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Notes on nesting, territoriality and behaviour of broadbills (Eurylaimidae, Calyptomenidae) and pittas (Pittidae) in Tawau Hills Park, Sabah, Malaysian Borneo

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SUMMARY.—Basic natural history and behavioural data are lacking for the majority of broadbills and pittas (Eurylaimidae, Calyptomenidae and Pittidae). We present a series of observations on these birds made during two visits to Tawau Hills Park, Sabah, Malaysia. During this period, we detected changes in temporal presence, detectability or vocal behaviour in various species. We also found habitat overlap on one ridgeline among four species of pitta. We observed a Green Broadbill *Calyptomena viridis* respond to our imitation of a call with a wing display. We discuss the social behaviour of Black-and-yellow *Eurylaimus ochromalus* and Banded Broadbills *E. javanicus*, including wing displays, territoriality, and in the first-named species, social groups comprising multiple adults. We also describe various nesting behaviours in these two species, including nest-construction techniques, incubation behaviour, nest defence, and the first described Banded Broadbill nest on Borneo. We found Dusky Broadbills *Corydon sumatranus* to frequently be the most conspicuous members of mixed-species flocks otherwise dominated by Cuculidae and Picidae. We analysed Black-crowned Pitta *Erythropitta ussheri* home range size and density in a colour-banded population, and found a potential hybrid or backcross with Garnet Pitta *E. granatina*. We observed that Blue-banded Pitta *E. arquata* make non-vocal sonations by striking their closed wings on their flanks, and discuss the immature male plumage of Blue-headed Pitta *Hydrornis baudii*.

The Old World suboscines, or Eurylaimides, are a passerine radiation that reach their highest diversity in South-East Asia. Within this region, the island of Borneo is home to three species of Calyptomenidae, five Eurylaimidae and nine Pittidae; six of these are endemic to the island (Phillipps & Phillipps 2014). Most knowledge of these birds comes from sporadic field observations, descriptions of specimens and phylogenetic analyses (e.g. Phillipps 1970, Raikow 1987, Prum 1993, Myers 1999, Prum *et al.* 2014, Zubkova & Korzun 2014). Prior to our work, there were no dedicated studies of these birds in the field on Borneo, although some Old World suboscines have been the subject of dedicated studies elsewhere (e.g., Zimmermann & Noske 2003, Zubkova 2017).

Here, we report our observations on natural history of the eurylaimid broadbills, pittas, and green broadbills made at Tawau Hills Park in Sabah, Malaysia (during six weeks in summer 2012 and three months in early 2013).

Methods

Tawau Hills Park is a national park managed by Sabah Parks, a state agency, in Tawau District in southern Sabah, near the border with Indonesia. The park was established in

1979 to protect the water basins of seven major rivers, and spans nearly 280 km² (Omar & Nais 1995). It supports primary lowland and hill dipterocarp forest, *kerangas*, and lower montane forest spread across three low mountains (Gunung Magdalena—1,312 m, Gunung Lucia—1,202 m and Gunung Maria—1,083 m; Omar & Nais 1995, Sabah Parks 2018). It is the only park in Sabah to protect lowland primary forest on volcanic soils (Tjia *et al.* 1992, Lakim 2008), and thus hosts some of the tallest tropical trees in the world, including a *Shorea faguettiana* that is 88.3 m tall (Dial *et al.* 2005, Seino *et al.* 2007). The park is surrounded by plantations.

Our visits to Tawau Hills were made on 20 June–1 August 2012 and 26 February–20 May 2013. The philosophy guiding these undergraduate-led expeditions is detailed in Winkler *et al.* (2017), but our goal was to document the natural history of Old World suboscines. Our research was concentrated within the 2 km² of old-growth forest around the park entrance (04°39.95'N, 117°88.92'E) and included patches of primary and secondary lowland and hill forest, freshwater swamps, riparian forest, and forest edge. We also briefly visited montane forest on Gunung Lucia.

Observations.—We took notes on the life history of all suboscines encountered. We spent most time off main trails, using paths in the study area and moving between them, particularly near Black-crowned Pitta *Erythropitta ussheri* territories (see Figs. 1, 9 and 11 for

