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OBSERVATIONS ON THE ECOLOGY, DISTRIBUTION AND BIOGEOGRAPHY OF FOREST BIRDS IN SABAH, MALAYSIA

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ABSTRACT. – From January 2004 to July 2008, we surveyed and collected birds at 15 sites in Sabah, Malaysian Borneo. This work was designed to (1) document bird occurrence in areas and habitats that had been poorly surveyed in the past, (2) provide specimens for molecular genetic studies of bird evolution in Borneo, and (3) examine the occurrence of forest birds in agricultural and industrial tree plantations. The research disclosed new elevational, habitat, and breeding records for numerous species. It also provided insight into the biogeography of lowland endemic species in Sabah and montane endemic species in Borneo. The hypotheses formulated from these biogeographic discoveries should serve as useful frameworks for future phylogeographic work on Bornean birds.

KEY WORDS. – Borneo, elevation, endemism, oil palm, peat swamp, Southeast Asian biogeography.

INTRODUCTION

In the last 30 years, the forests of Southeast Asia have changed dramatically as a result of logging and development (Curran et al., 2004; Sodhi et al., 2004; Koh & Wilcove, 2008). Typical of such change are forests in the Malaysian state of Sabah in northernmost Borneo. In 1970, only 16% of the land area of Sabah had been influenced substantially by humans (Thomas et al., 1976; Sheldon et al., 2001), but by the year 2000 more than 80% of the forest had been markedly disturbed (Marsh & Greer, 1992; McMorrow & Talip, 2001). Today, the only large stands of undisturbed forest remaining in Sabah are in parks (Kinabalu National Park and Crocker Range National Park) and special preserves (e.g., Danum Valley and Maliau Basin). At the

same time that the forests of Sabah have been changing, so has interest in the wildlife inhabiting those forests. Ecotourism and natural history research have boomed in the state in recent years and have produced a mass of new information on wildlife.

Much recent information on the birds of Borneo is being compiled and included in new publications, including an annotated checklist (Mann, 2008) and planned field guides (S. Myers and Q. Phillipps, pers. comm.). To contribute to the updating process, we report here on recent ornithological research in Sabah. Starting in January 2004 and ending in July 2008, we conducted a series of bird surveys and collections in Sabah. The purpose of the work was (1) to document bird occurrence in areas and habitats that had

been poorly surveyed in the past, (2) to collect specimens for studies of bird evolution in Borneo and Southeast Asia, and (3) to examine the use of agricultural and industrial tree plantations by Borneo's forest birds. By themselves, the many small facts we have collected during our surveys and subsequent studies may not appear profound, but together they provide substantial insight into the natural history of Bornean birds. Of special importance are emerging biogeographic patterns that shed light on the evolution of bird diversity in Borneo, particularly in regard to endemism. Also documented is evidence of recent shifts in bird distribution in Borneo promoted by the opening of montane forest by logging and plantation development, and perhaps also promoted by global warming. This new information should be of substantial interest to biogeographers, ornithologists, wildlife managers, birdwatchers, and other with a stake in Bornean birdlife.

MATERIALS AND METHODS

At each site described below (except Sabah Softwoods), we captured birds with mistnets and observed them informally in the wild. In some cases, we tape-recorded singing birds. These tape-recordings are archived at the Macaulay Library at Cornell University and are available online at www.animalbehaviorarchive.org. Specimens from the project were divided among several collections, depending on locality. Specimens from parks were split between the Sabah Park Collection and Louisiana State Museum of Natural Science (LSU). Specimens collected outside of parks were divided between Sabah Museum and LSU. Some specimens have been loaned permanently by LSU to the American Museum of Natural History and the University of Kansas Natural History Museum. At Sabah Softwoods, instead of making a collection, we conducted a formal point-count survey of birds as described by Styring et al. (2007).

Most of our descriptions of natural history are qualitative, but we have made some preliminary genetic comparisons among taxa. Unless otherwise specified, these are based on sequences of mitochondrial nicotinamide adenine dinucleotide dehydrogenase subunit 2 (ND2) DNA, as described by Sheldon et al. (2009b).

Work Sites

Inobang, Penampang, 30 May–1 June 2008. – Netted briefly at this site, just outside Crocker Range National Park (5°51'25"N 116°08'00"E). Elevation: 400 m. Habitat: upland secondary forest. Remarks: This site was of interest as a source of lowland specimens from the west coast for phylogeographic comparison with specimens from sites east across the Crocker Range.

Kinabalu National Park, 8–11 August 2004. – Netted swiftlets at the Park headquarters (6°00'19"N 116°32'36"E). Elevation 1500 m. Habitat: roads and buildings. Publications:

Samples from this collection were used by Moyle et al. (2008).

Kinabalu National Park, 24–28 February 2005. – Netted at Laban Rata (6°03.52'N 116°33.97'E) and Layang Layang (6°02.75'N 116°33.61'E). Elevation: at Laban Rata 3270 m, at Layang Layang 2730 m. Habitat: ericaceous forest. Publications: Samples from this collection were used by Moyle et al. (2008; 2009).

Kinabalu National Park, 20–25 June 2008. – Netted around park headquarters (6°00'19"N 116°32'36"E). Elevation: 1500 m. Habitat: primary and secondary montane forest.

