Ornithological survey of the mountains of the Huon Peninsula, Papua New Guinea

by Benjamin G. Freeman, Alexandra Class, Jennifer Mandeville, Suzanne Tomassi & Bruce M. Beehler

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Summary.—Based on field work conducted between 2009 and 2012 in the YUS Conservation Area on the Huon Peninsula, we present novel distributional information for 47 avian species. This includes range extensions, elevational records, demographic data and new records of species poorly known in New Guinea. Meyer's Goshawk *Accipiter meyerianus*, Rufous-throated Bronze Cuckoo *Chrysococcyx ruficollis*, Papuan Scrubwren *Sericornis papuensis*, Alpine Robin *Petroica bivittata*, Greater Ground Robin *Amalocichla sclateriana*, Yellow-breasted Bowerbird *Chlamydera lauterbachi* and a possible Rufous Monarch *Monarcha rubiensis* are recorded for the first time from the Huon Peninsula. The northern scarp of the mountains of the Huon Peninsula is shown to be a contact zone for several lowland species-pairs.

New Guinea is justly famed for its endemic avian radiations, best exemplified by the spectacular birds of paradise (Frith & Beehler 1998, Laman & Scholes 2012). Diversification of New Guinean bird lineages has been shaped by the island's geography, particularly the location and aspect of its mountain cordilleras (Diamond 1972, 1985, Heads 2002). New Guinea's highest and most extensive mountains are the Central Ranges, which form a continuous montane spine that stretches north-west–south-east along nearly the entire island. In addition, New Guinea has 19 outlying mountain ranges that vary in size and distance from the Central Ranges (Diamond 1985). New Guinea's mountains constitute a classic study system in island biogeography, and comparative study of avian distributions on the Central Ranges and outlying ranges has been used to infer historical patterns of speciation and community assembly (Diamond 1972, 1973).

The highest and most extensive of New Guinea's outlying ranges, with peaks of up to 4,120 m, are the Huon Mountains in north-east New Guinea, comprising the tectonically affiliated Finisterre, Saruwaged, Cromwell and Rawlinson ranges (Fig. 1). The Huon Mountains are geologically young; the majority of uplift occurred in the last one million years, and they continue to rise at a minimum rate of 0.8–2.1 mm / year (Abbott *et al*. 1997, Hovius *et al*. 1998). In comparison, the Central Ranges are similar in height (peaks up to 5,030 m) but much older; while a large degree of uncertainty remains, the majority of uplift is thought to have occurred *c*.5 million years ago (van Ufford & Cloos 2005).

The Huon Mountains are isolated from other montane regions by the lowland barrier of the Ramu / Markham Basin lowlands. The nearest montane regions are the adjacent Central Ranges, *c*.10–30 km distant, and the outlying Adelbert Mountains (highest peak *c*.1,700 m) *c*.30 km to the north-west (Fig. 1). This isolation has spurred allopatric speciation; the Huon Mountains are home to four endemic bird species—Spangled Honeyeater *Melipotes ater*, Huon Melidectes *Melidectes foersteri*, Huon Astrapia *Astrapia rothschildi* and Emperor Bird-of-Paradise *Paradisaea guilielmi*—while Wahnes's Parotia *Parotia wahnesi* is endemic to the Huon and Adelbert Mountains (Beehler *et al*. 1986). With the exception of Emperor Bird-of-Paradise, whose range abuts that of Lesser *P. minor* and Raggiana Bird-of-Paradise

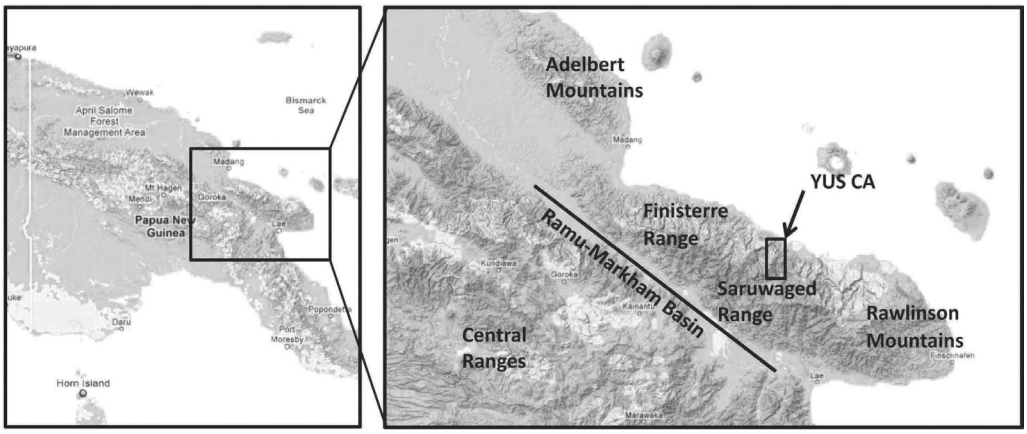

Figure 1. Map of New Guinea showing the location of the Huon Peninsula in relation to the Central Ranges and Adelbert Mountains. Field work took place within the YUS Conservation Area (YUS CA), in the Saruwaged Range of the Huon Peninsula.

P. raggiana at lower elevations, the Huon endemics are all allospecies, with closely related species in the Central Ranges. The Huon Mountains also harbour 24 endemic subspecies, with a further five endemic subspecies shared with the Adelbert Mountains (Coates 1985, Beehler *et al*. 1986, Coates 1990).