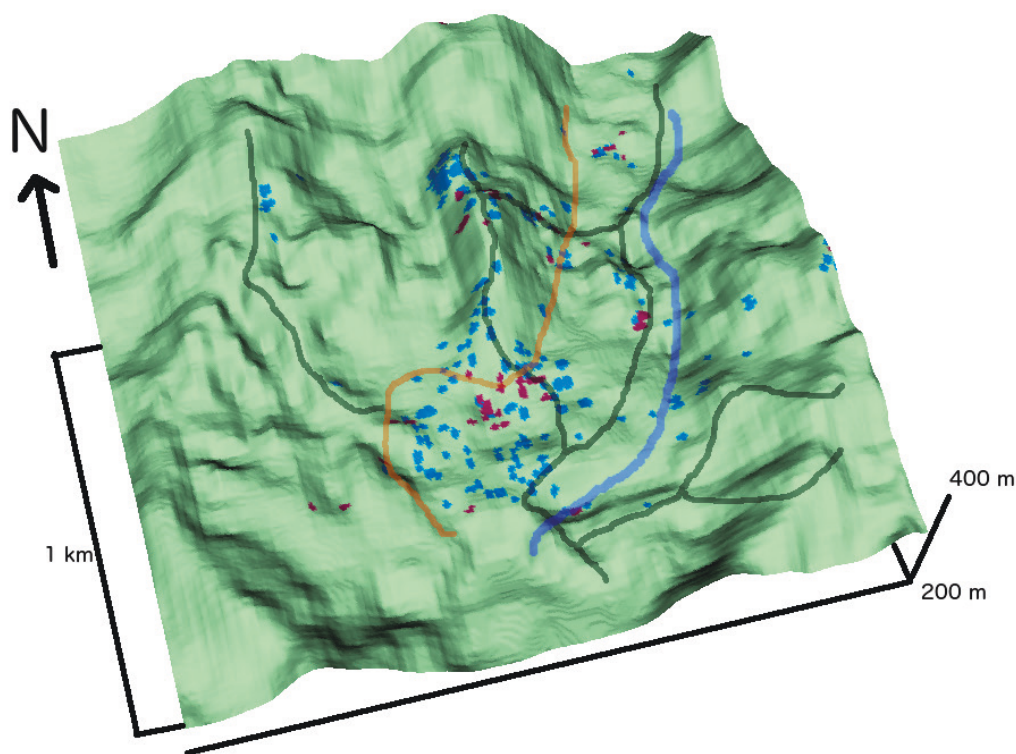


Figure 1. Map of the topography of our study area showing sightings of Black-and-yellow *Eurylaimus ochromalus* (blue) and Banded Broadbills *E. javanicus* (maroon) from both visits. Each point represents a sighting. Variation in point size and shape is an artefact of 3D plotting. This map demonstrates that Banded Broadbills occurred at a much-reduced density in the study area compared to Black-and-yellow Broadbills. Grey lines represent trails, the brown line represents a water pipeline, and the blue line represents the Tawau River. 3D map courtesy of JAXA (2015).

maps of the main study area). During both visits, a crew of 6–8 people spent 10–12 hours per day in the field (generally 06.00–18.00 h). We follow Clements *et al.* (2018) for species limits and names.

Spot mapping.—For some focal species, we recorded the locations of sightings and plotted these on a 3D topographic map of our main study area using data from the ALOS (Advanced Land Observing Satellite) Global Digital Surface Model, released by the Japan Aerospace Exploration Agency (© JAXA 2015). See Figs. 1, 9 and 11.

Home range estimates.—We used sightings and captures of individual Black-crowned Pittas, which were colour-banded, to plot each bird's home range (i.e. the area used by the individual on a daily basis) using a kernel density estimator (Powell 2000). Analyses were performed in R 3.2.1 (R Core Team 2015) using the function *kde2d* in the package *MASS* (Venables & Ripley 2002). Bandwidth was determined using a rule-of-thumb procedure of Scott (1992), employing a standard factor of 1.06. From our observations, we used a min. 7 and max. 119 points to calculate home range estimates.

Capture.—All captured birds were caught in 30-mm mesh, 3–12 m mist-nets. To target broadbills, we suspended two 12-m, four-trammel mist-nets, one above the other, 10–30 m above ground using a pulley system fastened to a scaffolding of para-chord that we placed in the trees. We had few passive captures in these mist-nets and used playback to target individuals. All of our playback tracks were .mp3 files downloaded from Xeno-canto (www.xeno-canto.org). All birds were handled under the approved Cornell IACUC protocol # 2001-0051 to DWW, and under an access license from Sabah Biodiversity Council and research permit issued by Sabah Parks.

Media collecting.—We collected high-quality audio and video recordings of vocalisations and behaviours. All of these are archived at the Macaulay Library of Natural Sounds (macaulaylibrary.org) and are publicly available online. We include Macaulay Library video catalogue numbers to cite videos of the behaviours we describe. To easily view the linked video, use the following URL with the catalogue number in question; e.g. <http://macaulaylibrary.org/asset/479590> links to the video catalogue number ML 479590.

Results

GREEN BROADBILL *Calyptomena viridis*

Encountered infrequently in the lowlands of Tawau Hills in 2012 and 2013 (despite regular visits to fruiting trees), but it was more common in the highlands in 2013. We observed the species ten times between 24 June and 26 July 2012, and twice in 2013, the latter during four visits to a strangler fig tree from 27 February to 4 March, and on a single visit to a fig tree 350 m away on the other side of a ridge on 7 April. Green Broadbills responded once to playback in 2012 (see below), but never in 2013. They were usually solitary, but we saw them in pairs several times, including on 27 February 2013, when a pair visited the understorey and made complex soft vocalisations while just out of sight. During a three-day excursion to Gunung Lucia in 2013, we heard *c.* 6 individuals at 850–940 m.

The species' scarcity in the primary forest lowlands of Tawau Hills during our visits (including July 2012) contrasts with the abundant breeding activity (and responsiveness to playback) in a degraded lowland forest in July 2014 (Pegan *et al.* 2018). Others have suggested that Green Broadbills are nomadic, as evidenced by broad and sporadic elevational records, and apparent rarity when fruit is scarce (Medway & Wells 1970, Fogden 1972; but see Lambert 1989). That the species tended to appear suddenly at Tawau Hills in places that they had not been before, and then disappear again, is consistent with this hypothesis.

On 24 June 2012, JAK observed a Green Broadbill respond to an imitation of its calls with a wing-raising display. JAK imitated the soft vocalisations of a lone male calling in the midstorey, whereupon the bird immediately flew directly and repeatedly overhead (c.5 m above ground). Each time the bird perched, it raised both wings so that their dorsal surfaces either touched or almost did so. Other displays in which Green Broadbills use their wings in various ways were summarised by Lambert & Woodcock (1996) and Wells (2007), although none was in response to vocal imitations or playback.

BLACK-AND-YELLOW BROADBILL *Eurylaimus ochromalus*

By far the commonest broadbills at our study site. We made spot maps of sightings (compiled in Fig. 1) which demonstrate that Black-and-yellow Broadbill occurs at a fairly high density throughout the areas we surveyed, relative to Banded Broadbill *E. javanicus* with which its home ranges overlapped.

Individuals (in pairs or small groups) often counter-sang in close proximity to other individuals or groups. They interspersed their frequent songs with throaty *keowrr* calls, which were used during sometimes aggressive confrontational interactions (as in a video JMH made at Sepilok Rainforest Discovery Centre, near Sandakan in north-east Sabah, ML 480277). Attempts to understand territoriality by colour-marking three individuals were largely unsuccessful because we only re-sighted birds twice: one on the day following its capture in the same general area; and the other at its nest, 137 m from the mist-nets, several days post-capture.

