maratua (Fishpool & Tobias, 2005). As in *C. malabaricus*, the Andaman population was previously considered a subspecies (Dickinson, 2003), but is now recognised as a full species, *P. fuscoflavescens* (Fishpool & Tobias, 2005; Gill & Donsker, 2014). The Maratua subspecies has the shiny black head and distinctive blue iris of *P. a. atriceps*, but instead of a yellow body, its plumage is entirely a mixture of dark grey and black. Maratua birds are also larger than *P. a. atriceps* (Bangs & Peters, 1927). Elsewhere in *P. atriceps* range, grey plumaged individuals occur as rare morphs (Dickinson & Dekker, 2002; Wells, 2007; pers. comm.), except on Bawean Island in the Java Sea, where grey individuals are more common than yellow (Hoogerwerf, 1966; van Balen, 1986; Dickinson & Dekker, 2002). The sister group of *P. atriceps* is a clade consisting of the Puff-backed Bulbul (*P. eutilotus*) and Black-and-white Bulbul (*P. melanoleucos*) (Moyle & Marks, 2006). We use *P. eutilotus* as outgroup for phylogeographic comparisons in this paper.

Black-naped Monarch (*Hypothymis azurea*) is distributed from India to Taiwan and south to the Lesser Sundas. It is a highly polymorphic species with 23 subspecies (Gill & Donsker, 2014) that vary mainly in shade and extent of blue feathering and degree of crest and breast markings (Coates et al., 2006). The Maratua population (*H. a. aeria*) differs from all other subspecies by lacking a distinctive black occipital patch and by possessing a narrower, less velvety, black crescent on its throat (Bangs & Peters, 1927; Rand, 1970). The closest relatives of *H. azurea* are Sulawesi’s *H. puella* (Sulawesi) and the Philippine’s *H. coelestis* and *H. helenae* (Fabre et al., 2012). We use the latter two species as outgroups in this study.

MATERIAL AND METHODS

We obtained DNA of *Copsychus stricklandii barbouri*, *Pycnonotus atriceps hodiernus*, *Hypothymis azurea aeria* from toe pads of Mjöberg’s study skins: two individuals of each from the Museum of Comparative Zoology, Harvard University (Table 1). We obtained DNA of other taxa from preserved tissues provided by tissues collections or by downloading DNA sequences from GenBank (Table 1). In all (Table 1), our comparisons included: for shamas—16 individuals of *Copsychus malabaricus* (three subspecies), eight *C. stricklandii* (two subspecies), and one *C. niger*

Table 1. Specimens compared in this study.

Species ¹	Subspecies	Downloaded GenBank or Specimen Numbers ²	Locality
<i>Copsychus malabaricus</i>	<i>interpositus</i>	HQ010913.1	Vietnam: Quang Nam
<i>Copsychus malabaricus</i>	<i>interpositus</i>	HQ010914.1	Myanmar: Sagaing
<i>Copsychus malabaricus</i>	<i>interpositus</i>	HQ010921.1	Myanmar: Sagaing
<i>Copsychus malabaricus</i>	<i>interpositus</i>	HQ010923.1	Myanmar: Sagaing
<i>Copsychus malabaricus</i>	<i>interpositus</i>	HQ010925.1	Myanmar: Sagaing
<i>Copsychus malabaricus</i>	<i>suavis</i>	HQ010908.1	Malaysia: Sarawak
<i>Copsychus malabaricus</i>	<i>suavis</i>	HM120190.1	Malaysia: Sarawak
<i>Copsychus malabaricus</i>	<i>suavis</i>	HQ010909.1	Malaysia: Sarawak
<i>Copsychus malabaricus</i>	<i>suavis</i>	LSUMNS B58587	Malaysia: Sarawak
<i>Copsychus malabaricus</i>	<i>suavis</i>	LSUMNS B73734	Malaysia: Sarawak
<i>Copsychus malabaricus</i>	<i>suavis</i>	HQ010911.1	Malaysia: Sarawak
<i>Copsychus malabaricus</i>	<i>tricolor</i>	HQ010912.1	Malaysia: Terengganu
<i>Copsychus malabaricus</i>	<i>tricolor</i>	HQ010933.1	Malaysia: Terengganu
<i>Copsychus malabaricus</i>	<i>tricolor</i>	HM120189.1	Malaysia: Johor
<i>Copsychus malabaricus</i>	<i>tricolor</i>	HQ010934.1	Malaysia: Johor
<i>Copsychus malabaricus</i>	<i>tricolor</i> (?)	HQ010910.1	Singapore
<i>Copsychus stricklandii</i>	<i>stricklandii</i>	HQ010915.1	Malaysia: Sabah
<i>Copsychus stricklandii</i>	<i>stricklandii</i>	HQ010917.1	Malaysia: Sabah
<i>Copsychus stricklandii</i>	<i>stricklandii</i>	HQ010920.1	Malaysia: Sabah
<i>Copsychus stricklandii</i>	<i>stricklandii</i>	LSUMNS B73450	Malaysia: Sabah
<i>Copsychus stricklandii</i>	<i>stricklandii</i>	LSUMNS B73454	Malaysia: Sabah
<i>Copsychus stricklandii</i>	<i>stricklandii</i>	LSUMNS B73488	Malaysia: Sabah
<i>Copsychus stricklandii</i>	<i>barbouri</i>	MCZ 235961	Indonesia: Maratua Is.
<i>Copsychus stricklandii</i>	<i>barbouri</i>	MCZ 235968	Indonesia: Maratua Is.
<i>Copsychus niger</i> *		HM120197.1	Philippines: Palawan
<i>Hypothymis azurea</i>	<i>aeria</i>	MCZ 235920	Indonesia: Maratua Is.
<i>Hypothymis azurea</i>	<i>aeria</i>	MCZ 235927	Indonesia: Maratua Is.
<i>Hypothymis azurea</i>	<i>azurea</i>	HQ010959.1	Philippines: Luzon
<i>Hypothymis azurea</i>	<i>azurea</i>	KUNHM 13983	Philippines: Camiguin Sur
<i>Hypothymis azurea</i>	<i>azurea</i>	HQ010958.1	Philippines: Mindanao
<i>Hypothymis azurea</i>	<i>azurea</i>	HQ010956.1	Philippines: Palawan
<i>Hypothymis azurea</i>	<i>azurea</i>	HQ010957.1	Philippines: Palawan
<i>Hypothymis azurea</i>	<i>prophata</i>	HQ01942.1	Malaysia: Terengganu
<i>Hypothymis azurea</i>	<i>prophata</i>	HQ010961.1	Malaysia: Sarawak
<i>Hypothymis azurea</i>	<i>prophata</i>	HQ010943.1	Malaysia: Sabah
<i>Hypothymis azurea</i>	<i>prophata</i>	HQ010944.1	Malaysia: Sabah
<i>Hypothymis azurea</i>	<i>prophata</i>	HQ010945.1	Malaysia: Sabah
<i>Hypothymis azurea</i>	<i>prophata</i>	HQ010946.1	Malaysia: Sabah
<i>Hypothymis azurea</i>	<i>prophata</i>	HQ010947.1	Malaysia: Sabah
<i>Hypothymis azurea</i>	<i>prophata</i>	HQ010939.1	Malaysia: Sarawak
<i>Hypothymis azurea</i>	<i>prophata</i>	HQ010940.1	Malaysia: Sarawak
<i>Hypothymis azurea</i>	<i>prophata</i>	HQ010941.1	Malaysia: Sarawak
<i>Hypothymis azurea</i>	<i>prophata</i>	HQ010950.1	Malaysia: Sarawak
<i>Hypothymis azurea</i>	<i>prophata</i>	HQ010951.1	Malaysia: Sarawak
<i>Hypothymis azurea</i>	<i>prophata</i>	HQ010948.1	Malaysia: Johor
<i>Hypothymis azurea</i>	<i>prophata</i>	HQ010960.1	Indonesia: Sumatra
<i>Hypothymis azurea</i>	<i>styani</i>	HQ010938.1	Vietnam: Quang Nam
<i>Hypothymis azurea</i>	<i>styani</i>	KUNHM 10293	China: Guangxi
<i>Hypothymis azurea</i>	<i>styani</i>	HQ010949.1	Myanmar: Sagaing
<i>Hypothymis azurea</i>	<i>styani</i>	HQ010952.1	Myanmar: Sagaing
<i>Hypothymis azurea</i>	<i>styani</i>	HQ010953.1	Myanmar: Sagaing
<i>Hypothymis azurea</i> ³		EF052695	Thailand
<i>Hypothymis coelestis</i> *	<i>coelestis</i>	KUNHM 19062	Philippines: Mindanao
<i>Hypothymis coelestis</i> *	<i>coelestis</i>	KUNHM 19063	Philippines: Mindanao
<i>Hypothymis helenae</i> *	<i>personata</i>	KUNHM 12536	Philippines: Camiguin