While the isolation of the Huon Mountains has promoted evolutionary divergence, the intervening lowlands of the Ramu / Markham Basin act as a geographic barrier limiting the colonisation of montane taxa from the Central Ranges. New Guinea's outlying ranges are in all instances species-poor compared to the Central Ranges (Diamond 1973, 1985, Beehler *et al*. 2012). The Huon Mountains are both large in extent and relatively close to the Central Ranges. Accordingly, the avifauna of the Huon Mountains is the most diverse of New Guinea's outlying ranges and far more so than that of the relatively small and isolated Adelbert Mountains (Pratt 1982, Diamond 1985).

New Guinea's montane avifauna provides a classic system in island biogeography (Diamond 1985), with distributional patterns in New Guinea's montane regions repeatedly used to infer processes of speciation, diversification and community assembly (Diamond 1970, 1973, Mayr & Diamond 2001). The accuracy of such studies is dependent on the quality of distributional data used in analyses. Here we present the results of extensive field work in the Saruwaged Range of the Huon Mountains—the most thorough avifaunal survey of the Huon Mountains conducted to date. Our surveys build on information garnered by early collectors (summarised in Stresemann 1923), and especially field work conducted in the Rawlinson and Saruwaged Ranges by E. Mayr in 1928–29 (>1,000 specimens collected; Mayr 1931, Haffer 2007). More recently, the Huon montane avifauna was surveyed by BMB (Mount Bangeta, Saruwaged Range, 19–28 September 1975, 1,400–3,750 m; 75 specimens in United States National Museum, Washington), by A. L. Mack, P. Igag, B. Benz, E. Scholes, R. Sinclair & W. Betz in 2001 and 2003 (Teptep area, Saruwaged Range), and by J. M. Diamond & K. D. Bishop in 2004 and 2006 (Wasaunon area, Saruwaged Range). Despite these prior unpublished surveys, we document five additions to the 86 montane species (defined as species largely distributed above 1,000 m) previously known from the Huon Mountains, comment on our records of poorly known species, and present several new elevational records. While our findings do not qualitatively alter the conclusions of previous studies of New Guinea's avian biogeography, new distributional information provides a more solid

basis for understanding the biogeography, diversification and community assembly of New Guinea's montane avifauna.

Methods

Surveys were conducted in the YUS Conservation Area (YUS CA, named after the Yopno, Urawa and Som Rivers) in Morobe Province. The YUS CA is Papua New Guinea's first recognised Conservation Area, a formally gazetted national designation given to lands pledged for conservation by traditional landowners (Fig. 1). The region is located between 05°45'–06°20'S and 146°30'–147°00'W. It protects *c*.76,000 ha of primary humid forest along an elevational gradient from the north coast to alpine heathlands and grasslands at 4,020 m in the Saruwaged Range. Field work took place in October–November 2009 and in June–July in 2010, 2011 and 2012, with a total of *c*.300 person-days.

We conducted our principal field work along an elevational transect through primary humid forest at 135–3,050 m (see Table 1 for locality information). Twenty-five 1-km trails were cut along contours at intervals of 120–200 m in elevation. We conducted aural censuses and extensive mist-netting along each trail. Aural censuses followed the Variable Circular Plot distance sampling methodology (Beehler *et al*. 1995, Beehler & Mack 1999, Camp & Reynolds 2009). Six census points were established along each contour track at 200-m intervals. A ten-minute sound census was conducted at each point and repeated twice each day for three days. Mist-netting surveys consisted of 36 12-m mist-nets arrayed over 600 m of each 1-km contour trail, and operated for 2.5 days per site (see Table 1 for mist-net effort). Captured individuals were weighed, measured (wing, tail, culmen, tarsus), scored for moult and photographed. We also took blood samples from the brachial vein from the majority of captured individuals. To identify previously captured individuals, we clipped the distal portion of the right three outer rectrices, permitting easy diagnosis of recaptures during the same season. We augmented our quantitative surveys with qualitative observations during the course of field work. Sound-recordings by BMB, BGF & AMC have been archived at the Macaulay Library of Natural Sounds at the Cornell Lab of Ornithology, Ithaca, NY, while georeferenced distributional data have been archived in the Avian Knowledge Network via eBird.

Results

To date we have recorded 267 species in the YUS CA, mist-netted 4,901 individual birds and vocally censused an additional 10,800 individuals over four field seasons. Here, we report novel distributional data for 47 species, including range extensions, elevational records, demographic data and new records of species poorly known in New Guinea. More detailed analyses of community composition will be presented elsewhere.

BLACK-MANTLED GOSHAWK *Accipiter melanochlamys*

Recently discovered on the Huon Peninsula, with sight records (Coates 1985) and a specimen collected from the YUS CA in 2001 (B. Benz, University of Kansas Natural History Museum, KU95811). Uncommon in montane forest in the YUS CA at *c*.1,700–3,000 m (BGF, ST photographs), we mist-netted three individuals at 1,790 m, 2,180 m and 2,420 m. We observed three other individuals, one as low as 1,090 m (BGF & AMC sighting, 15 July 2011).

MEYER'S GOSHAWK *Accipiter meyerianus*

We present the first record of this large montane goshawk for the Huon Peninsula (Beehler *et al*. 1986). BMB, JLM & ST observed an adult vocalising and giving a display flight for more

TABLE 1
Location of study sites in YUS for surveys conducted in 2009–12. Abbreviations for type of census: A = aural census using Variable Crcular Plot method, M = mist-net sampling, O = qualitative auditory and visual observations. Further information detailing survey methodology for both mist-net and aural censuses is presented in Methods. All mist-nets used were 12 m in length.