Despite frequent apparently confrontational behaviour, such as counter-singing, we rarely witnessed aggressive interactions such as chasing. Individuals we observed had a high level of tolerance for others in their territories or in close proximity. Even in areas where birds frequently counter-sang, individuals were often accompanied by several others silently perched nearby and only calling occasionally. In one territory, three adults—a female and two males—often approached together in response to playback and showed no signs of aggression to each other. Once, when only the two males appeared, they duetted after flying back and forth together, searching for the source of the vocalisations. Wells (2007) reported gatherings of up to five birds, but no ‘regular associations larger than pairs or pairs with offspring’.

Although other broadbills sometimes breed cooperatively (Phillipps 1970, Lambert & Woodcock 1996, Zubkova 2017), we never saw more than two Black-and-yellow Broadbills at or in the general vicinity of nests, except once when two females and an unmarked male briefly perched near an almost constructed nest belonging to a different (colour-marked) male. One of the females entered the nest for a few seconds, but all three birds departed shortly afterwards. Unseen birds sang and called throughout the event, but the colour-marked male did not arrive until 30 minutes later. The unmarked male never came near the nest again, and it is unlikely that he was engaged in cooperation.

Wing displays have been described for this species. These involve stereotypical raising of the wings, usually slightly above the back, accompanied by a slow opening and closing of the flight feathers (Lambert & Woodcock 1996). We observed such displays in a variety of contexts. Individuals frequently displayed after singing and after arriving in an area in response to playback. However, there were many situations in which a lone bird that had apparently been foraging would open its wings. On several occasions, we observed them spread just one wing at a time, and other times a spread wing was accompanied by a tail wag. When we approached birds along the canopy walkways at the Sepilok Rainforest Discovery Centre, we could hear soft vocalisations associated with these displays (Fig. 2, ML 480226), which were higher pitched and squeakier than similar calls of Banded

Broadbills (see below). We also sometimes witnessed gaping displays along with wing displays, during which an individual would open and close its bill in a deliberate fashion without making any sound (ML 479588, 480299). These displays may be enhanced by the striped pattern of the gape. However, it is sometimes difficult to distinguish these from non-display yawning or stretching (e.g. ML 480305). More information on the contexts of these displays would aid our understanding of the species' social behaviour.

Like Prentice (1988 *in* Lambert & Woodcock 1996), we observed a copulation following a wing-spreading display, and videoed the entire process (ML 471162). On 24 July 2012 at 07.58 h, an adult male and female perched on a horizontal branch c.6 m above ground. As the male flew in, the female spread her wings and opened her bill. The male then performed

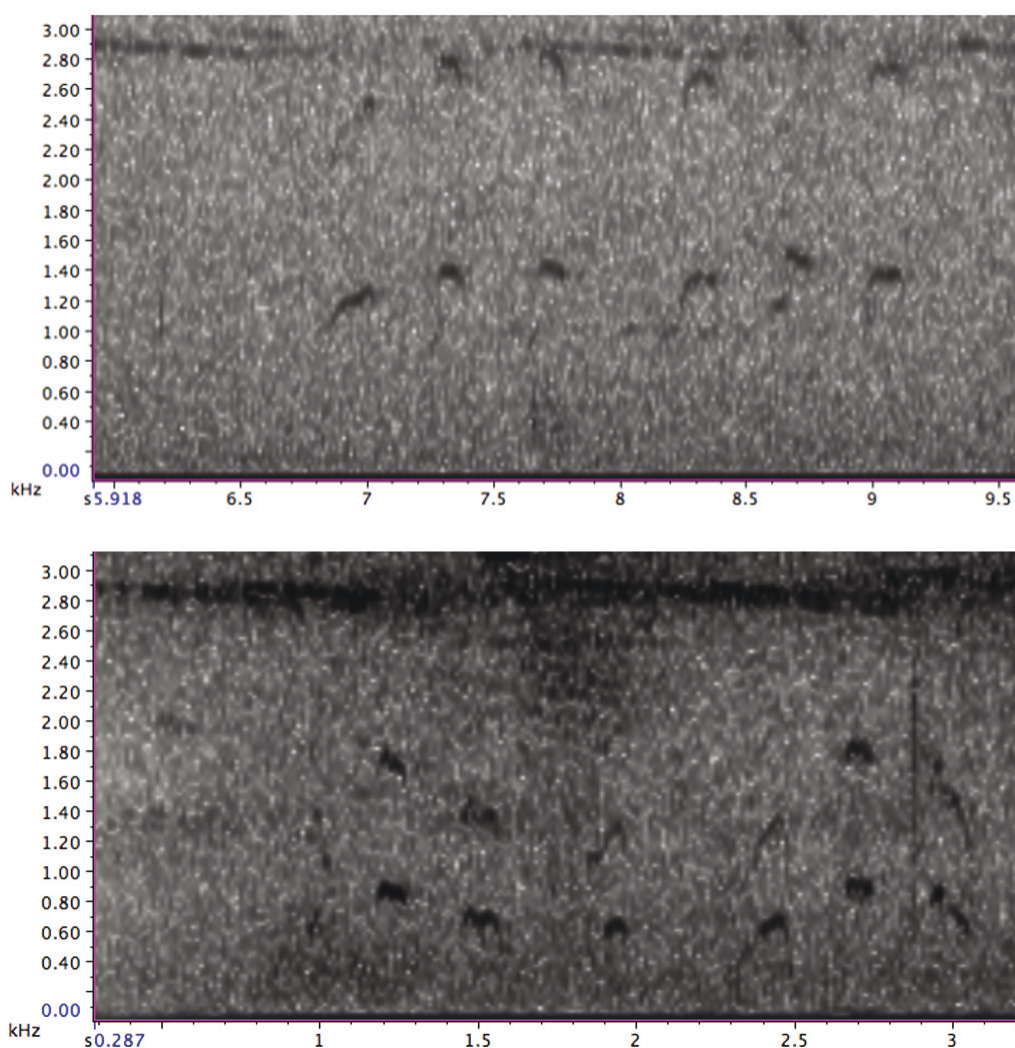


Figure 2. Spectrograms of the soft vocalisations made by *Eurylaimus* broadbills while performing spread-wing displays. In both species the duration of each note was c.0.12–0.2 seconds, given at a rate of 2–3 notes / second. Black-and-yellow Broadbill *E. ochromalus* calls (top, $n = 10$ in two bouts) ranged from 1.14 to 1.75 kHz (mean 1.45) and Banded Broadbill *E. javanicus* calls (above, $n = 6$ in one bout) from 0.61 to 0.88 kHz (mean 0.73). A set of harmonic notes is visible above the fundamental frequency in both spectrograms.