Klias Forest Reserve, 5–12 February 2004. – Worked in the northwest corner of Klias FR using the Forestry Department rest house as a base, about 8 km southwest of Beaufort (05°10'34"N 115°40'25"E). Elevation: sea level. Habitat: primary and secondary peatswamp forest and scrub. Results of this survey are reported in Sheldon et al. (2009a) and specimens were used in Sheldon et al. (2009b). Remarks: This site is of particular interest because it is one of the last remaining stands of accessible peatswamp in Sabah and home to some species that are rare or uncommon in Sabah, including Hook-billed Bulbul (*Setornis criniger*) and Grey-breasted Babbler (*Malacopteron albogulare*) (Sheldon, 1987).

Masikuan, Padas Damit, 3–4 June 2008. – Netted briefly at his site on Klias Peninsula ca. 25 km west of Beaufort (5°19'40"N 115°30'48"E). Elevation: sea level. Habitat: heavily disturbed swamp forest, scrub, and plantation. Remarks: This site was a source of coastal and west coast specimens.

Mt. Meliau, 22–31 May 2006. – We approached Mt. Meliau from the east through Pamol and the Meliau oil palm plantation to make camp on an old logging road on the north side of the Meliau River (05°50'44"N 117°10'57"E). We set nets from the base camp up to a ridge northeast of Mt. Meliau proper (05°52'08"N 117°09'59"E). Elevation: 75 – 1067 m. Habitat: logged forest on ultrabasic soils to 400 m; primary ultrabasic forest at higher elevation. This forest consisted mainly of narrow, pole-like trees, interspersed with thickets of climbing bamboo. Remarks: We were interesting in discovering whether montane species inhabit the ultrabasic forest at higher elevations.

Mendolong and Mt. Lumaku, 15–18 January 2005. – This site included two locations ca. 25 km southeast of Sipitang: one near the Sabah Forest Industries plantation rest house (4°54.181'N 115°41.522'E), and the other on the flanks of Mt. Lumaku (4°51.027'N 115°41.963'E). Elevation: 550 m in the plantation and 1100 m on Mt. Lumaku. Habitat: scrub adjacent to *Acacia* plantation and, on Lumaku, small stands of primary forest on ridges surrounded by heavily logged slopes. Remarks: This site is important not only for its elevation but also its location in the taxic transition zone between Sarawak and Sabah. Publications: Samples

from this collection were used by Haines (2007) and Sheldon et al. (2009b)

Sabah Softwoods, 23 June–12 July 2005. – Sabah Softwoods Sdn. Bhd. is an exotic tree plantation in the Tawau District of southeastern Sabah. We surveyed birds near its headquarters at Brumas, ca. 50 km NNW of Tawau (4°37'N, 117°44'E). Elevation: 150 – 200 m. Habitat: logged forest on steep hills, scrub, *Albizia* (*Paraserienthis*) *falcataria*, *Accacia mangium*, and oil palm. Remarks: Our survey was a follow-up to previous work at Sabah Softwoods (Mitra & Sheldon, 1993).

Serinsim Substation, Kinabalu National Park, 17 January–1 February 2004. – This substation is located in the northeastern corner of Kinabalu Park (6°17'36"N 116°42'29"E), ca. 30 km south of Kota Marudu. Elevation: 200 – 450 m. Habitat: Mainly heavily disturbed scrub and forest and lightly logged dipterocarp forest. Remarks: We were interested in Serinsim because no birds have been collected on the mainland of northern Sabah since colonial times. Publications: Results of this survey are reported by Sheldon et al. (2009c) and specimens were used in Sheldon et al. (2009b).

Tawau Hills Park, 23 January–10 February 2005. – Work was conducted in two areas in the Park: near the headquarters (4°23.87'N 117°53.28'E) and on Mt. Lucia (4°27.63'N 117°53.34'E). Elevation: 280 m at the headquarters; 900 – 1150 m on Mt. Lucia. Habitat: near the headquarters, secondary forest and oil palm plantation; on Mt. Lucia, primary forest. Remarks: Mt. Lucia is of interest for its isolated montane bird population. Publications: Samples from this collection were used by Haines (2007) and Moyle et al. (2009)

Trus Madi, 21 July–2 August 2005. – This survey was based at the Forestry Department rest house located at 1450 m on the highest logging road on the north side of the mountain (05°35'09"N 116°29'26"E). We also set nets and observed birds for brief periods at four other locations: the helicopter platform at 1629 m (5°34'12"N 116°28'58"E), 26–28 July 2005; Taman Bunga at 2350 m (5°33'27"N 116°30'03"E), 29–30 July 2005; the summit at 2600 m (5°33'20"N 116°30'34"E), 29 July 2005; and northeast of the rest house at 1600m (05°35'25"N 116°29'38"E), 30 July – 1 August 2005. Habitats: logged lower montane forest and primary upper montane and ericaceous forest. Publications: Older reports include Sheldon & Francis (1985) and Moyle & Wong (2002). Samples from the 2005 collection were used by Gawin (2006) and Haines (2007).

Ulu Kimanis Substation, Crocker Range National Park, 14–18 June 2008. – Netted briefly at this site ca. 53 km south of Kota Kinabalu (5°30'17"N 116°00'48"E). Elevation: 565 m at the substation headquarters. Habitat: upland primary and secondary forest and gardens. Remarks: This site was a source of lowland specimens from the west coast for phylogeographic comparison with sites east across the Crocker Range. Because of its extensive plantings

of bananas and gingers, Ulu Kimanis headquarters had a remarkable number of spiderhunters of various species.

Ulu Lauhon, Maligan Range, 5–11 June 2008. – We made a substantial collection at this site ca. 58 km SSE of Sipitang (4°34'28"N 115°41'45"E). Elevation: 1700 – 1800 m. Habitat: roadside scrub, heavily logged lower montane forest, and some primary forest on ridges. Remarks: This site is important not only for its elevation but also its location in the taxic transition zone between Sarawak and Sabah.