Site name	Elevation (m)	Latitude	Longitude	Type of census	Mist-net hours	Years
Nanaiya 2 Camp Bottom	143	05°55′31.6″S	146°52′88.4″E	M, A	1,004	2012
Nanaiya 2 Camp Lower	230	05°55′80.6″S	146°52′275″E	M	1,096	2010
Nanaiya 2 Camp	258	05°55′89″S	146°52′11.8″E	M, A	1,452	2012
Nanaiya 2 Camp Upper	300	05°56′48.8″S	146°51′93.5″E	M, A	1,196	2012
Nanaiya 1 Camp	390	05°57′048″S	146°51′535″E	M	1,082	2010
Baiks Camp	610	05°55′864″S	146°49′769″E	M	1,102	2010
D'Kina Camp	620	05°57′10.6″S	146°52′40.7″E	M, A	1,536	2012
Waganon Camp	750	05°57′55.4″S	146°52′076″E	M	1,056	2011
D'Kina Camp Upper	808	05°57′69.2″S	146°52′56.1″E	M, A	1,364	2012
Gutganaknon Camp	910	05°57′593″S	146°50′551″E	M	1,099	2010
Waganon Camp Upper	1,000	05°58′60.9″S	146°52′48.7″E	M, A	857	2012
Sombom Camp Lower	1,090	05°58′983″S	146°52′341″E	M	1,067	2011
Sapmanga Village	1,100	06°04′35.30″S	146°49′17.11″E	O	NA	2010, 2011
Gormdan Village	1,250	06°03′2.21″S	146°49′1.96″E	O	NA	2009, 2010, 2011
Langmang Camp	1,360	05°58′207″S	146°49′484″E	M	1,084	2010
Sombom Camp	1,510	06°00′152″S	146°52′910″E	M	1,098	2011
Sombom Camp Upper	1,660	06°00′852″S	146°52′587″E	M	1,035	2011
Kolmit Camp	1,790	05°58′639″S	146°49′810″E	M, A	1,089	2010
Kolmit Camp Upper	1,900	05°58′848″S	146°49′742″E	M	724	2011
Gamben Wagain Lower	2,040	05°59′310″S	146°49′839″E	M	1,017	2011
Camp 11 (Gamben Wagain)	2,150	06°00′13.7″S	146°49′25.9″E	M, A	2,201	2010, 2011
CL 11.5 (Youngurong Camp Lower)	2,280	06°01′094″S	146°49′900″E	M, A	1,038	2010, 2011
CL 12 (Youngurong Camp)	2,420	06°01′642″S	146°50′328″E	M, A	1,065	2010
Boksawin Land	2,550	06°05′16.39″S	146°51′44.38″E	M	569	2012
Camp 13 Lower (Kotom)	2,700	06°03′44.5″S	146°52′34.8″E	M, A	760	2011
Camp 13 (Yabem Daron)	2,821	06°04′18.9″S	146°52′35.2″E	M, A	900	2011
Wasaunon Camp	2,936	06°05′54.3″S	146°54′89.6″E	M, A	1,178	2011

than ten minutes on 6 June 2011 at 2,400 m above Boksawin village. Boksawin inhabitants reported this location to be a traditional nest site for the species. The vocalisation of this pale-morph adult was a forced *wih-i-yu*, with three calls given in four seconds.

PYGMY EAGLE *Hieraaetus weiskei*
New Guinea endemic, recently split from Australian Little Eagle *H. morphnoides* (Gjershaug *et al*. 2009), which was previously thought to be confined to elevations below 2,000 m (Beehler *et al*. 1986). BGF & AMC observed a soaring individual in good light for two minutes on 30 June 2011 at 2,420 m.

NEW GUINEA SCRUBFOWL *Megapodius affinis*
Widespread in lowlands of New Guinea, but previously unknown above 2,100 m (Beehler *et al*. 1986). We commonly observed it in montane forest in the YUS CA at 2,120–2,950 m (BMB sound-recordings at 2,950 m, 2010 and 2011). While we have not located any nest mounds in the YUS CA, local informants report that it nests commonly near sea level and in montane forest above *c*.2,500 m, but not at intervening elevations.

BRONZE GROUND DOVE *Gallicolumba beccarii*
Restricted to elevations above 1,200 m on mainland New Guinea (Baptista *et al.* 1997), it ranges far lower in the YUS CA, with individuals mist-netted as low as 390 m (AMC photograph). The presence of this small forest dove at low elevations is perhaps related to the apparent absence of several lowland dove species as yet unrecorded from the YUS CA (although reported for the Huon Peninsula by Coates 1985), including the medium-sized White-bibbed Ground Dove *G. jobiensis* (Diamond & LeCroy 1979).

PHEASANT PIGEON *Otidiphaps nobilis*
The previous highest-elevation record of this foothill species was 1,900 m (Beehler *et al*. 1986); BGF & AMC heard its distinctive two-note whistle at 2,050 m on 14 June 2011.

GOLDIE'S LORIKEET *Psitteuteles goldiei*
Known only from the Huon Peninsula by sight records presented by Coates (1985), BGF observed four in a flowering tree at 1,330 m on 11 July 2011 (BGF sound-recordings, video). This tree also attracted *c*.75 Little Red Lorikeets *Charmosyna pulchella*, 40 Red-collared Myzomelas *Myzomela rosenbergii* and a Pygmy Lorikeet *Charmosyna wilhelminae*. On 20 July 2011, BGF & AMC observed and sound-recorded a flock of *c*.40 *P. goldiei* in a flowering tree at 1,600 m, with four Papuan Lorikeets *Charmosyna papou* and *c*.10 Little Red Lorikeets. These are our only observations of Goldie's Lorikeet despite months of field work at appropriate elevations, suggesting that the species is relatively uncommon in the YUS CA.

PYGMY LORIKEET *Charmosyna wilhelminae*
Uncommon and probably overlooked throughout its ample New Guinea range (Beehler *et al*. 1986), BGF observed one in good light on 11 July 2011 in a flowering tree at 1,330 m (see Goldie's Lorikeet), foraging next to much larger Little Red Lorikeets *C. pulchella*.