Species ¹	Subspecies	Downloaded GenBank or Specimen Numbers ²	Locality
<i>Hypothymis helena</i> *	<i>helena</i>	KUNHM 20342	Philippines: Luzon
<i>Pycnonotus atriceps</i>	<i>atriceps</i>	LSUMNS B36320	Malaysia: Sabah
<i>Pycnonotus atriceps</i>	<i>atriceps</i>	LSUMNS B57464	Malaysia: Sabah
<i>Pycnonotus atriceps</i>	<i>atriceps</i>	LSUMNS B58500	Malaysia: Sarawak
<i>Pycnonotus atriceps</i>	<i>atriceps</i>	KUNHM 12317	Malaysia: Sarawak
<i>Pycnonotus atriceps</i>	<i>atriceps</i>	KUNHM 12633	Philippines: Palawan
<i>Pycnonotus atriceps</i>	<i>atriceps</i>	KUNHM 12639	Philippines: Palawan
<i>Pycnonotus atriceps</i>	<i>atriceps</i>	KUNHM 12642	Philippines: Palawan
<i>Pycnonotus atriceps</i>	<i>atriceps</i>	GU112683.1	Philippines: Palawan
<i>Pycnonotus atriceps</i>	<i>hodiernus</i>	MCZ 235903	Indonesia: Maratua Is.
<i>Pycnonotus atriceps</i>	<i>hodiernus</i>	MCZ 235907	Indonesia: Maratua Is.
<i>Pycnonotus eutilotus</i> *	monotypic	DQ402236.1	Malaysia: Sabah

¹Names follow the classification of Gill and Donsker (2014). *Outgroup taxa.

²“Downloaded GenBank numbers” refers to sequences from previous studies: DQ (Moyle & Marks, 2006), EF (Fuchs et al., 2007), GU (Oliveros & Moyle, 2010), HM (Lim et al., 2010), and HQ (Lim et al., 2011). “Specimen numbers” refers to material (preserved tissues or museum skins) used to produce new sequences in this study. GenBank numbers of sequences produced by this study are KP208752–KP208775. Museum abbreviations: AMNH, American Museum of Natural History, New York, New York; KUNHM University of Kansas Natural History Museum, Lawrence, Kansas; LSUMNS, Louisiana State University Museum of Natural Science, Baton Rouge, Louisiana; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts; NMNH, US National Museum of Natural History, Washington, D.C.; UWBM, University of Washington Burke Museum, Seattle, Washington.

³Exact collecting locality and subspecies not specified (Fuchs et al., 2007).

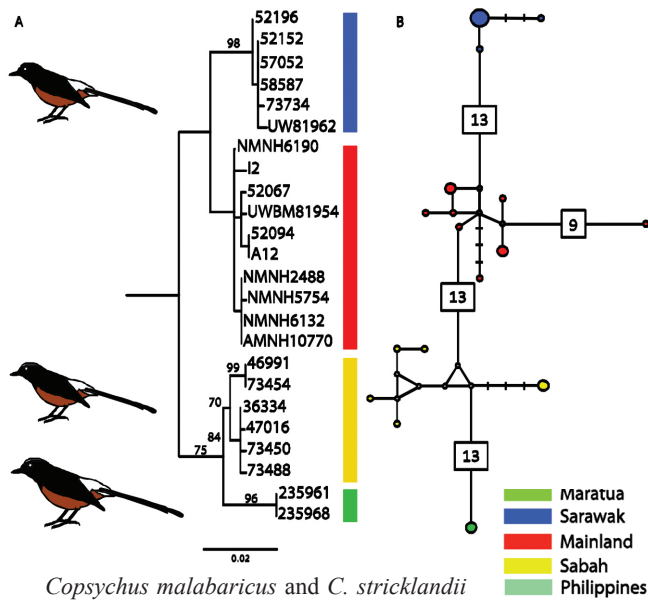


Fig. 3. ND2 phylogeographic tree and haplotype network of populations of White-rumped Shama, *Copsychus malabaricus* (top figure), and White-crowned Shama, *C. stricklandii* (bottom two figures). A, Maximum likelihood bootstrap tree. Numbers by branches are bootstrap support (70% and above). Labels are specimen numbers; B, Haplotype network. Circle size indicates proportion of individuals with a given haplotype, and cross hatches indicate nucleotide changes (larger numbers of changes are noted in square boxes).