Ulu Rukuruku, 13–19 August 2004. – This site includes a Class I forest reserve within the Tawai Forest Reserve, ca. 8 km east of Telupid (5°36.940'N, 117°11.660'E). Elevation: 130 m. Habitat: primary and disturbed kerangas on ultrabasic soils and primary and disturbed forest growing on a complex of ultrabasic and limestone soils. Remarks: This site was of interest for endemic ultrabasic forest species, such as Grey-breasted Babbler (*Malacopteron albogulare*) and Scarlet-breasted Flowerpecker (*Prionochilus thoracicus*) (Davies & Payne, 1982).

RESULTS

Key Distributional and Taxonomic Observations

Bornean Swiftlet (*Collocalia dodgei*). – Cranbrook et al. (2005) and Moyle et al. (2008) described the occurrence of this endemic swiftlet at higher elevations on Mt. Kinabalu. Moyle et al. (2008) suggested it might also occur on other mountains in Borneo, but has not been recognized because of its similarity to the Glossy Swiftlet (*C. esculenta*), which is common up to ca. 1600 m. This prediction proved true, as we captured an individual of Bornean Swiftlet at 1800 m on a logging road at Ulu Lauhon in the Maligan Range. It was genetically identical to the *C. dodgei* specimens from Mt. Kinabalu (GenBank # FJ798744). Unfortunately, we cannot provide useful wing measurements, as the outer primaries in the specimen are still sheathed. The bird is very small, noticeably smaller in the field than Glossy Swiftlet, with which it was feeding over a logging road.

Bornean Barbet (*Megalaima eximia*). – We captured this species on Trus Madi (1450 m) and Mt. Lucia (900 m), where it was often heard calling. A specimen from Mt. Lucia disputes the endemic Mt. Kinabalu subspecies *M. e. cyanea*, which has a blue forehead and throat. The Mt. Lucia specimen also had a blue forehead and throat, but was immature. The blue coloring is likely to be a characteristic of young birds.

Bornean Leafbird (*Chloropsis kinabaluensis*). – Specimens from Trus Madi provide additional evidence that the montane blue-winged leafbird of Borneo, formerly *C. cochinchinensis flavocincta*, is a species distinct from the lowland form, *C. c. viridinucha*, found in Borneo outside of Sabah (Wells et al., 2003). Not only does the female *C. kinabaluensis* have a black throat like the male, which

distinguishes it from *C. cochinchinensis* (Peters, 1940), but there are additional distinguishing characteristics. Only the male--not the female--has a blue malar stripe (moustache), and the female has green plumage surrounding the black on the head and throat (as in MacKinnon & Phillipps, 1993), as opposed to yellow in the male. (A juvenile male we collected had female plumage.) The parapatric distribution of *C. kinabaluensis* in highland areas and *C. cochinchinensis* in lowland areas of Borneo is strong *a priori* evidence of species distinction (see Discussion).

Straw-headed Bulbul (*Pycnonotus zeylanicus*). – This species was previously one of the most common birds of padi and river edges in Sabah. Now it is rare. For example, in surveys at Sabah Softwoods in 1982, Mitra and Sheldon (1993) commonly recorded it along rivers in *Albizia falcataria* groves. However, it was not recorded in surveys in 2005 at Sabah Softwoods in any habitat. Indeed, the only location where we have found it in the last five years is on the Kinabatangan River near Sukau. Others have recorded it along rivers at Danum Valley (S. Myers pers. comm.). This species appears to have been extirpated from most of its range in Sabah (and other areas in Borneo), presumably by pet traders (Holmes, 1997).

Oriental Magpie-Robin (*Copsychus saularis*). – We collected individuals of this species at Klias FR, Mendolong, Serinsim, and Tawau Hills and examined specimens from other localities in Sabah (Sheldon et al., 2009b). In principle, three subspecies occur in Borneo (Collar, 2005): (1) *musicus* in the southwest, with a white belly and black and white tail; (2) *adamsi* in Sabah, with a dark belly and all black tail; and (3) *pluto* in eastern Kalimantan, with a dark belly and white in the tail. Our molecular comparisons, however, show only two genetic groups: *musicus* types (with white bellies and white in the tail) and *adamsi/pluto* types (with black bellies and usually white in the tail). It appears that *musicus* has invaded Borneo relatively recently from the west and is hybridizing extensively with (presumably native) black-bellied birds (Mees, 1986), resulting in a variety of plumage combinations and possibly swamping the black-bellied form. We found individuals of the two genotypes together on Klias Peninsula and at Ulu Kimanis. Those of *musicus* genotype had typical *musicus* plumage, but those of *adamsi/pluto* genotype had either black bellies and a little white in the tail or white bellies and substantial white in the tail. Thus, hybridization of *musicus* and *adamsi* appears to be extensive on the western side of Sabah, and it may be difficult nowadays to find individuals with the all-black *adamsi* plumage. (Historically, *adamsi* occurred on the coast from Tuaran up to Banggi and Balambangan islands and down through Sandakan to Tawau.)