BREHM'S TIGER PARROT *Psittacella brehmii*
Resident in the Central Ranges at 1,500–2,600 m, *P. brehmii* inhabits higher elevations in the YUS CA, from 1,750 m to at least 3,050 m, and is abundant at *c*.2,700–3,050 m (40 mist-netted individuals in 2011). This expanded elevational distribution is perhaps due to the absence on the Huon Peninsula of Painted Tiger Parrot *P. picta*, which replaces the present species above *c*.2,500 m in the Central Ranges (Diamond 1972). On more than ten occasions, BMB found the species foraging on the ground in forest interior for fruit or fallen flower buds.

PESQUET'S PARROT *Psittrichas fulgidus*
Threatened by hunting pressure throughout much of New Guinea and rare above 1,000 m, with a handful of records up to 2,000 m (Beehler *et al*. 1986). We observed it on a daily basis at 600–2,420 m in the YUS CA, a new high-elevation record for this distinctive New Guinea endemic.

CHESTNUT-BREASTED CUCKOO *Cacomantis castaneiventris*
A resident of hill forest at 500–2,300 m (Beehler *et al*. 1986), it ranges lower in the YUS CA. JLM mist-netted one individual at 250 m on 18 July 2012 and a second individual at 300 m on 23 July 2012 (JLM photographs).

RUFOUS-THROATED BRONZE CUCKOO *Chrysococcyx ruficollis*
Previously unknown from the Huon Peninsula (Beehler *et al*. 1986), we regularly heard the species in montane forest in the YUS CA between *c*.2,100 m and 3,000 m, where it appears to be an uncommon resident. JLM & ST mist-netted one at 2,850 m on 11 June 2011 (BMB photographs).

RUFOUS OWL *Ninox rufa*
This lowland species was previously known to occur only below 2,000 m (Marks *et al*. 1999). BGF & AMC observed and recorded one at our 2,150 m camp in June 2011 (e.g., AMC recording 22 June 2011). The species' vocalisation is a soft, low-pitched double hoot, *hu-hu*. This individual (or pair) frequently remained active until well after dawn (e.g., BGF observation of one vocalising in flight at 06.50 h on 26 June 2011). Additionally, AMC observed a Rufous Owl attempting to predate a mist-netted Rufous-backed Honeyeater *Ptiloprora guisei* at 07.45 h at 1,900 m on 20 June 2011.

PACIFIC SWIFT *Apus pacificus*
A rare winter visitor to the New Guinea region, recorded principally from the southern watershed of New Guinea during the boreal winter, in October–March (Beehler *et al*. 1986). We are aware of just one previous record from the Huon Peninsula—a sighting at Wasu Station in mid November (Coates 1985). AMC & BGF observed four of these distinctive large, fork-tailed swifts flying high in a flock of *Collocalia* sp. on the overcast afternoon of 10 July 2010 at 380 m. This is an unusual date, and suggests that some individuals may over-summer in New Guinea instead of returning to their Asian breeding grounds.

BLACK-BELLIED CUCKOO-SHRIKE *Coracina montana*
A resident of montane forest at 770–2,800 m, mainly found at 1,000–2,450 m (Coates 1990), JLM & ST mist-netted one at 2,850 m on 11 June 2011, and BMB additionally heard this canopy species at 2,800 m on 10 June 2011.

BLUE JEWEL-BABBLER *Ptilorrhoa caerulescens*
Fairly common at 220–590 m, where 13 of the sexually monomorphic *P. c. neumanni* were mist-netted (AMC, BGF, JLM photographs; Coates 1990). Despite intensive mist-netting effort, we did not mist-net or observe Dimorphic Jewel-babbler *P. geislerorum*, which was formerly considered conspecific with Blue Jewel-babbler (Coates 1990). The absence of *geislerorum* from the YUS CA is somewhat surprising; it co-occurs with Blue Jewel-babbler in the Adelbert Mountains to the west and also on the northern slope of the Central Ranges in south-east New Guinea (Coates 1990), and might therefore be expected throughout the Huon Peninsula.

SPOTTED JEWEL-BABBLER *Ptilorrhoa leucosticta*
A montane species previously recorded up to 2,700 m (Boles 2007), BGF observed three individuals at close range at 2,900 m on 19 May 2012.

RUSSET-TAILED THRUSH *Zoothera heinei*
Few records of this rare foothill forest species from New Guinea, including several from the Adelbert Mountains and Huon Peninsula (Beehler *et al*. 1986). Previously considered conspecific with Scaly Thrush *Z. dauma* (Collar 2005). AMC & BGF mist-netted one at 1,360 m on 20 June 2010 (AMC photograph); this was the only individual captured despite intensive mist-netting at appropriate elevations.

PAPUAN SCRUBWREN *Sericornis papuensis* / **BUFF-FACED SCRUBWREN** *Sericornis perspicillatus*
Papuan Scrubwren, previously unknown from the Huon Peninsula (Beehler *et al*. 1986), was first found in the YUS CA in 2004 (J. Diamond pers. comm.). Subsequent surveys revealed it to be uncommon at 1,900–2,420 m, but abundant at 2,700–2,940 m (20–30 individuals mist-netted at high-elevation locations). Papuan Scrubwren's elevational distribution in the YUS CA overlaps with the similarly sized Buff-faced Scrubwren at *c*.1,900–2,500 m. Papuan Scrubwren differs strongly in its vocalisations from Buff-faced Scrubwren, and is distinguished by its brownish-buff (not grey) crown and forecrown, warm-brown (not buff-orange) face, dark subterminal tail-band and hazel-brown irides (AMC & BGF photographs). While Gregory (2007) stated that Buff-faced Scrubwren possesses a dark subterminal tail-band, we found this to be true in only 8% of mist-netted Buff-faced Scrubwrens ($n = 25$); most had plain brown tails completely lacking any dark banding. In comparison, 93% of mist-netted Papuan Scrubwrens ($n = 28$) had obvious dark subterminal tail-bands (AMC, BGF photographs). At least in the YUS CA, our data concur with Diamond's (1972) suggestion that the presence of a subterminal tail-band is helpful in distinguishing these two species.