Figure 3. Black-and-yellow Broadbill *Eurylaimus ochromalus* nest, 2013 (Eric R. Gulson-Castillo). Inset: Black-and-yellow Broadbill holding a green object just before bringing it to its nest, from video ML 471552 (© Brian Magnier)

the same displays. They did not wag their tails, as they did in the display described by Prentice (1988). Following several repetitions by both individuals, they copulated. The male then perched to the left of the female and continued to perform wing displays but the female did not (similar to Prentice 1988). Four seconds later the female briefly pecked the male's bill while he continued displaying. The male continued displaying his wings until after the female departed a few seconds later.

We observed one active nest (see Fig. 3) in late July 2012, and four between 9 March and 22 April 2013. An additional new nest construction attempt was observed briefly on 9 May 2013. The five nests were high in trees (c.20–35 m above ground). Most were at least partially shaded by a leafed branch or vine, but that in July 2012 was suspended from a brushy vine tangle dangling in the open away from the tree's trunk, exposing the nest to full sunlight. All of the nests swayed freely in wind. Some nests were concealed, but others were conspicuous. We never noticed bee or wasp hives in the vicinity of nests (Lambert & Woodcock 1996, Smythies 1999), despite searching for them. The appearance of the nests was consistent with previous descriptions (summarised in Lambert & Woodcock 1996, Bruce 2003, Wells 2007). When incubating, the bird's blue bill was often visible in the nest entrance (as in Norman 1964), but birds also frequently hunkered down and were invisible inside the chamber.

We inferred that the nest discovered on 12 July 2012 contained eggs because adults spent long periods of time inside it, probably incubating. Two nests in 2013 were discovered during nest construction between 29 March and 2 April. One nest in 2013, discovered on 13 March (when inferred to be in the incubation stage, due to long visits by adults), was predated between 19 and 21 March. Another of the 2013 nests was found completed on 27 February, but no birds were in attendance. Ten days later, we observed visiting adults

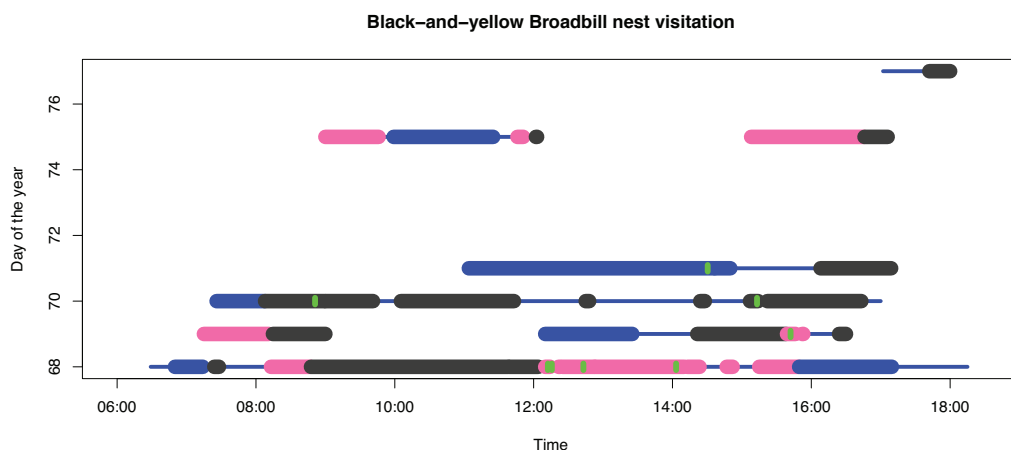


Figure 4. Graphical summary of nest visitation by Black-and-yellow Broadbills *Eurylaimus ochromalus* during incubation at one nest in 2013. Y axis = day (where day 68 = 9 March) and x axis = time of day. Thin blue lines represent time periods during which nest watches occurred, thicker lines represent visits by broadbills. Colour of thicker lines represents sex: pink = female, blue = male, dark grey = unsexed. Individuals could not always be sexed due to the angle that they approached the nest; these three colours probably represent just two individuals. When visit breaks are too short to be visible, they are marked with a small green line.

and discovered that incubation had commenced. The broadbills never laid eggs in the two nests that were discovered under construction, instead abandoning them as soon as they were complete. Some birds construct nests without using them (e.g. Verner & Engelsens 1970, Berg *et al.* 2006), but it is possible that our presence (which did not deter the birds from continuing construction efforts) might have prompted them to delay incubation. One of these nests belonged to a colour-marked individual, and we continued to see this male nearby after the birds stopped visiting it.

Both members of a pair participated in nestbuilding. Addition of material appeared to occur in three distinct parts of the nest: the roof, near the nest's attachment to the branch; the sides; and the internal chamber, where most attention was focused late in the process. Birds added material with vigorous head-shaking like Banded Broadbills, but they did not appear to pull loose material from the sides inwards to the chamber (see Banded Broadbill account). The chamber was formed from within, often by the birds pressing their head or breast against the walls. Visits with material tended to last 15–100 seconds, with visits by the female generally longer than those by the male. Sex ratio associated with the number of visits made to the nest seemed equal, with both adults working on the sides and chamber, but the roof was predominantly built by the male. Visit length increased as building progressed.