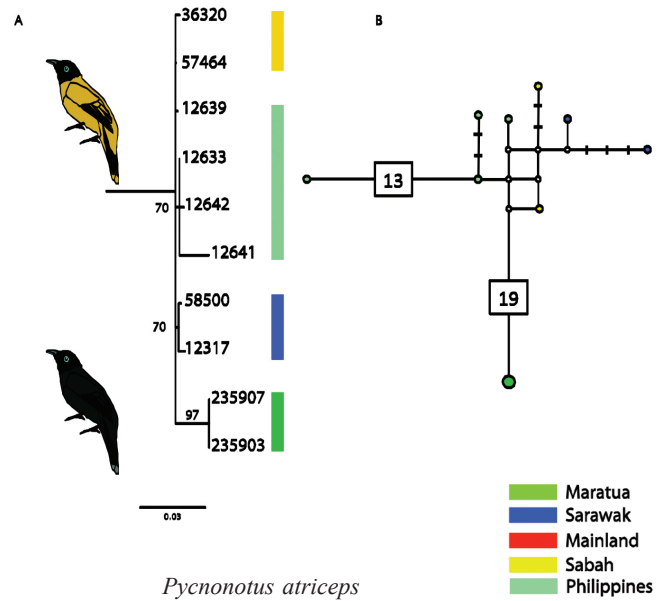


Fig 4. ND2 phylogeographic tree and haplotype network of Black-headed Bulbul (*Pycnonotus atriceps*) populations. A, Maximum likelihood bootstrap tree. Numbers by branches are bootstrap support (70% and above). Labels are specimen numbers. B, Haplotype network. Circle size indicates proportion of individuals with a given haplotype, and cross hatches indicate nucleotide changes (larger numbers of changes are noted in square boxes).

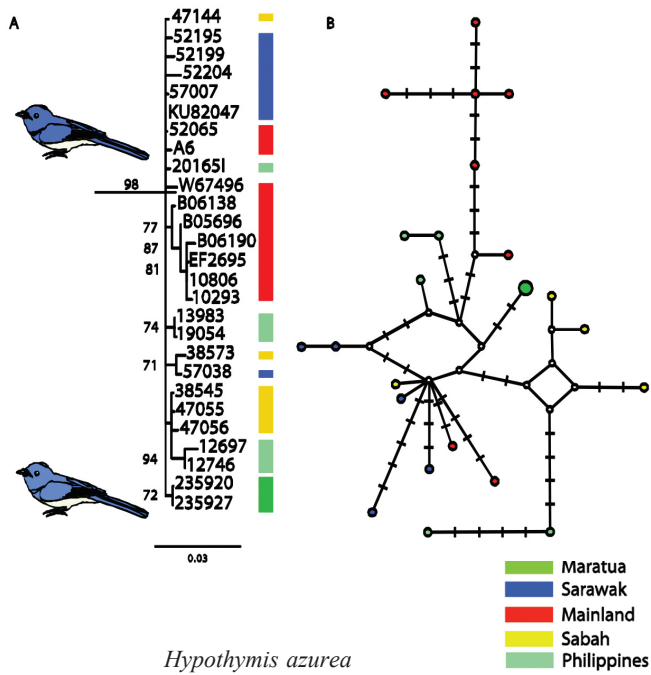


Fig. 5. ND2 phylogeographic tree and haplotype network of Black-naped Monarch (*Hypothymis azurea*) populations. A, Maximum likelihood bootstrap tree. Numbers by branches are bootstrap support (70% and above). B, Haplotype network. Circle size indicates proportion of individuals with a given haplotype, and cross hatches indicate nucleotide changes (larger numbers of changes are noted in square boxes).

as outgroup; for bulbuls—10 *Pycnonotus atriceps* (two subspecies) and one *P. eutilotus* as outgroup; and for monarchs—27 *Hypothymis azurea* (at least four subspecies) and two each of *H. coelestis* and *H. helenae* as outgroups.

DNA was extracted from preserved tissues using a Qiagen DNeasy kit following the manufacturer’s protocol. To extract toe-pad DNA, we used a Qiagen QIAmp DNA kit and applied the methods of Moyle et al. (2011). We sequenced mtDNA NADH dehydrogenase subunit 2 (ND2) using alternate methods depending on the DNA source. For amplification of DNA from preserved tissues, we used primers L5215 (Hackett, 1996) and HTrpC (STRI), as per Lim et al. (2010). DNA was amplified in 25 µL reactions using Qiagen HotStarTaq plus DNA Polymerase kit. For amplification toe-pad DNA, we designed five pairs of internal primers from the preserved-tissue sequences (Table 2). These primers were used to amplify 250–300 nucleotide sections of the ND2 gene, which were then concatenated. All post-PCR products were sent to Beckman Coulter Genomics for sequencing. Complementary strands were aligned using Geneious version R6 by Biomatters (www.geneious.com). GenBank numbers of tissues sequenced in this study are KP208752–KP208775.

Population genetic statistics were computed using Arlequin 3.5 (Excoffier & Lischer, 2010). Phylogeographic trees of

Table 2. Primers used to amplify and sequence DNA from study specimen toe pads.