BICOLOURED MOUSE-WARBLER *Crateroscelis nigrorufa*
Patchily distributed throughout foothill elevations of New Guinea, this species is restricted to a very narrow elevational belt (Beehler *et al*. 1986). We found Bicoloured Mouse-warblers in the YUS CA at 1,660–1,900 m, and they were abundant at 1,790 m, where we mist-netted 41 individuals (15% of all mist-net captures at this site). The local abundance of this generally rare species is surprising; in comparison, there are just 38 specimen records of Bicoloured Mouse-warbler from anywhere in New Guinea in the ORNIS database. Bicoloured Mouse-warbler is replaced at lower elevations by Rusty Mouse-warbler *C. murina* and at high elevations by Mountain Mouse-warbler *C. robusta*, although in the YUS CA it is sympatric with the latter at 1,790–1,900 m.

BLACK FANTAIL *Rhipidura atra*
Common throughout New Guinea's mountains at 700–3,200 m (mainly 1,000–2,150 m) (Boles 2006). AMC & BGF mist-netted a female-plumaged bird at 610 m in July 2010 (AMC photograph). It is also present at relatively high elevations in the YUS CA, e.g., JLM & ST mist-netted a male at 2,710 m on 15 June 2011 (JLM photograph) and BMB observed this species at 2,900 m on 19 October 2009.

YELLOW-BREASTED BOATBILL *Machaerirhynchus flaviventer* / **BLACK-BREASTED BOATBILL** *M. nigripectus*
Boatbills replace one another elevationally in New Guinea forests. Yellow-breasted Boatbill inhabits forests below 1,300 m and Black-breasted Boatbill those above 1,130 m (Coates 1990). Despite this general pattern, boatbills appear to be absent at *c*.1,000–1,300 m in many well-studied regions of New Guinea (Diamond 1972), and a similar gap may also exist in primary forest in the YUS CA. However, BMB & BGF observed singing male Yellow-

breasted and Black-breasted Boatbills within 0.5 km along a trail in secondary forest at, respectively, 1,000 m and 1,100 m on 6 June 2011. We suggest that, at least in secondary forest, these congeners occupy abutting elevational distributions in the YUS CA.

RUFOUS MONARCH *Monarcha rubiensis*
Known from the lowland forests of northern New Guinea, from the Bird's Neck to the headwaters of the Ramu River and Madang region, this species has not been previously recorded from the Huon Peninsula (Beehler *et al*. 1986, Coates *et al*. 2006). In July 2010, BGF observed an apparent female of this rarely seen bird at close range as it foraged with a noticeably smaller Hooded Monarch *M. manadensis* at 230 m. However, two bouts of mist-netting (2010, 2012) in appropriate lowland forest habitat failed to confirm the species' presence. This should be the target of future field work in the area, as it would constitute an important range extension across an important biogeographic boundary formed by the Ramu Basin.

SHINING FLYCATCHER *Myiagra alecto*
Widespread across New Guinea's lowlands, but we are unaware of documented records from the Huon Peninsula. It is uncommon at low elevations in the YUS CA, with five mist-netted at 220 m by BGF & AMC in 2010 (BGF photographs), and two additional individuals mist-netted at 250 m by JLM in 2012 (JLM photographs).

OCHRE-COLLARED MONARCH *Arses insularis* / **FRILLED MONARCH** *A. telescophthalmus*
Formerly considered conspecific, these taxa differ markedly in plumage and distribution (Coates *et al*. 2006). Ochre-collared Monarch inhabits tropical lowland forest in the northern watershed of New Guinea (Beehler *et al*. 1986), and is the common *Arses* in the YUS CA, being regularly mist-netted and observed daily below 800 m (AMC photographs). However, AMC & BGF identified a male Frilled Monarch at close range on 7 July 2010 at 230 m, by its pure white breast and head. Subsequently, at 390 m, AMC & BGF mist-netted a male *Arses* with a faint buff-coloured upper breast and head (BGF photographs), in sharp contrast to the rufous head / breast of the common Ochre-collared Monarchs. Two more pale-headed / breasted individuals were mist-netted by JLM & BMB in 2012 at 300 m (JLM photographs). These two taxa co-occur near Wasu Station, *c*.20 km east of the YUS CA, where they appear to partially segregate altitudinally, Frilled Monarch occurring principally at lower elevations (Coates 1990, Coates *et al*. 2006). Our observations of Frilled Monarchs at 230–390 m and Ochre-collared Monarchs at 230–1,200 m tentatively corroborate this hypothesised pattern. We additionally suggest that the three mist-netted male *Arses* with pale buff-coloured heads / breasts were hybrids; largely Frilled Monarch-like in phenotype but with some characteristics of Ochre-collared Monarch.

BLACK-THROATED ROBIN *Poecilodryas albonotata*
We present a high-elevation record of this montane species, which is typically found below 2,750 m (Coates 1990). JLM & ST mist-netted one at 2,940 m on 21 June 2011 (JLM, ST photographs).

ALPINE ROBIN *Petroica bivittata*
Patchily distributed in the Central Ranges but previously unknown from the Huon Peninsula (Beehler *et al*. 1986). D. Bishop & J. Diamond observed this distinctive species in montane forest at 3,000 m in the YUS CA on more than five occasions during their 2004 field

work (J. Diamond pers. comm.). In addition, BGF twice observed a small party in May 2012 at 2,900 m (BGF sound-recordings).