White-rumped Shama (*Copsychus malabaricus*). – In general, the White-crowned Shama, *C. stricklandii*, is considered the shama of Sabah and *C. malabaricus* occurs elsewhere in Borneo. However, *C. malabaricus* enters the western side of Sabah. The Sabah Park Collection has a specimen from Mendolong (#16761), a male collected in

secondary forest on 4 November 1998, and there are early records from the Padas River district (Smythies, 1957). Conversely, *C. stricklandii* extends and overlaps with *C. malabaricus* to the Lawas region of Sarawak (Smythies, 1957). On the eastern side of Sabah, *C. malabaricus* has been reported to reach Silam near Lahad Datu (Smythies, 1957). Apparent introgressed individuals of *C. stricklandii* were caught in Danum Valley, inland of Silam, in 1976 (Kiew, 1977). These birds had white crown feathers extensively tipped in black. Davison (1999) reviewed the species status of *C. malabaricus* and *C. stricklandii*. He concluded that they hybridize over a wide area (in some cases hundreds of kilometers), and their status as species depends on the stability of their hybrid zone. Genetically, the two taxa are quite distinct between Sabah and Bintulu, Sarawak (uncorrected ND2 distance, 2.6% – 3.2%). Because they are also distinct morphologically, we treat them as different species (see Discussion).

Bornean Forktail (*Enicurus borneensis*). – Moyle et al. (2005) demonstrated that the highland form of *E. leschenaulti* in Borneo (*E. l. borneensis*) is different phylogenetically and morphologically from the lowland form, *E. l. frontalis* (see Discussion). As such, the endemic montane form is a different species. We suggest Bornean Forktail as an appropriate name for *E. borneensis*.

Streaky-breasted Spiderhunter (*Arachnothera affinis*). – Confusion still exists concerning this species and its similar congener, Grey-breasted Spiderhunter, *A. modesta* (Mann, 2008). *Arachnothera modesta* is a lowland species that does not occur in Sabah; only *A. affinis* is found in the state (in both the lowlands and mountains; see Discussion). Comparison of mitochondrial ND2 and ND3 genes between lowland and montane specimens from Sabah confirmed they are all *A. affinis* (Haines, 2007). At Ulu Kimanis, we netted many individuals of this species. Males averaged ca. 27 g, females 20 g. The much larger size of the males may cause birdwatchers to think there are two species.

Pygmy White-eye (*Oculocincta squamifrons*). – Netted on Mt. Lucia at 1000 – 1100 m in primary forest. Previously, it was recorded on nearby Mt. Magdalena by the British Museum expedition of 1956 at ca. 1200 m (Smythies, 1957). Genetic comparisons with other white-eyes (Moyle et al., 2009) indicate that *Oculocincta* is a member of a clade with *Lophozosterops* (Wallacean white-eyes) that is embedded among Philippine babblers (*Dasycrotapha*, *Sterrhoptilus*, and *Zosterornis* previously in *Stachyris*). This unusual group is sister to typical white-eyes (*Zosterops*).

Mountain Black-eye (*Chlorocharis emiliae*). – Netted at Laban Rata (3270 m) and also on Mt. Trus Madi (at 1600 and 2600 m). The Trus Madi specimens were used in a genetic comparison of Sabah and Sarawak populations (Gawin, 2006). The Laban Rata specimens were used in a phylogenetic study of white-eye relationships (Moyle et al., 2009), which found *Chlorocharis* to be a typical white-eye embedded within *Zosterops*.

Other Species Accounts

The species records below were included because they supplement substantially the information on distribution and breeding in Smythies (1999), Sheldon et al. (2001), Moyle (2003) and Mann (2008). We have not mentioned marginal increases in elevation or breeding records of common species. (These are included in unpublished reports available from the authors.) We have, however, included records of rarer birds, even if the information was predictable from earlier knowledge. The quality of the information is indicated by its source, i.e., whether it is based on mistnetting, observation, or voice (=recorded).

Oriental Honey-Buzzard (*Pernis ptilorhyncus*). – Observed in 7 year old *Acacia* at Sabah Softwoods.

Blue-breasted Quail (*Coturnix chinensis*). – Recorded in oil palm at Sabah Softwoods.

Scaly-breasted Partridge (*Arborophila charltonii*). – Recorded in 7 year old *Acacia* at Sabah Softwoods.

Crested Partridge (*Rollulus rouloul*). – Numerous individuals were netted commuting to the oil palm plantation at Tawau Hills Park headquarters from adjacent forest. This species was also observed in the oil palm at Sabah Softwoods.

Crested Fireback (*Lophura ignita*). – Three males were displaying to a female in 7 year old *Acacia* at Sabah Softwoods.

Pink-necked Green Pigeon (*Treron vernans*). – Birds in breeding condition were collected at Klias FR on 9 February 2004: testes 14x5 mm, 16x8 mm, yolked egg 15x15 mm.

Plaintive Cuckoo (*Cacomantis merulinus*). – An individual with a shelled oviduct egg was collected on 7 February 2004 at Klias FR.

Little Bronze Cuckoo (*Chrysococcyx minutillus*). – Recorded in old tall trees at Sabah Softwoods in *Eucalyptus*, *Acacia*, and *Albizia* groves.

Chestnut-winged Cuckoo (*Clamator coromandus*). – Two were netted in thick primary peatswamp forest at Klias FR in February 2004. These records suggest this scarce migrant may prefer coastal or peatswamp forest for overwintering.

Bornean Ground Cuckoo (*Carpococcyx radiatus*). – Recorded numerous times in recent years in the riverine forest along the Menanggul River, Sukau. A voice recording is stored at Macaulay Library, ML# 129446.

Rajah Scops Owl (*Otus brookii*). – The Sabah Park Collection has a mounted male specimen collected at 1650 m on Mt. Kinabalu on 20 August 1998.

Collared Owlet (*Glaucidium brodiei*). – Recorded on Mt. Lucia at 950 m.