Name	Species	Primer Sequence
R1	<i>Pycnonotus atriceps</i>	GCAATGGCTGAGGTCAGGAT
F2	<i>Pycnonotus atriceps</i>	TAACCCACCCAGTGTGCATGC
R2	<i>Pycnonotus atriceps</i>	CCTAGGGCGGTGGATAGGAT
F3	<i>Pycnonotus atriceps</i>	CCCATCACTACTTACTTGCATGGC
R3	<i>Pycnonotus atriceps</i>	GGTAGGAATCCAGTTAATGGGG
F4	<i>Pycnonotus atriceps</i>	CTCCTACTAACCTACTCTCCC
R4	<i>Pycnonotus atriceps</i>	GGTTAGAGGTGTGTGGTGGG
F5	<i>Pycnonotus atriceps</i>	CGCCTTGCATACTGCGCAAC
R1	<i>Copsychus malabaricus/stricklandii</i>	AGTGGAATGGGGCTAGTCCT
F2	<i>Copsychus malabaricus/stricklandii</i>	AACCTGTCTACAGCATGCC
R2	<i>Copsychus malabaricus/stricklandii</i>	ATCCTCCTAGGGCTGTGGAG
F3	<i>Copsychus malabaricus/stricklandii</i>	CCCCACACTACTAGTTACCATAGC
R3	<i>Copsychus malabaricus/stricklandii</i>	TTAAGGGCGAGGAATACGGC
F4	<i>Copsychus malabaricus/stricklandii</i>	CCTACAGCCCCAAATTAGCC
R4	<i>Copsychus malabaricus/stricklandii</i>	ATTGTTGCTGCTGGGGCTAT
F5	<i>Copsychus malabaricus/stricklandii</i>	ACAGGCTTCCCTCCCCAAATG
R1	<i>Hypothymis azurea</i>	TGAGCCTTGCAAGACTTCTG
F2	<i>Hypothymis azurea</i>	TGCCTGATCCTAACAGCAGC
R2	<i>Hypothymis azurea</i>	CTATTCATCCTCCTAGGGCAG
F3	<i>Hypothymis azurea</i>	CCTCGCACTCACTCAACCCAAC
R3	<i>Hypothymis azurea</i>	GAGAAATACGGCTGCAGTGATTAGGG
F4	<i>Hypothymis azurea</i>	CTACAACCCAAAGCTCACCC
R4	<i>Hypothymis azurea</i>	GCCTAGCAGGGATAGCAGTG
F5	<i>Hypothymis azurea</i>	CAGGACATAGCCCCTACAGC

each species or species group were estimated by maximum likelihood (ML) using Garli 2.0 (Zwickl, 2006). Nodal support was tested with 200 bootstrap replicates. Appropriate ML substitution models were selected based on the Akaike Information Criterion implemented in jModelTest 2 (Guindon & Gascuel, 2003; Darriba et al., 2012). The best-fit substitution model for *P. atriceps* was TIM2+G, for *C. stricklandii*, GTR+G, and for *H. azurea*, TrN+I. Bootstrap consensus trees and bootstrap values were calculated using SUMTREES (Sukumaran & Holder, 2010). Uncorrected proportional genetic distances among populations within each species or species group were generated using Mega5 using both complete and pairwise divergence (Tamura et al., 2011; Fregin et al., 2012). Median joining haplotype networks were constructed with the program Network v. 4.6 (Bandelt et al., 1999) to visualise geographic relationships within each species.

RESULTS

ND2 sequence lengths of individuals in the three species ranged from 841 to 1,041 nucleotides. *Copsychus malabaricus/stricklandii* had 65 (6.2%) variable sites and 51 (4.9%) parsimony-informative sites, *Pycnonotus atriceps* 192 (18.4%) variable sites and 25 (2.4%) parsimony-informative sites, and *Hypothymis azurea* 64 (6.1%) variable sites and 29 (2.8%) parsimony-informative sites. We found 18 haplotypes in 24 individuals of *C. malabaricus/stricklandii*, 9 haplotypes in 10 individuals of *P. atriceps*, and 26 haplotypes in 27 individuals of *H. azurea* (Table 3). Average divergence values (Table 4) between Maratua and the next closest populations were: *Copsychus stricklandii barbouri* to *C. s. stricklandii* (Sabah) 2%, *Pycnonotus atriceps hodiernus* to *P. a. atriceps* (Sabah) 2.5%, *Hypothymis azurea aerea* to *H. a. prophata* (Sabah) 0.6%.

ML trees and haplotype networks depicted three different phylogeographic patterns in the three species. The *Copsychus malabaricus/stricklandii* tree (Fig. 3A) had the most hierarchical structure, with the Maratua population (*C. s. barbouri*) as sister to the Sabah population (*C. s. stricklandii*), and this clade as distinct from *C. malabaricus*. Within *C. malabaricus*, the Sarawak population (*C. m. suavis*) was distinct from the Malay Peninsula and Indochinese populations. The *Copsychus malabaricus/stricklandii* haplotype network largely mirrored the phylogeographic tree (Fig. 3B). One individual from the mainland (red color in Fig. 3B) is nine steps removed from the other mainland taxa. This individual (Table 1; GenBank no. HQ010910.1) is from Singapore (no specimen) and possibly had been imported from elsewhere in SE Asia. The *Pycnonotus atriceps* tree and network (Fig. 5) indicated that Maratua individuals are well differentiated from members of other populations, whereas the other populations showed little phylogeographic structure. Three of the Philippine individuals formed a marginally distinct clade, while a fourth Philippine individual was largely differentiated from the others. The Maratua population of *Hypothymis azurea* was not distinct phylogeographically from the other sampled populations (Fig. 6). Although several branches leading to small groups

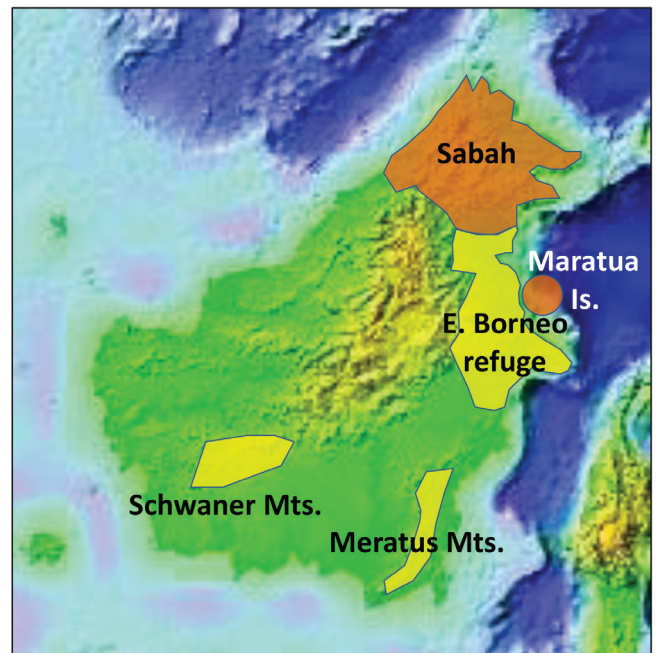


Fig. 6. Borneo map showing possible Pleistocene rainforest refuges (yellow and orange) and the modern distribution of *Copsychus stricklandii* (orange).

of individuals had moderate support, there was no clear hierarchical structure in the tree or network.