GREATER GROUND ROBIN *Amalocichla sclateriana*
An enigmatic species previously known only from high montane forests in the Snow Mountains of east-central New Guinea and the Owen Stanley Range in south-east New Guinea (Beehler *et al*. 1986). We present the first record for the Huon Peninsula; BMB, JLM & ST mist-netted one at 2,710 m on 17 June 2011 (BMB photographs). Given the species' restricted distribution, our record is a major surprise. The bird had a black bill, brown irides, pink legs and appeared to be smaller than Central Range populations, with the following measurements taken in the field: wing chord (unflattened) = 94 mm, tarsus = 41 mm, tail = 68 mm, exposed culmen = 13.7 mm, weight = 54.7 g. All of these are outside the range of variation of the species' two known populations (Mayr & Rand 1937). Additional material may reveal the new population to be distinct from the two described subspecies.

LESSER GROUND ROBIN *Amalocichla incerta*
Common in the YUS CA at 1,660–2,420 m, BGF & AMC mist-netted a juvenile at 1,360 m on 20 June 2010 (AMC photographs). This record supports Diamond's hypothesis (1972) that juveniles tend to be distributed at the fringes of a species' elevational distribution.

REGENT WHISTLER *Pachycephala schlegelii*
Common in the YUS CA at 1,780–3,050 m, BGF & AMC mist-netted a juvenile at 1,360 m on 20 June 2010 (AMC photographs) This provides a second example of a juvenile observed well beyond the species' typical elevational distribution (Diamond 1972).

VARIABLE PITOHUI *Pitohui kirhocephalus*
Widespread in New Guinea's lowlands, the species is patchily distributed on the Huon Peninsula and largely absent from the Huon Gulf to Collingwood Bay (Beehler *et al*. 1986). In the YUS CA, it is common in forests at 140–750 m (AMC, BGF photographs). The closely related Hooded Pitohui *P. dichrous* generally replaces it at higher elevations, although both species occur syntopically in the YUS CA in a wide zone of overlap at *c*.140–750 m.

VARIED SITTELLA *Daphoenositta chrysoptera*
Previously known from the Huon Peninsula only from sight records presented by Coates (1990), AMC & BGF observed a flock of 8–10 individuals of both sexes on 9–10 June 2010, at our 2,150 m camp. On both dates, the flock was observed for 3–5 minutes foraging in the canopy, flying from tree to tree and calling incessantly. BMB observed small flocks at the same location in 2010–11, and we additionally observed flocks of 4–8 birds on three occasions in June 2011 in Gormdan village at 1,300 m.

RED-CAPPED FLOWERPECKER *Dicaeum geelvinkianum*
A lowland species generally found below 1,500 m, rarely to 2,350 m (Beehler *et al*. 1986), BMB observed and heard one singing at 2,420 m in forest interior on 12 July 2010.

SPOTTED BERRYPECKER *Melanocharis crassirostris*
Widespread and uncommon throughout the mountains of New Guinea (Beehler *et al*. 1986), it is fairly common in the YUS CA at *c*.1,700–2,300 m, where we frequently observed small groups in flowering trees. Despite this species' strong preference for the canopy, we mist-netted 11 in forest understory (nine females and two males; BGF photographs).

FOREST MELIPHAGA *Meliphaga montana* / **SCRUB MELIPHAGA** *M. albonotata*
These congeners exhibit consistent habitat preferences: Forest Meliphaga prefers primary forest while Scrub Meliphaga primarily inhabits secondary forest and disturbed landscapes, and is 'apparently absent in forest interior' (Higgins *et al*. 2008). However, we mist-netted both species syntopically in primary forest interior at 1,360 m in June 2010 (AMC, BGF photographs), and additionally mist-netted a Forest Meliphaga in young secondary forest near Gormdon village at 1,300 m on 8 June 2011. While the white-eared *Meliphaga* species generally segregate by habitat throughout New Guinea, these observations support Coates' (1990) observations that habitat preferences are not absolute.

CINNAMON-BROWED MELIDECTES *Melidectes ochromelas* / **HUON MELIDECTES** *M. foersteri*
Patchily distributed throughout New Guinea and previously considered restricted to a narrow elevational range at 1,100–1,800 m in the Huon Mountains (Higgins *et al.* 2008), Cinnamon-browed Melidectes is present at higher elevations in the YUS CA, where it is fairly common at 1,640–2,420 m (AMC photograph). The endemic Huon Melidectes *M. foersteri* replaces it in montane forests within the YUS CA at *c*.2,400–3,050 m, and presumably at higher elevations as well.

YELLOW-BREASTED BOWERBIRD *Chlamydera lauterbachi* / **FAWN-BREASTED BOWERBIRD** *C. cerviniventris*
These congeners are reported to co-occur only in the headwaters of the Ramu and Markham Rivers and near Dumpu along the Ramu River (M. LeCroy pers. comm.). We present the first record of Yellow-breasted Bowerbird from the Huon Peninsula (Beehler *et al*. 1986, Coates 1990). R. Jensen was shown the four-walled bower of this species at Worin village (*c*.1,500 m) in 2007, where local informants confirmed its presence in the Urawa drainage. BMB observed Fawn-breasted Bowerbirds at Sapmanga station (1,000 m) in 2009, and received reports of two-walled bowers of this species in this area, while Dono Ogate reported both two-walled and four-walled bowers near Yawan village (1,600 m) in 2009. Thus, both of these open-country bowerbirds apparently inhabit the YUS ecosystem, one of the few places where they co-occur.