Short-tailed Frogmouth (*Batrachostomus poliolophus*). – Netted on Mt. Trus Madi in primary forest at 1650 m. Its main food was beetles.

Sunda Frogmouth (*Batrachostomus cornutus*). – The Sabah Park Collection has two specimens collected on Balambangan Island on 25 and 27 May 2003.

Waterfall Swift (*Hydrochous gigas*). – The Sabah Park Collection has six specimens collected at Batu Kapur on Balambangan Island on 23 May 2003.

Diard's Trogon (*Harpactes diardi*). – Netted in secondary peatswamp scrub 0.5 km from substantial forest at Klias FR.

Rufous Piculet (*Sasia abnormis*). – Netted up to 1450 m on Trus Madi.

Rufous Woodpecker (*Celeus brachyurus*). – Netted in primary peatswamp at Klias FR and in ultrabasic forest at Ulu Rukuruku.

Great Slaty Woodpecker (*Mulleripicus pulverulentus*). – Observed excavating a nest hole in a 9 year old *Albizia* tree at Sabah Softwoods on 11 July 2005. The site was ca. 200 m from logged native forest.

Hose's Broadbill (*Calyptomena hosii*). – Sabah Museum has a specimen collected on Mt. Lumaku on 20 July 1996 in disturbed forest (no elevation).

Dusky Broadbill (*Corydon sumatranus*). – Observed at Sabah Softwoods in 7 year old *Acacia*. It is also commonly recorded on the edge of the Kinabatangan River at Sukau.

Giant Pitta (*Pitta caerulea*). – Commonly recorded along the Kinabatangan River near Sukau.

Blue-banded Pitta (*Pitta arquata*). – Recorded at Sabah Softwoods in steep, logged forest and at Bumbalai Hill in Tawau Hills Park. The Sabah Park Collection has a specimen from a ridge in Tawau Hills Park. Sabah Museum has a specimen from Tagodon, a submontane site on the western side of the Crocker Range, east of Penampang. This scarce species seems to prefer steep forest sites.

Lesser Cuckooshrike (*Coracina fimbriata*). – Parent birds were observed feeding a recent fledgling on 31 May 2006 at Meliau base camp.

Black-and-white Bulbul (*Pycnonotus melanoleucos*). – Netted in primary and secondary ultrabasic forest at Ulu Rukuruku and Meliau.

Grey-bellied Bulbul (*Pycnonotus cyaniventris*). – Common in ultrabasic roadside scrub at Meliau.

Flavescent Bulbul (*Pycnonotus flavescens*). – A few recorded at 1500 m in roadside scrub on Trus Madi; more common in the ericaceous forest at the summit (2300 – 2600 m).

Olive-winged Bulbul (*Pycnonotus plumosus*). – Netted at 1600 m along a logging road at Ulu Lauhon.

Grey-cheeked Bulbul (*Alophoixus bres*). – Netted in primary ultramafic forest at Ulu Rukuruku and Meliau.

Yellow-bellied Bulbul (*Alophoixus phaeocephalus*). – Netted in primary ultramafic forest at Ulu Rukuruku.

Hook-billed Bulbul (*Setornis criniger*). – Netted in peatswamp at Klias FR. Two specimens were in breeding condition on 8 February 2004 (testes 10x5 mm and 8x8 mm).

Streaked Bulbul (*Ixos malaccensis*). – Common in ultramafic forest at Meliau.

Buff-vented Bulbul (*Iole olivacea*). – Common in ultramafic roadside scrub at Meliau, and also at other sites in Sabah in edge habitat.

Chestnut-capped Thrush (*Zoothera interpres*). – Netted in both primary and secondary forest along the Serinsim River, where an individual in breeding condition was collected on 29 January 2004 (testes 8x4 mm). A. Biun (pers. comm.) reported that several nests were found by Park staff in August 1998 along the Serinsim River. The nests were near the ground or up to 3 m high. They were cups built of twigs and placed in saplings. Most nests contained 2 eggs or 2 chicks.

Fruithunter (*Chlamydochaera jefferyi*). – We observed an adult feeding a recent fledgling at Kinabalu Park on 12 April 2002.

Temminck's Babbler (*Pellorneum pyrrogenys*). – Netted in ultrabasic forest at 1000 m on Mt. Meliau.

Short-tailed Babbler (*Malacocincla malaccensis*). – Netted at 1600 m in heavily logged, roadside scrub at Ulu Lauhon.

Horsfield's Babbler (*Malacocincla sepiarium*). – A specimen in breeding condition was netted in old secondary forest at Serinsim: 27 January 2004, testes 8x5 mm.

Grey-breasted Babbler (*Malacopteron albogulare*). – Netted at Klias FR in peatswamp and at Ulu Rukuruku in ultrabasic forest.

Bornean Wren Babbler (*Ptilocichla leucogrammica*). – Netted in primary ultrabasic forest at Ulu Rukuruku.

Mountain Wren Babbler (*Napothera crassa*). – Observed at the summit of Trus Madi (2600 m) foraging on tree trunks in the ericaceous forest.

Eyebrowed Wren Babbler (*Napothera epilepidota*). – Netted on Mt. Trus Madi at 1450 m in dark woods near streams and observed on Mt. Lucia at 1000 m in a dense tangle on a ridge.

Striped Tit Babbler (*Macronous gularis*). – Netted at 1600 m at Ulu Lauhon and 1450 m on Mt. Trus Madi, in both cases in scrub along logging roads.

Fluffy-backed Tit Babbler (*Macronous ptilosus*). – A specimen in breeding condition was netted at Klias FR: 7 February 2004, 15 mm oviduct yolk.