DISCUSSION

Biogeography and plumage patterns. All three of our study taxa, *Copsychus malabaricus/stricklandii*, *Pycnonotus atriceps*, and *Hypothymis azurea*, are widely distributed in Southeast Asia and have morphologically distinct populations on isolated islands. It is tempting, therefore, to suggest that some of the plumages found on oceanic islands such as Maratua may represent morphology of an early wave of Sundaic colonisers, whereas those on continental islands represent later arriving colonisers. This possibility was raised by Fooden (1995), who suggested that dark pelaged Long-tailed Macaques (*Macaca fascicularis*) that occur on oceanic islands surrounding Sundaland, including Maratua (*M. f. tua*), are relicts of early inhabitants of the region. These dark forms were presumed to have been replaced on all continental islands by *M. f. fascicularis*, a lighter pelaged, possibly more recent invader (also see Abegg & Thierry, 2002). However, plumage variation across our three study taxa is complex, and in only one case, the shama, does the plumage pattern occurring on Maratua provide insight into a possible ancestral distribution. Morphology and genetic variation in the Maratuan monarch and bulbul, although perhaps not indicating ancestral distributions, still provide logical explanations for the evolution of their plumages on Maratua.

We suggest the following scenario for the biogeographic history of *Copsychus stricklandii* populations. The white crown of *C. stricklandii* appears to have developed in an eastern Bornean rainforest refuge in the early Pleistocene. At the time of this development, *C. stricklandii*'s ancestors

Table 3. Sampling and diversity values for populations: n = number of individuals, h = number of haplotypes, var = number of variable sites, Hd = haplotype diversity, SD = standard deviation and π = nucleotide diversity.

Population	n	h	var	Hd \pm SD	$\pi \pm$ SD
<i>Pycnonotus atriceps</i>					
Maratua	2	1	0	0	0
Sarawak	2	2	4	1.0 \pm 0.50	0.0038 \pm 0.0043
Sabah	2	2	4	1.0 \pm 0.50	0.0039 \pm 0.0043
Philippines	4	4	18	1.0 \pm 0.18	0.0086 \pm 0.0060
mean	2.5	2.25	6.5	0.75	0.004075
<i>Hypothymis azurea</i>					
Maratua	2	1	0	0	0
Sabah	5	5	17	1.0 \pm 0.13	0.0078 \pm 0.0051
Sarawak	6	6	20	1.0 \pm 0.10	0.0072 \pm 0.0045
Mainland	9	9	25	1.0 \pm 0.05	0.0314 \pm 0.0172
Philippines	5	5	18	1.0 \pm 0.13	0.0340 \pm 0.0210
mean	5.4	5.2	16	0.8	0.01608
<i>Copsychus malabaricus / stricklandii</i>					
Maratua	2	1	0	0	0.0050 \pm 0.0033
Sabah	6	6	9	1.0 \pm 0.10	0.0012 \pm 0.0011
Sarawak	6	3	3	0.93 \pm 0.12	0.0057 \pm 0.0034
Mainland	10	8	11	0.96 \pm 0.06	0.0050 \pm 0.0033
mean	6	4.5	5.75	0.72	0.003

would have been allopatric relative to the black-crowned *C. malabaricus*, which was most likely restricted to western Sundaland (and perhaps western Borneo) in the early to mid-Pleistocene. This scenario is based on a variety of evidence. The genetic distance between the white- and black-crowned shamas is substantial (>3%; Table 3; Lim et al., 2010; Lim et al., 2011), especially in view of the overall similarity of these taxa (Collar, 2004). Also, the two shamas exhibit limited hybridisation where they currently come in contact near the Sabah border (Gawin, 2014). (This is known for the Malaysian side of Sabah; hybridisation has not been studied on the Indonesian side.) Furthermore, allopatric divergence in the two shama populations accords well, spatially and temporally, with phylogeographic evidence of Pleistocene subdivisions in several other groups of vertebrates caused by presumed dry habitat in central Sundaland (Bird et al., 2005; Wilting et al., 2012). These other groups include not only birds (Lim et al., 2011), but also reptiles, amphibians, and several orders of mammals (e.g., Brandon-Jones, 1998; Gorog et al., 2004; Meijaard & Groves, 2004; Wilting et al., 2012). We also know that the rainforest required by *C. stricklandii* existed continuously in the mountains and some coastal areas of eastern Borneo since the Miocene, even when other parts of Sundaland were drier (Morley, 2012; Morley & Morley, 2013). The locations of refuges for *C. malabaricus* in western Sundaland, however, are less well established (Fig. 6). The Mentawai Islands and mountains of Sumatra are the most likely places for refugial rainforest because of orographic precipitation in those locations (e.g., Brandon-Jones, 1998; Wilting et al., 2012). Among possible western refuges on Borneo, the Schwaner Mountains and associated lowlands were suggested for lowland rodents (Gorog et al., 2004).

In respect to Maratua, the mid-Pleistocene refuge of white-crowned shamas was likely near the Bornean coast adjacent to the island, and it would have provided the stock for the Maratua's invasion (Fig. 6). The separation of *C. s. barbouri* (Maratua) from *C. s. stricklandii* (mainland Borneo) occurred early enough for the two populations to accrue a genetic distance of ca. 2% (Table 3). Currently, *C. s. stricklandii* is restricted to northeastern Borneo (essentially Sabah). Its positional shift was probably in response to a redistribution of refugial rainforest, as evidenced by the co-occurrence of many vertebrate rainforest endemics in Sabah (Sheldon et al., 2001; Sheldon et al., 2009; Gawin et al., 2014). More recently, presumably following expansion of rainforest in central Sundaland (Cannon et al., 2009), *C. malabaricus* moved from western Borneo/Sundaland across Borneo to meet *C. stricklandii*, leading to their parapatric distribution roughly in alignment with Sabah's border.