LESSER BIRD-OF-PARADISE *Paradisaea minor* / **EMPEROR BIRD-OF-PARADISE** *P. guilielmi*
Distributed in the northern watershed of New Guinea, *P. minor* occurs 'irregularly to the northern slope of [the] Huon' (Beehler *et al*. 1986: 232). AMC & BGF observed females on several occasions in the YUS CA, identified by their brown mantle and diagnostic whitish underparts. We only observed this species at 220 m; at higher elevations it is replaced by the closely related *P. guilielmi*, which is common between 390 m and *c*.1,400 m. Raggiana Bird-of-Paradise *P. raggiana* is common in the north-east Huon Peninsula (Mayr 1931), and readily hybridises with *P. minor* where the two species' distributions overlap in the Ramu / Markham basin (Rand & Gilliard 1967). We therefore suggest that a Raggiana / Lesser hybrid zone is located east of the YUS ecosystem along the north coast of the Huon Peninsula.

MOUNTAIN DRONGO *Chaetorhynchus papuensis*
Common resident of New Guinea foothill forests at 600–1,600 m (Beehler *et al*. 1986) and as low as 200 m, this species is rarely recorded in lowland forests (Beehler *et al*. 1995, Coates 1990). We observed and mist-netted Mountain Drongo at 300–2,150 m (AMC, BGF,

JLM photographs). Additionally, we repeatedly mist-netted both Mountain and Spangled Drongos *Dicrurus hottentottus* in primary forest at 300 m, contradicting Beehler *et al*.'s (1986) assertion that the two species rarely occur together.

TORRENT-LARK *Grallina bruijni*
A distinctive inhabitant of fast-flowing creeks and rivers at 400–2,400 m (Beehler *et al*. 1986), BGF and AMC found small groups of Torrent-larks along the Sari River down to 280 m in the YUS CA. It remains unclear why Torrent-larks do not occur further downstream than this; the river remains fast flowing and rocky to at least 200 m, and the ecologically similar Torrent Flyrobin *Monachella muelleriana* is present to at least 200 m.

Discussion

The Huon Mountains are considered to be relatively well surveyed by ornithologists (e.g., Mayr 1931, Rand & Gilliard 1967, Diamond 1985, Beehler *et al*. 1986, Coates 1990). However, our comprehensive surveys uncovered six additions to the montane avifauna (species largely distributed above 1,000 m) of the Huon Peninsula. While a relatively small number, these six additions represent a 6.9% increase in the known diversity of the Huon Peninsula montane avifauna, from 86 to 92 species (Coates 1985, Beehler *et al*. 1986, Coates 1990).

The montane avifauna of the Huon Peninsula is the product of colonisation from the Central Ranges (Diamond 1985). Separated by the lowlands of the Ramu / Markham Valleys, montane taxa on the Huon Peninsula have diversified in allopatry, producing five species and 24 subspecies endemic to the Huon Mountains (Coates 1985, Beehler *et al*. 1986, Coates 1990). An additional one species and five subspecies are shared endemics of the Huon and Adelbert Mountains, thought to represent cases of colonisation from one outlying montane region to the other (e.g., from the Huon Mountains to the Adelberts or vice versa; Pratt 1982, Diamond 1985).

Our records additionally provide insight into the lowland avifauna of the Huon Peninsula. This avifauna is depauperate compared to that of the adjacent lowlands of the Ramu Basin (Beehler *et al*. 1986). For example, we did not record Northern Cassowary *Casuarius unappendiculatus*, Victoria Crowned Pigeon *Goura victoria*, White-bibbed Ground Dove, Brown Lory *Chalcopsitta duivenbodei*, Papuan Babbler *Garritornis isidorei*, Tawny Straightbill *Timeliopsis griseigula*, Twelve-wired Bird-of-Paradise *Seleucidis melanoleucus* and Trumpet Manucode *Manucodius keraudrenii* in the YUS CA, all of which regularly occur in lowland forests of the Adelbert region (Beehler *et al*. 1986). However, our records of Blue Jewel-babbler, Shining Flycatcher, Variable Pitohui and Lesser Bird-of-Paradise from the YUS CA—lowland species thought to be absent from the north slope of the Huon Mountains—demonstrates that biogeographical barriers between the Huon Peninsula and the nearby Ramu Basin are weaker than previously considered (Beehler *et al*. 1986) for lowland species. The coastal plain in the YUS CA is very narrow (*c*.3–4 km), typical of the northern fringe of the Peninsula. We suggest that the geometry of this *c*.250 km ribbon-like strip of lowland forest may have led to higher extinction and lower colonisation rates through time, possibly explaining the apparent absence of some species from lowland forests of the YUS CA and the generally patchy distributions of lowland species on the north slope of the Huon Mountains.

Biogeographical inference of diversification and community assembly.—Molecular studies are rapidly increasing our ability to infer drivers of speciation in New Guinean birds (Dumbacher *et al*. 2008, Irestedt *et al*. 2009, Nyári *et al*. 2009, Jønsson *et al*. 2010, Deiner *et al*. 2011, Driskell *et al*. 2011). However, inferring mechanisms of diversification

from distributional data (Diamond 1973, Diamond 1986) continues to remain workable, especially in the absence of phylogeographic and population genetic data.