White-necked Babbler (*Stachyris leucotis*). – Netted in primary ultrabasic forest at Ulu Rukuruku and observed in primary dipterocarp forest at Mt. Lucia (700 m). This scarce species was also captured by Moyle (2003) at the Crocker Range National Park headquarters near Keningau. It appears to prefer steep slopes.

Chestnut-rumped Babbler (*Stachyris maculata*). – Specimens in breeding condition collected at Klias: 7 February 2004, testes 9x5 mm, 9 mm yolk and enlarged oviduct.

White-browed Shrike Babbler (*Pteruthius flaviscapis*). – Netted at 2340 m on Trus Madi in ericaceous forest.

Brown Fulvetta (*Alcippe bruneicauda*). – Netted at 500 and 1000 m on Mt. Meliau in primary ultrabasic forest. We also observed (apparent) family groups collecting nesting material at Ulu Kimanis on 16-17 June 2008.

Chestnut-crested Yuhina (*Yuhina everetti*). – Netted at 1000 m in ultrabasic forest at Meliau.

Golden-bellied Gerygone (*Gerygone sulphurea*). – Common at 1450 m and recorded up to 1800 m on Trus Madi; also at 1800 m at Ulu Lauhon. A bird was observed collecting nesting material in 5 year old *Acacia* at Sabah Softwoods on 10 July 2005.

Bornean Stubtail (*Urosphena whiteheadi*). – Netted and observed on Trus Madi (1450 – 2200 m) and netted at Ulu Lauhon (1700 m).

Sunda Bush Warbler (*Cettia vulcania*). – Two males in breeding condition were collected on Trus Madi on 29 July 2005 (testes 7x5 mm and 5x4 mm) at 1500 m. A young bird collected at 2350 m had distinctly buffy-yellow, rather than greyish-white, underparts and supercilium. We also netted this species at 3270 m on Kinabalu and recorded it at Ulu Lauhon (1700 m).

Mountain Leaf Warber (*Phylloscopus trivirgatus*). – Recorded from 1450 – 2600 m on Trus Madi. The birds were the bright yellow form, *P. t. sarawacensis*. It was also netted at Ulu Lauhon (1700 m).

Yellow-breasted Warbler (*Seicercus montis*). – Recorded at Mt. Lucia (1050 m) and netted at Ulu Lauhon (1700 m).

Yellow-bellied Warbler (*Abroscopus superciliaris*). – Family groups observed and netted at Mt. Meliau (100 – 1000 m) in ultrabasic forest; also observed on Trus Madi (1450 m), and Mt. Lucia, and netted on Kinabalu in a headquarter's garden (1600 m).

Rufous-tailed Tailorbird (*Orthotomus sericeus*). – Netted at Ulu Lauhon (1700m).

Ashy Tailorbird (*Orthotomus ruficeps*). – Sympatric with *O. atrogularis* in ultrabasic scrub at Meliau. A bird in breeding condition was collected at Klias FR on 6 February 2004 (testes 5x3 mm).

Spotted Fantail (*Rhipidura perlata*). – Netted in ultrabasic forest at Ulu Rukuruku and Mt. Meliau.

Pied Fantail (*Rhipidura javanica*). – Recorded in oil palm at Brumas and up to 1100 m on Mt. Lumaku. Birds in breeding condition were collected at Klias FR on 8-9 February 2004 (testes 9x4 mm, yolk 12 mm, respectively).

Grey-headed Canary Flycatcher (*Culicicapa ceylonensis*). – Observed on Mt. Lucia, Mt. Lumaku (1100 m), and Ulu Lauhon (1600 m).

Verditer Flycatcher (*Eumyias thalassina*). – Observed at Ulu Kimanis in logging forest (500 m).

Hill Blue Flycatcher (*Cyornis banyumas*). – Recent specimen records indicate that this species is fairly common in submontane forest. LSU has specimens from the Crocker Range National Park headquarters (1000 m) and Mt. Lucia (900 m). The Sabah Museum has specimens from Sayap (1000 m), Ulu Tomani (selectively logged forest southwest of Tenom), Ulu Senagang (near Keningau on the west side of the Crocker Range), and Long Pasia.

Mugimaki Flycatcher (*Ficedula mugimaki*). – Netted on Mt. Lumaku (1100 m, 17 January 2005) and Mt. Kinabalu (3270 m, 25 February 2005). An apparent summering male, which was assuming adult plumage, was observed at 2600 m on Trus Madi (29 July 2005).

Fulvous-chested Jungle-Flycatcher (*Rhinomyias olivacea*). – Caught at Serinsim and Masikuan. We found this species at Serinsim in scrub and old forest, where one would normally expect Grey-chested Jungle Flycatcher (*R. umbratilis*). A male at Serinsim was in breeding condition (testes 7x4 mm on 27 January 2004).

Grey-chested Jungle Flycatcher (*Rhinomyias umbratilis*). – Common in the peatswamp forest at Klias FR and ultrabasic forest at Meliau.

Purple-throated Sunbird (*Nectarinia sperata*). – This species was unusually common in the ultrabasic forest and scrub from 100 - 1000 m on Mt. Meliau.

Scarlet-breasted Flowerpecker (*Prionochilus thoracicus*). – This poor-soil forest specialist was common in the primary and secondary forest at Klias FR, Ulu Rukuruku, and Mt. Meliau (up to 1000 m). A male with testes 5x4 mm was collected at Klias on 8 February 2004.

Plain Sunbird (*Anthreptes simplex*). – Netted from 100 – 1000 m in ultrabasic forest at Meliau.