Pycnonotus atriceps hodiernus, the other genetically distinct Maratuan taxon, appears to have had a different biogeographic history than the shama, at least in respect to its plumage evolution. Individuals with grey plumage like those on Maratua appear as rare morphs in various parts of the species' range, although none has been recorded on Borneo (Smythies, 1999; Dickinson & Dekker, 2002; Wells, 2007; pers. comm.). Apart from Maratua, the only location in Sundaland where grey individuals are common is Bawean Island in the Java Sea (Fig. 3B; Hoogerwerf, 1966; van Balen, 1986; Dickinson & Dekker, 2002). Why dark morphs exist in Sundaland has always puzzled ornithologists. They occur not only in *P. atriceps*, but also in some other Sundaic rainforest passerines (e.g., *Terpsiphone paradisi* and *Philentoma pyrhoptera*). Studies of yellow versus black plumages in bananquits (*Coereba flaveola*), which appear

Table 4. Uncorrected proportional ND2 divergence values (complete deletion of missing nucleotides/pairwise deletion of missing nucleotides).

Locality	Maratua	Sabah	Sarawak	Palawan
<i>Copsychus malabaricus/stricklandii</i>				
Sabah	0.02/0.02			
Sarawak	0.036/0.036	0.029/0.030		
Malay Pen.	0.032/0.032	0.023/0.023	0.02/0.02	
<i>Pycnonotus atriceps</i>				
Sabah	0.023/0.023			
Sarawak	0.025/0.025	0.005/0.005		
Palawan	0.026/0.026	0.008/0.008	0.009/0.009	
<i>Hypothymis azurea</i>				
Sabah	0.007/0.008			
Sarawak	0.008/0.008	0.007/0.008		
Palawan	0.009/0.008	0.011/0.011	0.012/0.011	
Mainland	0.010/0.009	0.012/0.012	0.012/0.011	0.013/0.012

on different islands in the Caribbean, have shown that the difference is based on a single nucleotide substitution influencing melanin synthesis (Theron et al., 2001). In other cases, grey and yellow plumages are directly related by relative levels of lutein concentration (Brush & Johnson, 1976; Remsen & Graves, 1995). Thus, plumage change in *P. atriceps* is probably the result of a relatively simple recessive genetic difference, which is expressed on Maratua and Bawean because of founder effect and drift. In larger *P. atriceps* populations, the recessive grey morph would be swamped by the dominant yellow plumage.

We have not examined the phylogeography of the Bawean population of *P. atriceps*, but Bawean has a different history than Maratua in respect to isolation and habitat. Unlike Maratua, Bawean is a continental island that would have been attached to Borneo and Java during multiple glacial events, most recently during the last glacial maximum (ca. 18 ka). As such, its bulbul population would have been subject to substantial gene flow. However, unlike eastern Borneo, Bawean lies in a region that would have been drier and probably devoid of rainforest at various times in the Pleistocene (Bird et al., 2005; Morley, 2012). Thus, its bulbul population may have been subject to multiple bottlenecks, invasions, drift, and other small population effects, allowing gray plumage to predominate.

Maratua's *Hypothymis azurea* population, although possessing a somewhat different plumage than the population on adjacent Borneo, is genetically similar not only to its Bornean neighbors but to all other populations we examined (Table 4, Fig. 6). Its lack of genetic distinctiveness would seem to reflect *H. azurea*'s substantial dispersal capabilities. Its morphological distinctiveness on Maratua and elsewhere, resulting in 23 morphologically defined subspecies, would suggest a highly plastic plumage.

Taxonomy. We have not evaluated the degree of gene flow influencing Maratua's populations of shama and bulbul, which

would provide a better assessment of their status as biological species than our mitochondrial dataset (Lim et al., 2014). Nevertheless, the genetic and morphological distinctiveness of *Copsychus stricklandii barbouri* and *Pycnonotus atriceps hodiernus* on Maratua are enough to call them phylogenetic species, and probably even biological species.

Conservation. The Maratuan Shama has become noticeably rarer in the last few years. The Indonesian government is developing the island as a tourist destination and has recently built an airport. The influx of construction workers has apparently resulted in the capture of many birds for the pet trade, causing what was once an abundant forest species to become rare and in danger of extirpation (QP, personal observation). Even without this immediate danger, Maratua's shama and bulbul deserve special protection because of their genetic distinctiveness, inherently small population sizes, and interesting evolutionary trajectories.

ACKNOWLEDGEMENTS

We especially thank Harvard University (Scott Edwards and Jeremiah Trimble) for providing toe pads of Maratua specimens for this study. The American Museum of Natural History, Louisiana State Museum of Natural Science, University of Kansas Natural History Museum, U.S. National Museum of Natural History, and University of Washington Burke Museum also kindly provided tissues for the study. We are also very grateful to the Malaysian Chief Minister's Department and the governments of Sabah and Sarawak for permission to undertake and help with research in Malaysian Borneo and to the government of the Philippines for permission to work there. The manuscript was improved from comments by Clare Brown, Ryan Burner, Frank Rheindt, Subir Shakya, David Wells, and an anonymous reviewer. This research was cleared by LSU's institutional animal care and use facility and funded by NSF DEB-0228688, NSF DEB-1241059, Coypu Foundation of Louisiana, Louisiana State University, and Universiti Malaysia Sarawak.