The geographical distributions of many genera of New Guinea lowland birds show patterns of allospecies occupying different regions of the island (e.g., northern vs. southern watershed; Beehler *et al*. 1986, Diamond 1986). Speciation in these systems is inferred to occur allopatrically due to the isolating effect of vicariant barriers, a hypothesis recently supported by a detailed phylogeography of a polytypic New Guinea lowland bird (Deiner *et al*. 2011). Our discoveries of Lesser Bird-of-Paradise in the YUS CA (with the closely related Raggiana Bird-of-Paradise known from the north-east Huon Peninsula and the Ramu / Markham basin), co-occurrence of and possible hybridisation between Ochre-collared and Frilled Monarchs, and both Yellow-breasted and Fawn-breasted Bowerbirds in the YUS CA demonstrate that the Huon Peninsula is an important zone of secondary contact for allopatric lowland taxa, as suggested by Mack & Dumbacher (2007). The importance of the Huon Peninsula and Ramu / Markham Basin as a driver of diversification in the lowland avifauna of New Guinea is further supported by subspecific taxonomy; 28 widespread lowland species exhibit subspecific breaks on or near the Huon Peninsula, most of which are represented by one subspecies on the Huon Peninsula, Markham Valley and adjacent Central Ranges, and by a different subspecies in the Adelbert Mountains and Ramu Basin (Mack & Dumbacher 2007).

Diamond (1972) observed that many New Guinea bird species exhibit patchy distributions. He hypothesised that local extinctions of montane taxa along the continuous Central Ranges occurred stochastically in small populations and provided the isolation necessary for divergence and speciation to occur. Diamond used the disjunct distributions of New Guinea montane species, including Greater Ground Robin, as evidence for this hypothesis. Our discovery of Greater Ground Robin in the highland forests of the Huon Peninsula is biogeographically surprising, as the species is currently unknown from apparently suitable habitat in the Central Ranges adjacent to the Huon Peninsula. We suggest that patchy distributions of montane taxa represent a form of the 'drop-out' phenomenon described by Diamond (1972), but that this pattern is likely to be the result of complex and dynamic histories of colonisation and extinction driven by climatic cycles and biotic processes rather than by stochastic local extinctions.

Competition between closely related species is thought to play an important role in structuring avian communities in New Guinea (Diamond 1973, Diamond 1986). This hypothesis is supported by distributional patterns of elevational replacements, where closely related species (usually congeners) inhabit abutting distributions along an elevational gradient. We recorded numerous examples of this phenomenon in the YUS CA, including many genera with sequences of three elevational replacements (e.g., *Crateroscelis*, *Melidectes*). While the 'middle' taxon of these 'trios' is often patchily distributed throughout New Guinea (Diamond 1972), we found 'middle' taxa to always be present in the YUS CA and in some cases to be more abundant (Bicoloured Mouse-warbler) or to occupy a wider elevational distribution (Cinnamon-browed Melidectes) compared to the adjacent Central Ranges.

The importance of interspecific competition to the maintenance of parapatric range borders in species that replace one another elevationally is supported by examples of enlarged altitudinal distributions in the absence of a competitor (usually congeneric). Diamond (1973) illustrated this phenomenon by comparing the elevational ranges of Rufous-backed Honeyeater *Ptiloprora guisei* in the Huon and Central Ranges. This species is resident at *c*.1,700–2,500 m in the Central Ranges, replaced above 2,500 m by its close relative Black-backed Honeyeater *P. perstriata*. Black-backed Honeyeater is absent in the Huon

Mountains, however, and Rufous-backed Honeyeater expands its climatic niche, inhabiting a broad elevational zone at *c*.1,660–3,500 m (higher than the scope of our studies in the YUS CA) in the Huon Peninsula. We comment on two additional examples of climatic niche expansion in the absence of a congener on the Huon Peninsula. First, Brehm's Tiger Parrot *Psittacella brehmi* is present at *c*.1,700–2,500 m in the Central Ranges where it co-occurs with the closely related Painted Tiger Parrot (*c*.2,500–3,200 m). Brehm's Tiger Parrot inhabits a wider distribution—from 1,750 m to at least 3,000 m—in the YUS CA, and is abundant at high elevations (2,500–3,000 m). As first suggested by Diamond (1972), this scenario may reflect niche expansion of Brehm's Tiger Parrot on the Huon Peninsula due to the absence of its competing congener. Similarly, the normally montane Bronze Ground Dove inhabits lowland and foothill forests in the Huon; while more tentative, this elevational expansion is perhaps associated with the apparent absence of several lowland ground dove species in the YUS CA.

Conclusion

We completed a comprehensive survey of the avifauna of the YUS CA in the Huon Mountains of New Guinea, using both mist-netting and aural censuses between 135 m and 3,050 m. The new information regarding avian distributions in New Guinea garnered during our field work implies that current knowledge remains incomplete, but confirms the important role of the Huon Peninsula in the diversification of both the island's lowland and montane avifaunas. Our distributional records reveal that the montane avifauna of New Guinea continues to be an excellent system in which to investigate biogeography, diversification and community assembly. Our many elevational records may suggest that some species are expanding their distributions upslope in response to climate change. We recommend further biodiversity surveys of New Guinea's montane regions, with collecting to document plumage variation and facilitate identification of difficult groups (e.g. *Meliphaga*), and continued monitoring of bird populations to investigate the possibility that species range boundaries are shifting in response to climate change. Finally, we recommend field surveys in all under-surveyed mountain regions using large arrays of mist-nets (>35) deployed at many elevational intervals, complemented by aggressive sound-recording by individuals knowledgeable with New Guinea bird song.

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Addresses: Ben G. Freeman, Dept. of Ecology and Evolutionary Biology, Cornell University, W257 Corson Hall, Ithaca, NY; and Cornell Lab of Ornithology, 159 Sapsucker Woods Road, Ithaca, NY, USA, e- mail: bgf27@cornell.edu. Alexandra Class, Cornell Lab of Ornithology, 159 Sapsucker Woods Road, Ithaca, NY, USA. Jennifer Mandeville, 327 Harper Place, Apt. 2, Highland Park, NJ 08904, USA. Suzanne Tomassi, 7358 28th Avenue SW, Seattle, WA, USA. Bruce M. Beehler, Science and Knowledge Division, Conservation International, 2011 Crystal Drive, Arlington, VA 22202, USA.