Everett's White-eye (*Zosterops everetti*). – Common in large flocks at Sabah Softwoods in older groves of *Albizia* and *Acacia*.

Bornean Bristlehead (*Pityriasis gymnocephala*). – Observed in 7 year old *Acacia* at Sabah Softwoods. It has also been seen in *Acacia* near Sepilok Orangutan Reserve (K. Ickes, pers. comm.).

Tawny-breasted Parrotfinch (*Erythrura hyperythra*). – Observed on Trus Madi in primary forest from 1700 – 2350 m. At 2350 m, a flock of ca. 10 individuals was observed in a coniferous tree. Its call is a high-pitched note with a burry quality and a tremor (very finch-like). Compared to the illustration in MacKinnon & Phillipps (1993), the birds had more black on the forehead and only males (or adults) had blue on the head. The belly and flanks were the same green color as the back and wings. The breast was much paler than illustrated, much more like the bird depicted in Robson (2000).

Black Magpie (*Platysmurus leucopterus*). – Observed in 10 year *Albizia* at Sabah Softwoods.

House Crow (*Corvus splendens*). – Now a common resident in the Filipino Market in Kota Kinabalu.

DISCUSSION

Biogeographic patterns. – Recent work in the field and laboratory has disclosed interesting patterns in the distribution and biogeography of Bornean birds. The most important of these patterns relate to the evolution of lowland endemics in Sabah and montane endemics in Borneo as a whole.

In its lowlands, Sabah has endemic bird species that are complemented by close congeners in other parts of Borneo. An example is the White-fronted Falconet (*Microhierax latifrons*) in Sabah, which is replaced by the Black-thighed Falconet (*M. fringillarius*) elsewhere. Other examples are the Black-and-crimson Pitta (*Pitta ussheri*) versus Garnet

Pitta (*P. granatina*) and the shamas *Copsychus stricklandii* and *C. malabaricus*. There are also numerous lowland subspecies endemic to Sabah, such as *Copsychus saularis adamsi* discussed above (Mann, 2008:18, provides an extensive list). Molecular comparisons suggest that some of Sabah's endemic lowland bird populations may represent remnants of native Bornean taxa that have been replaced on the rest of the island by closely related, relatively recent invaders from the west (Moyle et al., 2005; Sheldon et al., 2009b). These invaders would have colonized Borneo from Sumatra, Malaya, or mainland Asia via land bridges exposed during lowered sea levels in glacial periods of the mid-Pleistocene (Heaney, 1986; Inger & Voris, 2001). This scenario is suggested not only by the morphological distinctiveness of Sabah's populations, but also by a genetic dichotomy in Borneo; some bird populations from western Borneo are closer genetically to populations in Malaya and Sumatra than to those in Sabah. This is true of several taxa, including forktails (*Enicurus leschenaulti*; Moyle et al., 2005), magpie-robins (*Copsychus saularis*; Sheldon et al., 2009b), and shamas (*C. malabaricus*; Sheldon et al. in preparation).

The hypothesis that some of Sabah's lowland birds are relicts of once widely distributed populations, and that western invaders are moving eastward and may eventually overrun Sabah, must be tempered by the observation that a variety of ecologically disparate organisms—with presumably different dispersal capabilities—share the taxic discontinuity between Sabah and the rest of Borneo. This is true of birds (e.g., canopy falconets, terrestrial pittas, forest shamas, and open-country magpie-robins) and also mammals; for example, tree-shrews, bats, and various rodents exhibit population, subspecies, and species discontinuities between Sabah and the rest of Borneo (Medway, 1977; Payne et al., 1985; Han, 2000; Gorog et al., 2004; S. Murray, pers. comm., M. T. Abdullah, pers. comm.). It is unlikely that such distinct groups would invade from the west at the same time and move across Borneo at the same rate so that all are poised at the same moment on the border of Sabah. Moreover, we have evidence that *Copsychus saularis* and *C. malabaricus* invaded Borneo about a million years ago (Sheldon et al., 2009b; in preparation), certainly long enough for their genes to have diffused throughout the entire island.

A variety of paleontological, ecological, physiographic, and genetic forces probably have played a role in shaping Sabah's distinctive lowland bird and mammal faunas. Sabah is a small, almost peninsular, part of Borneo that is adjacent to Palawan and the Sulu Archipelago in the north and bordered by fairly substantial mountains in the west (Maligan and Crocker ranges) and south (Maitland and Witt ranges). Philippine taxa undoubtedly have invaded Sabah periodically and may have hybridized with indigenous taxa, adding to their distinctiveness. Lowland populations to the west and south of Sabah probably have been deterred from invading the state by its bordering mountains. Potential invaders may also have been influenced by altered distributions of forest and other habitats caused

by paleoclimatic changes (e.g., Bird et al., 2005; Mann, 2008). Perhaps most importantly, there may be genetic tension zones that inhibit the eastward diffusion of genes by reducing the inherent fitness of hybrids (Barton & Hewitt, 1985). This reduction in gene flow would not necessarily be related to environmental conditions, nor would it occur in the same place for all taxa, thus making the zone difficult to find without extensive molecular comparisons. Detailed exploration and examination of the molecular population genetic composition of taxa throughout Borneo and surrounding areas will be required to identify all the forces that have created Sabah's distinct lowland faunas.