LITERATURE CITED

- Abegg C & Thierry B (2002) Macaque evolution and dispersal in insular south-east Asia. *Biological Journal of the Linnean Society*, 75: 555–76.
- Bandelt H-J, Forster P & Röhl A (1999) Median-joining networks for inferring intraspecific phylogenies. *Molecular Biology and Evolution*, 16: 37–48.
- Bangs O & Peters JL (1927) Birds from Maratua Island, off the east coast of Borneo. *Occasional Papers of the Boston Society of Natural History*, 5: 235–42.
- Becking LE, Renema W, Santodomingo NK, Hoeksema BW, Tuti Y & de Voogd NJ (2011) Recently discovered landlocked basins in Indonesia reveal high habitat diversity in anchialine systems. *Hydrobiologia*, 677: 89–105.
- Bintanja R, van de Wal SW & Oelemans J (2005) Modelled atmospheric temperatures and global sea levels of the past million years. *Nature*, 437: 125–128.
- Bird MI, Taylor D & Hunt C (2005) Palaeoenvironments of insular Southeast Asia during the last glacial period: a savanna corridor in Sundaland? *Quaternary Science Reviews*, 24: 2228–2242.
- Brandon-Jones D (1998) Pre-glacial Bornean primate impoverishment and Wallace's line. In: Hall R & Holloway JD (eds.) *Biogeography and Geological Evolution of SE Asia*. Backhuys Publishers, Leiden. Pp. 393–403.
- Brush AH & Johnson NK (1976) The evolution of color differences between Nashville and Virginia's warblers. *Condor*, 78: 412–414.
- Cannon CH, Morley RJ & Bush ABG (2009) The current refugial rainforests of Sundaland are unrepresentative of their biogeographic past and highly vulnerable to disturbance. *Proceedings of the National Academy of Sciences of the United States of America*, 106: 11188–11193.
- Chasen FN (1935) A handlist of Malaysian birds. *Bulletin of the Raffles Museum*, 11: 1–389.
- Coates BJ, Dutson GCL & Filardi CE (2006) Family Monarchidae (monarch-flycatchers). In: Del Hoyo J, Elliott A & Christie D (eds.) *Handbook of the Birds of the World Volume 11*. Lynx Edicions, Barcelona. Pp. 244–329.
- Collar NJ (2004) Species limits in some Indonesian thrushes. *Forktail*, 20: 71–87.
- Collar NJ (2005) Family Turdidae (thrushes). In: del Hoyo J, Elliott A & Christie D (eds.) *Handbook of the birds of the world*, Vol. 10. Lynx Edicions, Barcelona. Pp. 514–807.
- Darriba D, Taboada GL, Doallo R & Posada D (2012) jModelTest 2: more models, new heuristics and parallel computing. *Nature Methods*, 9: 772.
- de Voogd NJ, Becking LE & Cleary DF (2009) Sponge community composition in the Derawan islands, NE Kalimantan, Indonesia. *Marine Ecology Progress Series*, 396: 169–180.
- Deignan HG (1959) Harry Cusheir Raven's travels in eastern Borneo. *Sarawak Museum Journal*, 9: 267–269.
- Dickinson E & Dekker R (2002) Systematic notes on Asian birds. A preliminary review of the Pycnonotidae. *Zoologische Verhandelingen*, 25: 93–114.
- Dickinson EC (2003) *The Howard & Moore Complete Checklist of the Birds of the World*, 3rd Edition. Christopher Helm, London, 1056 pp.
- Excoffier L & Lischer HEL (2010) Arlequin suite ver 3.5: A new series of programs to perform population genetics analyses under Linux and Windows. *Molecular Ecology Resources*, 10: 564–567.
- Fabre PH, Irestedt M, Fjeldså J, Bristol R, Groombridge JJ, Irham M & Jönsson KA (2012) Dynamic colonization exchanges between continents and islands drive diversification in paradise-flycatchers (*Terpsiphone*, Monarchidae). *Journal of Biogeography*, 39: 1900–1918.
- Fishpool LDC & Tobias JA (2005) Family Pycnonotidae In: Del Hoyo J, Elliott A & Christie D (eds.) *Handbook of the Birds of the World Volume 10*. Lynx Edicions, Barcelona. Pp. 124–250.
- Fooden J (1995) Systematic review of Southeast Asian longtail macaques, *Macaca fascicularis* (Raffles, 1821). *Fieldiana Zoology*, 81: 1–206.
- Fregin S, Haase M, Olsson U & Alström P (2012) Pitfalls in comparisons of genetic distances: A case study of the avian family Acrocephalidae. *Molecular Phylogenetics and Evolution*, 62: 319–328.
- Fuchs J, Cruaud C, Couloux A & Pasquet E (2007) Complex biogeographic history of the cuckoo-shrikes and allies (Passeriformes: Campephagidae) revealed by mitochondrial and nuclear sequence data. *Molecular Phylogenetics and Evolution*, 44: 138–153.
- Gawin DF (2014) Population genetic and hybridization studies of three Bornean birds species: Mountain Black-eye (*Chlorocharis emiliae*), White-rumped Shama (*Copsychus malabaricus*), and Oriental Magpie-Robin (*Copsychus saularis*) In: *Biological Sciences*. Louisiana State University, Baton Rouge, Louisiana.
- Gawin DF, Rahman MA, Ramji MFS, Smith BT, Lim HC, Moyle RG & Sheldon FH (2014) Patterns of avian diversification in Borneo: the case of the endemic Mountain Black-eye (*Chlorocharis emiliae*). *The Auk: Advances in Ornithology*, 131: 86–99.
- Gill F & Donsker D (2014) IOC World Bird List (v 4.1). URL <http://www.worldbirdnames.org/>.
- Gorog AJ, Sinaga MH & Engstrom MD (2004) Vicariance or dispersal? Historical biogeography of three Sunda shelf murine rodents (*Maxomys surifer*, *Leopoldamys sabanus* and *Maxomys whiteheadi*). *Biological Journal of the Linnean Society*, 81: 91–109.
- Guindon S & Gascuel O (2003) A simple, fast and accurate method to estimate large phylogenies by maximum-likelihood". *Systematic Biology*, 52: 696–704.
- Hackett SJ (1996) Molecular phylogenetics and biogeography of tanagers in the genus *Ramphocelus* (Aves). *Molecular Phylogenetics and Evolution*, 5: 368–382.
- Hoogerwerf A (1966) Notes on the islands of Bawean (Java Sea) with special reference to the birds. *The Natural History Bulletin of the Siam Society*, 21: 313–340.
- Kellogg R (1944) A new macaque from an island off the east coast of Borneo. *Proceedings of the Biological Society of Washington*, 57: 75–76.
- Kuenen PH (1947) Two problems of marine geology: atolls and canyons. *Verhandelingen der Koninklijke Nederlandsche Akademie van Wetenschappen, afdeling Natuurkunde*.
- Lim HC, Chua VL, Benham PM, Oliveros CH, Rahman MA, Moyle RG & Sheldon FH (2014) Divergence history of the Rufous-tailed Tailorbird (*Orthotomus sericeus*) of Sundaland: Implications for the biogeography of Palawan and the taxonomy of island species in general. *Auk*, 131: 629–642.
- Lim HC, Rahman MA, Lim SLH, Moyle RG & Sheldon FH (2011) Revisiting Wallace's haunt: Coalescent simulations and comparative niche modeling reveal historical mechanisms that promoted avian population divergence in the Malay Archipelago. *Evolution*, 65: 321–34.
- Lim HC, Zou F, Taylor SS, Marks BD, Moyle RG, Voelker G & Sheldon FH (2010) Phylogeny of magpie-Robins and shamas (Aves: Turdidae: *Copsychus* and *Trichixos*): implications for island biogeography in Southeast Asia. *Journal of Biogeography*, 37: 1894–906.
- Meijaard E & Groves C (2004) The biogeographical evolution and phylogeny of the genus *Presbytis*. *Primate Report*, 68: 71–90.
- Miller GS (1913) Fifty-one new Malayan mammals. *Smithsonian Miscellaneous Collections*, 61: 1–30.