Both adults participated in incubation (Fig. 4). Entries and exits were swift and easily missed, making birds difficult to sex unless the visit was recorded on video and analysed later. Of a sample of 32 videoed visits at one nest during incubation, the female was identified visiting twice as frequently as the male (14 female, seven male, 11 unidentified due to the angle of entrance / exit). Within this small sample of visits, the mean incubation bout also differed between the sexes, with males remaining on average 75 minutes ($n = 7$) and females 38 minutes ($n = 14$; the mean duration for birds of unknown sex was 36 minutes, $n = 11$). When an adult departed, the nest was often unattended for several minutes before the presumed mate arrived; these off-periods were substantially shorter than on-periods, usually less than 15 minutes in duration, although they occasionally lasted >30 minutes to nearly an hour.

Both sexes defended the nest. In 2012, we observed a Prevost's Squirrel *Callosciurus prevostii* foraging in a nest tree for 30 minutes, during which period the broadbills were apparently absent. The squirrel eventually came to a vine near the nest whereupon both pair members suddenly appeared and made very fast vertical dives near the squirrel. Although the birds did not appear to make physical contact, the squirrel jumped from the vine and landed in a tree below. We never witnessed nest parasitism, although known broadbill nest parasites (e.g. Indian Cuckoo *Cuculus micropterus*) were abundant at the study site.

We occasionally saw broadbills carry triangular green objects (probably leaves) into the nest chamber during incubation. Other broadbills often line their nests with green leaves (Wells 2007, Zubkova 2017), although Wells (2007) noted that a Black-and-yellow Broadbill nest he inspected lacked them. Once we caught an image on video that could be sexed, and it was the male holding the leaf (ML 471552; Fig. 3).

We did not observe nestlings (or feeding behaviour indicating their presence) at any of the five nests we found. One nest in 2012 was abandoned during incubation; one in 2013 was predated (and visibly torn) during incubation; two in 2013 were abandoned prior to incubation; and one in 2013 was in a tree that came into leaf subsequently, blocking the nest from view (whether it later produced nestlings is unknown). Around six weeks after the nest in 2013 was predated, we observed a pair in the early nestbuilding stages c.20 m away.

We saw fledglings twice, once each on 16 July 2012 and 20 March 2013. In the latter case, the bird was accompanied by three other birds—one adult of each sex and one of unknown age and sex. Both fledglings matched descriptions in Lambert & Woodcock (1996) and Myers (2009).

BANDED BROADBILL *Eurylaimus javanicus*

Encountered daily, but at lower density than Black-and-yellow Broadbill (Fig. 1). These species have been reported at similar densities in Sarawak (Fogden 1976), but our observation that Banded Broadbill is less common agrees with observations from Brunei (C. F. Mann pers. comm.).

This species shared the Black-and-yellow Broadbill's repertoire of wing and bill displays (see above). Such displays have not been previously reported for Banded Broadbill (Lambert & Woodcock 1996, Wells 2007). The context and patterns of these were similar to Black-and-yellow Broadbill displays. We also saw displays performed near a nest (ML 479554). Birds displayed both when accompanied by conspecifics, and apparently when alone. Soft calls accompanying displays were lower pitched and less squeaky than those made by Black-and-yellow Broadbills when wing-displaying (ML 480261; Fig. 2).

We found what appears to be the first nest of the species to be described on Borneo (Smythies 1999). It was under construction and suspended from the thick, serrated, drooping leaves of a large epiphytic *Pandanus* sp. (Fig. 5) growing c.15–20 m above ground in the lowest crotch of a *Koompassia excelsa* tree at the edge of a clearing with a densely vegetated swamp, at c.290 m elevation. The completed nest, which we subsequently collected and is now in the Sabah Parks Vertebrates Collection, was 25 cm tall, 22.5 cm wide and 15 cm deep. Its outward appearance was of a rounded, oblong tangle of vines (c.1 mm thick, some with leaves), narrow black fibres, twigs (c.2–3 mm thick) and scattered leaves. The entrance to the inner chamber was near the top of the tangle, directly below the *Pandanus* leaves from which the nest was suspended. It faced away from the tree trunk and the epiphyte, and was 54 mm tall by 58 mm wide. Mean thickness of the walls around the entrance was 35 mm. Diameter of the inner cavity at the nest entrance was 11.6 cm; the inner cavity was lined with thick, flat grass stems and leaves.



Figure 5. Banded Broadbill *Eurylaimus javanicus* nest during late construction, with an adult exiting at the lower left (© Kayleigh Chalkowski). Inset: close-up of the nest chamber after the nest was abandoned and collected, showing lining material (Eric R. Gulson-Castillo).

The nest leant against the tree trunk. It was almost entirely supported by a 44 mm-thick bundle of fibres slung around one of the *Pandanus* leaves, but some stray vines were connected to other leaves nearby. The location was relatively unobscured by branches and received ample sunlight: this *Koompassia excelsa* was an emergent and the nest was sited well above the tangles and saplings of the adjacent swamp. Similar to a nest described in Peninsular Malaysia (Myers 1999), our nest was close to a bees' nest sited within the tree trunk, which had an entrance tunnel two-thirds of the way up. However, the bees were not aggressive and ignored observers, including on the three occasions when we climbed the tree after the nest had been abandoned, suggesting these were sweat bees (F. Lambert pers. comm.), which do not sting.