In the mountains of Borneo, a different biogeographic story is emerging for birds. At least some montane endemics are more closely related to congeners in Java than to similar taxa in the lowlands of Borneo. Molecular and morphological comparisons have shown that the montane Bornean Swiftlet, *Collocalia dodgei*, is more closely related to *C. linchi* of Java than to *C. esculenta* in the lowlands of Borneo (Somadikarta, 1986; Moyle et al., 2008). Previously both taxa were considered parapatric subspecies of *C. esculenta*. In a similar case, the Bornean Forktail (*Enicurus borneensis*) appears to be more closely related to *E. leschenaulti leschenaulti* of Java than to *E. l. frontalis* in the lowlands of Borneo (Moyle et al., 2005). (Wells, 2007, mentioned alternative relationships for the two taxa based on juvenile plumages, but provided no details.)

Based on morphological comparisons, Davison (1999) argued that Borneo's montane Streaky-breasted Spiderhunter (*Arachnothera affinis everetti*) is most closely related to the Javan form (*A. a. affinis*), whereas its lowland counterpart, *A. modesta concolor*, is the same subspecies as the form in Sumatra. An interesting twist on this example is that it supports both the explanation for lowland patterns of endemism in Sabah and the montane pattern of endemism in Borneo. *Arachnothera modesta* is a fairly recent invader from Sumatra, judging from the similarity of the Sumatran and Bornean forms. It occurs in most, but not all, of the lowlands of Borneo. Where *A. modesta* occurs in lowland areas, it is replaced in the mountains by *A. affinis*. However, *A. modesta* is not found in Sabah. In Sabah, the erstwhile montane form, *A. affinis*, occurs in both the mountains and lowlands. Presumably, in the future, if *A. modesta* invades Sabah, *A. affinis* will become restricted to higher elevations.

The Bornean Leafbird (*Chloropsis kinabaluensis*) presents a case remarkably like the spiderhunter. Previously, it was considered to be a parapatric subspecies of the widespread lowland species, *C. cochinchinensis* (Smythies, 1999). Wells et al. (2003) have now separated it as an endemic Bornean species. We predict that genetic comparisons of these taxa will show that the lowland *C. cochinchinensis* is a relatively recent invader from western Sundaland (as it does not occur in Sabah) and the montane *C. kinabaluensis* will be most closely related to the Javan taxon, *C. cochinchinensis nigricollis*.

Other patterns. – Our surveys disclosed some other interesting patterns in Sabah's birds. A remarkable number of species was breeding at Klias Forest Reserve in early February 2004. Groups in breeding condition included: pigeons (*Treron vernans*), cuckoos (*Cacomantis merulinus*), woodpeckers (*Sasia abnormis*), swallows (*Hirundo tahitica*), bulbuls (*Pycnonotus goiavier*, *P. simplex*, and *Setornis criniger*), thrushes (*Trichixos pyrrhopygus* and *Copsychus saularis*), babblers (*Malacopteron albogulare*, *Macronous ptilosis*, *Stachyris nigricollis*, *S. maculata*, and *S. erythroptera*), warblers (*Orthotomus ruficeps*), flycatchers (*Rhipidura javanica*, *Rhinomyias umbratilis*, and *Hypothymis azurea*), flowerpeckers (*Prionochilus thoracicus*, *P. xanthopygius*, and *Dicaeum trigonostigma*), sunbirds (*Anthreptes singalensis*, *Hypogramma hypogrammicum*, and *Aethopyga siparaja*), and waxbills (*Lonchura malacca*). Wells (1976) and Sheldon et al. (2001) previously reported congregations of parrots, pigeons, bulbuls, and other frugivores breeding along Sabah's southwestern coast in late winter months, when fruit is plentiful. Numerous species were also found breeding at Serinsim in January, as reported by Sheldon et al. (2009c).

Our survey at Ulu Lauhon in the Meligan Range produced several remarkable elevational records. This site, at 1700 – 1800 m, had recently been cleared for the development of *Acacia mangium* plantation. Thus, an opportunity was created for lowland scrub-dwelling birds to travel high into the mountains and mix with resident montane species. At 1700 m, such lowland species as *Pycnonotus goiavier*, *P. simplex*, *P. plumosus*, *Malacocincla malaccense*, *Macronous gularis*, and *Orthotomus sericeus* occurred alongside the montane species expected at this elevation, such as *Pycnonotus flavescens*, *Alophoixus ochraceus*, *Hemixos flavala*, *Stachyris nigriceps*, *Cettia vulcania*, and *Orthotomus cucullatus*. Although recent logging seems to have been the cause of these high elevation records, the possibility that temperature changes from global warming had some influence (Colwell et al., 2008) should be considered in light of the recent discovery of elevational shifts in moths on Mt. Kinabalu (Chen et al., 2009).

Surveys in the ultrabasic forests of eastern Sabah, at Ulu Rukuruku and Mt. Meliau, revealed the expected poor-soil specialists *Malacopteron albogulare* and *Prionochilus thoracicus*. We did not encounter *Setornis criniger* at those sites, however. It appears largely restricted to peat swamp in Sabah (Sheldon, 1987). The forest at Ulu Rukuruku also yielded *Stachyris leucotis*, a scarce species, and the Bornean endemic *Ptilocichla leucogrammica*. On Mt. Meliau (1336 m), we were particularly interested in investigating the occurrence of montane species. The 1956 British Museum expedition failed to find any montane birds there (R. Sims, unpublished manuscript), but we expected them because of the proximity of Mt. Meliau to the Crocker Range and the presence of such species on several isolated peaks in Sabah (e.g., Mt. Lucia). Although we did not spend much time at high elevation, we confirmed the presence of at least two montane species on Meliau, *Pellorneum pyrrogenys* and *Yuhina everetti*. Undoubtedly others occur there as well.

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