- Morley RJ (2012) A review of the Cenozoic palaeoclimate history of Southeast Asia. In: Gower DJ, Johnson KG, Richardson JE, Rosen BR, Rüber L & Williams ST (eds.) *Biotic Evolution and Environmental Change in Southeast Asia*. Cambridge University Press, Cambridge, UK. Pp. 79–114.
- Morley RJ & Morley HP (2013) Mid Cenozoic freshwater wetlands of the Sunda region. *Journal of Limnology*, 72(s2): 18–35.
- Moyle RG & Marks BD (2006) Phylogenetic relationships of the bulbuls (Aves: Pycnonotidae) based on mitochondrial and nuclear DNA sequence data. *Molecular Phylogenetics and Evolution*, 40: 687–695.
- Moyle RG, Taylor SS, Oliveros CH, Lim HC, Haines CL, Rahman MA & Sheldon FH (2011) Diversification of an insular Southeast Asian genus: Phylogenetic relationships of the spiderhunters (Aves: Nectariniidae). *Auk*, 128: 777–788.
- Musser G & Calafia D (1982) Results of the Archbold Expeditions. No. 106. Identities of rats from Pulau Maratua and other islands off East Borneo. *American Museum Novitates*, 2726: 1–30.
- Ng PK & Tomascik T (1994) *Orcovita saltatrix*, a new genus and species of anchialine varunine crab (Crustacea: Decapoda: Brachyura: Grapsidae) from Kakaban Island, Indonesia. *Raffles Bulletin of Zoology*, 42: 937–48.
- Oliveros CH & Moyle RG (2010) Origin and diversification of Philippine bulbuls. *Molecular Phylogenetics and Evolution*, 54: 822–32.
- Phillipps Q & Phillipps K (2011) *Phillipps' Field Guide to the Birds of Borneo*, Second Edition. John Beaufoy Publishing, Oxford.
- Rand AL (1970) Species formation in the blue monarch flycatchers genus *Hypothymis*. *Natural History Bulletin of the Siam Society*, 23: 353–65.
- Remsen JV & Graves WS (1995) Distribution patterns and zoogeography of *Atlapetes* brush-finches (Emberizinae) of the Andes. *Auk*, 112: 210–24.
- Riley JH (1930) Birds from the small islands off the northeast coast of Dutch Borneo. *Proceedings of the United States National Museum*, 77: 1–23.
- Sheldon FH, Lim HC, Nais J, Lakim M, Tuuga A, Malim P, Majuakim J, Lo A, Schilthuizen M, Hosner PA & Moyle RG (2009) Observations on the ecology, distribution, and biogeography of forest birds in Sabah, Malaysia. *Raffles Bulletin of Zoology*, 57: 577–586.
- Sheldon FH, Moyle RG & Kennard J (2001) *Ornithology of Sabah: history, gazetteer, annotated checklist, and bibliography*. *Ornithological Monographs*, 52: 1–285.
- Smythies BE (1999) *The Birds of Borneo*, 4th Edition. Natural History Publications (Borneo), Kota Kinabalu, 710 pp.
- Sukumaran J & Holder MT (2010) DendroPy: a Python library for phylogenetic computing. *Bioinformatics*, 26: 1569–1571.
- Tamura K, Peterson D, Peterson N, Stecher G, Nei M & Kumar S (2011) MEGA5: Molecular Evolutionary Genetics Analysis using Maximum Likelihood, Evolutionary Distance, and Maximum Parsimony Methods. *Molecular Biology and Evolution*, 28: 2731–2739.
- Theron E, Hawkins K, Bermingham E, Ricklefs RE & Mundy NI (2001) The molecular basis of an avian plumage polymorphism in the wild: A melanocortin-1-receptor point mutation is perfectly associated with the melanic plumage morph of the bananaquit, *Coereba flaveola*. *Current Biology*, 11: 550–557.
- Tomascik T, Mah AJ, Nontji A & Moosa MK (1997) The ecology of the Indonesian seas. Part two. Chapters 13–23. *Periplus*, Singapore.
- van Balen S (1986) Short note on the occurrence of grey phase Black-headed Bulbuls *Pycnonotus atriceps* especially on Java. *Kukila*, 2: 86–7.
- Voris HK (2000) Maps of Pleistocene sea levels in Southeast Asia: shorelines, river systems and time durations. *Journal of Biogeography*, 27: 1153–1167.
- Wells DR (2007) *The Birds of the Thai-Malay Peninsula*, Volume 2, Passerines. Christopher Helm, London, 800 pp.
- Wilting A, Sollmann R, Meijaard E, Helgen KM & Fickel J (2012) Mentawai's endemic, relictual fauna: is it evidence for Pleistocene extinctions on Sumatra? *Journal of Biogeography*, 39: 1608–1620.
- Zwickl DJ (2006) Genetic algorithm approaches for the phylogenetic analysis of large biological sequence datasets under the maximum likelihood criterion. University of Texas, Austin, Texas. 115 pp.