Upon discovery on 11 March 2013, both adults visited the site silently with nesting material, hovering beside the tree. The nestbuilding process was then observed in a series of two-hour watches between 11 and 29 March (Fig. 6). Long, tangled fibres (including vines) were draped over the base of some of the *Pandanus* leaves, near its centre. The birds generally visited the nest singly, bringing one piece of material to the top or side of the tangle. On visits to the roof of the nest, the bird generally wedged its bill into the top of the tangle, rapidly shaking its head to affix the fibre, which was left to hang freely over either side. The chamber was formed once a large number of fibres had been draped over the *Pandanus* leaves. When visiting the side of the nest, the bird would integrate some material and then grab a previously placed piece emanating from the tangle and push this material inwards, shaking its head to affix the piece to the back wall of the nest, while flaring its tail. As the nest formed, the main nestbuilding activity shifted from the exterior to the chamber. Material was added to the roof during nine of 24 observed visits between 07.00 and 09.00 h

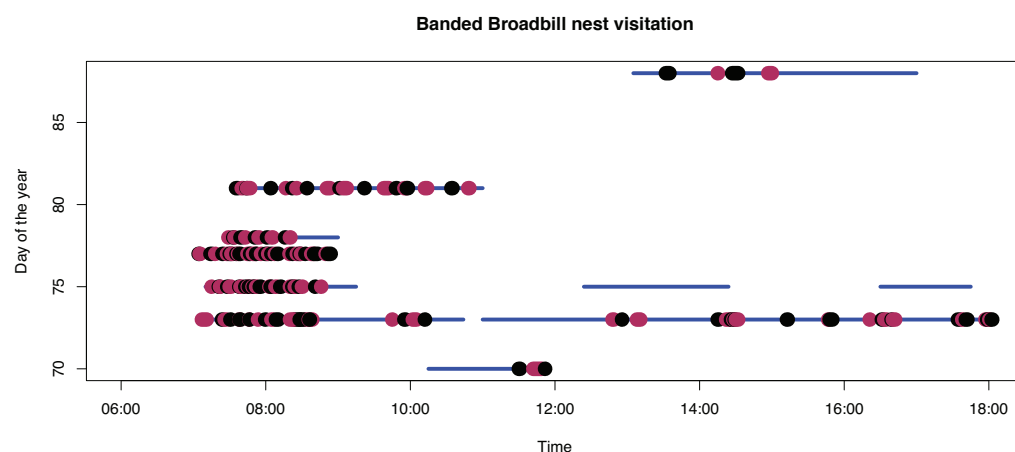


Figure 6. Graphical summary of nest visitation by Banded Broadbills *Eurylaimus javanicus* during nest construction. Y axis = day (day 70 = 11 March) and x axis = time of day. Thin blue lines represent time periods during which nest watches occurred, thicker lines visits by broadbills. The colour of each visit alternates to highlight visits with short intervening breaks, which would otherwise appear to blend into a single line; colour does not represent sex or individual.

on 14 March, five of 28 visits between 07.00 h and 09.00 h on 16 March, and one of 66 visits between 07.00 and 09.00 h on 18 March; all other visits brought material to the sides of the nest or the chamber, which was not well formed on 14 March, but neat and recognisable by 16 March. To work on the chamber, a bird would enter, turn around so that it was facing outwards, then reach down or sideways to grab the end of a free fibre, and pull it inwards. This was often repeated several times during each visit. By the time the chamber was well formed, the base of the nest consisted of a large wad of fibres curling from the sides of the nest inwards. The nestbuilding techniques described here are generally consistent with those reported for Black-and-red *Cymbirhynchus macrorhynchos* and Dusky Broadbills (Zubkova 2017).

Division of labour between the sexes was not closely observed because sexing this species at a distance is difficult. Occasionally, while a bird was working on the nest the other member of the pair would join it. Once, on 18 March, one bird sang as it clung to the outside of the nest near the chamber.

On 29 March, one bird stayed in the nest for 1.8 hours during the watch and was still present when we departed at the end of the day. We observed relatively little activity in the two hours beforehand—all visits involved the adult visiting the chamber for a brief period. We interpreted this to signify the presence of eggs and that incubation had begun. It is possible that incubation started before this: Banded Broadbill sometimes continues nest construction after incubation has begun (Wells 2007). As with incubating Black-and-yellow Broadbills, we could sometimes observe the adult's blue bill in the nest entrance (Myers 1999 specifically did not see this). We observed several incubation bouts on 30 March, but during our watches over the next few days, all activity ceased. There was no sign of activity when we collected the nest on 9 April, 2.5 weeks after the earliest possible start of incubation and well before any nestlings would have fledged.

Videos of this nest being constructed can be seen at ML catalogue numbers 479337, 479428–438, 479527–544, 479590, 479998, 480004 and 480006. ML 479590 shows nestbuilding behaviour by both pair members, including an instance in which the male became tangled on a vine and had to struggle for 50 seconds to get free.

DUSKY BROADBILL *Corydon sumatranus*

Observed in groups of 8–12 individuals in the lowlands on eight occasions in 2012 (most in early July) and four times in 2013; also once on Gunung Lucia in 2013. We generally located them by their far-carrying calls, given consistently. Birds were observed both sides of the Tawau River in 2012, but in 2013 we generally saw them on the ridge west of the river. We usually saw flocks during the morning but also observed loud activity, including nestbuilding, well into the midday hours (although the species is reportedly crepuscular: Lambert & Woodcock 1996). One of the few times we saw the species in late afternoon was also the only time it was silent. On this occasion, on 2 March 2013, ERGC observed a small flock in a tall *Macaranga hypoleuca* tree with clusters of very small flowers. They sallied after insects while foraging and occasionally hovered immediately below a flower, but it was unclear if they were eating flowers or small insects.

Groups of Dusky Broadbills mostly appeared to be accompanied by mixed-species flocks. The broadbills' vocalisations were very audible over several hundred metres, making them the most obvious members of these flocks. The other birds consistently included species of Cuculidae and Picidae, including Raffles's *Rhinortha chlorophaea*, Red-billed *Zanclostomus javanicus* and Chestnut-breasted Malkohas *Phaenicophaeus curvirostris*; an unidentified small coucal *Centropus* sp.; and Maroon *Blythipicus rubiginosus*, Orange-backed *Reinwardtipicus validus*, Checker-throated *Chrysophlegma mentale*, Crimson-winged *Picus puniceus*, Grey-and-buff *Hemicircus concretus*, Buff-necked *Meiglyptes tukki* and Buff-rumped Woodpeckers *M. tristis*. Other species recorded sporadically near these flocks were Slender-billed Crow *Corvus enca*, Black Magpie *Platysmurus leucopterus*, Greater Racket-tailed Drongo *Dicrurus paradiseus*, Red-naped Trogon *Harpactes kasumba* and Maroon-breasted Philentoma *Philentoma velata*. We have found no mention of Dusky Broadbills associating with mixed-species flocks in the literature, but Norman (1964) reported a noisy flock at Kalabakan (near Tawau) in the company of Red-bearded Bee-eaters *Nyctyornis amictus*, unspecified hornbills (Bucerotidae) and Bat Hawks *Macheiramphus alcinus*. SCO also observed multiple Dusky Broadbills and Banded Broadbills in a clearing on the ridge west of the Tawau River on 7 March 2013. Both species vocalised frequently as they repeatedly flew back and forth across the clearing, but no interactions were observed. It was unclear whether Dusky Broadbill acted as a nuclear species in the flocks we observed, but it was certainly the loudest species and generally the only species that vocalised regularly.

We twice encountered groups constructing nests (Fig. 7). Reports of Dusky Broadbill breeding behaviour are relatively common (Lambert & Woodcock 1996), probably because the species is very vocal around nests, which they visit in large



Figure 7. Dusky Broadbill *Corydon sumatranus* nest during early construction with an adult perched on top (© Brian Magnier)

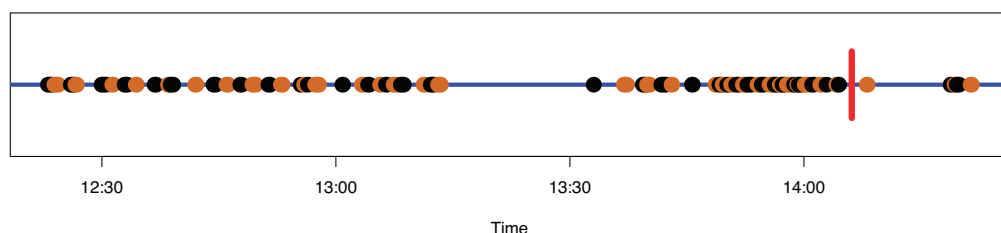
Dusky Broadbill nest visitation 29 June 2012

Figure 8. Graphical summary of nest visitation by Dusky Broadbills *Corydon sumatranus* during the early nestbuilding period. X axis = time of day. The thin blue line represents a continuous nest watch, the thicker lines visits by broadbills. The colour of each visit alternates to illustrate visits with short intervening breaks, which would otherwise appear to blend into a single line; colour does not represent sex or individual. Red line represents disturbance. We watched the nest until 18:00 h, but no birds visited after 14:21 h.

groups. We found the first group building on 29 June 2012 and another on 15 July 2012. Both dates are typical for the species, yet late compared to other nests reported on Borneo (Lambert & Woodcock 1996, Myers 2009). The first nest was suspended from a long rattan whip directly above the park's main trail (c.700 m from the headquarters), very close to the river. The second was in a low, swampy area off the trail, further to the east, near a Black-crowned Pitta territory.

Only the first nest was observed in detail (Fig. 8). At this nest, a flock of c.8 birds worked amid a cacophony of constant calling. The birds generally took turns, bringing material one at a time, and added each piece of stick, vine, leaf or moss atop the growing pile, sometimes with a head-shaking motion similar to that used by *Eurylaimus* broadbills (see above). We observed the 'winding' behaviour described by Zubkova (2017), in which a flying bird latches the loose end of a fibre to the top of the nest, then spirals downwards while balanced on the side of the nest, to place the other end of the fibre near the base. However, we also frequently saw birds simply place a new piece of material atop the tangle of fibres (both behaviours visible in ML 471148). Young individuals, identified by their paler, smaller throat patches and paler bills, were present and called loudly with the others (ML 471545–546). Although immatures did not actively participate in nest construction while we watched, their presence is consistent with suggestions that the species breeds cooperatively (Lambert & Woodcock 1996, Zubkova 2017).

This nestbuilding attempt was abandoned the same day we discovered the nest, at c.14.20 h, after we began setting up a rope system for a hide in the trees nearby. Although they appeared unperturbed by our presence, the ropes we launched into the trees may have disturbed them sufficiently to abandon. The nest was still quite small and far from complete. However, the second nest, which was only observed by JPH, was also abandoned after just one day of building, and JPH did not disturb the birds in any way that would have obviously caused the birds to abandon.

BLACK-CROWNED PITTA *Erythropitta ussheri*

The most common representative of the Pittidae in our study area. Unlike other pittas, their singing behaviour did not change noticeably between the two visits, except when pairs were tending a nest, when they became silent (see Gulson-Castillo *et al.* 2017 for a detailed description of parental care at a nest in 2013). Our observations were biased towards times when birds were singing—a simple, prolonged, whistle. We heard the subtle 'wing-clap' sonation (Pegan *et al.* 2013) often during both periods, although only ever from a recently singing bird departing a perch (ML 181755, 4:03). After bouts of singing, pittas often moved

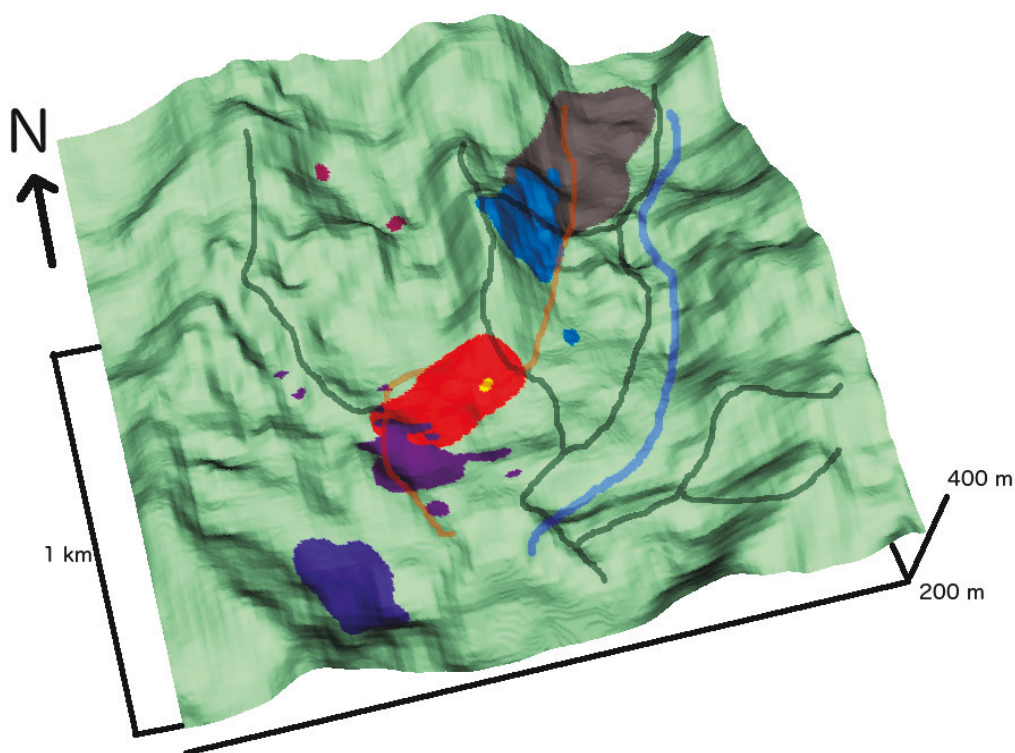


Figure 9. Map of the topography of our study area showing home ranges of five pairs of colour-banded Black-crowned Pittas *Erythropitta ussheri* observed in 2013. Coloured shapes represent the 95th percentile of a kernel density of sightings of each pair. Colours represent different pairs' territories. The location of a nest is marked by a yellow point. The map demonstrates the approximate number and size of Black-crowned Pitta home ranges, including apparent overlap between two pairs' home ranges. Kernel densities were calculated in R using the function *kde2d* with default bandwidth. We had only four sightings at one territory (maroon points near the upper left corner) and display points rather than kernel density. Grey lines represent trails, the brown line a pipeline, and the blue line the Tawau River. 3D map courtesy of JAXA (2015).

through the understorey and across the forest floor, perching on logs and roots to sing occasionally as they flipped over leaves, foraging. Once, JMH observed a pitta climb 2 m up a buttress to inspect a clump of leaf litter against the trunk.

Because we followed individuals in our study area closely and colour-banded most of them in 2013, we were able to use our sightings to calculate 95th percentile kernel densities of home ranges for each pair. One bird was colour-banded in 2012 and occupied the same area in both 2012 and 2013. Fig. 9 shows the estimated home ranges for five pairs, as well as a few sightings for a sixth pair in an area that we visited infrequently. Two pairs' home ranges either overlapped slightly or had abutting boundaries (red with purple, and grey with pale blue in Fig. 9). Neighbouring birds sang in response to each other's presence or to playback in the boundary area, and birds in the northern two territories frequently counter-sang at opposite sides of a gully. The active nest we found belonged to birds in the southern set of adjoining home ranges, and is shown on the map as a yellow point. All territories were associated with a tangled swamp or stream, usually the former, and some also included a segment of drier slope on the neighbouring ridge.

The plotted density kernels are probably fairly representative of the home range occupied by each pair, although without radio-tracking data we cannot eliminate the

possibility that these areas were merely those parts of their territories in which the birds were most detectable (i.e. where they sing most frequently, or where the topography was most accessible). Indeed, small points outside the main territories, displayed as part of the pale blue and purple home ranges on Fig. 9, demonstrate that birds sometimes visited areas where we usually did not detect them. The calculated areas of the home ranges are as follows: 6.5 ha; 5.3 ha; 14.4 ha; 4.4 ha; and 4.3 ha. However, these areas are affected by the number of points used to calculate them, and should be taken as very approximate estimates—larger sample sizes led to smaller estimates of range size. Phillipps & Phillipps (2014) interpreted Fogden (1976) finding two individuals within 20 ha to signify that the species' home range size is c.10 ha, which is consistent with our findings. Using radio telemetry, Lambert & Howes (in prep. in Lambert & Woodcock 1996; F. Lambert pers. comm.) estimated, based on the small area used by individuals in their study, as many as 21–22 pairs per km² in Danum Valley, which is much greater than the density we observed at Tawau Hills; within the 3 km² area of Fig. 9 we found six pairs. Danum Valley may possess more suitable habitat than the area we surveyed in Tawau Hills, which contains numerous steep, drier ridges.

All home ranges except one appeared to harbour a pair (the other held a single individual). One member of each pair (probably the male) sang more frequently and tended to be more brightly coloured (similar to Rainbow Pittas *Pitta iris*; Zimmermann & Noske 2003). The putative females sang much less often—we would generally hear them once or twice during a prolonged visit to a territory. They occupied the same area as putative males and their songs did not elicit an aggressive response from the latter. Their songs were distinctly higher pitched than putative male songs. We subsequently used blood samples to determine the sex of captured individuals, which confirmed this (Gulson-Castillo *et al.* 2017).

We trapped a bird that appeared to be a hybrid or backcross with Garnet Pitta *Erythropitta granatina*. We took photographs, blood, audio and feather samples from this individual. This bird shared a territory with a male Black-crowned Pitta and sang less often than the latter, but more frequently than a typical female. We used the blood sample to confirm that the bird was female; it was the only female we caught that appeared to be just as brightly coloured as its mate (Fig. 10). The dark purplish feathers in the upper mantle of all Black-crowned Pittas (including the unusual bird's mate) have a slight reddish tint at the fringes. In the presumed hybrid, a bright red streak emanated from these red-tinted feathers in the upper mantle and ended on the central crown (Fig. 10). This streak was not as broad or long as the red crown of a Garnet Pitta and although each so-marked feather was



Figure 10. A presumed hybrid or backcrossed female Black-crowned *Erythropitta ussheri* × Garnet Pitta *E. granatina* (right), showing brighter coloration than other female Black-crowned Pittas and a streak of red on the head and nape; at left is her presumed mate (© Katherine Lauck)

mostly red, their tips were still black (Fig. 10). This is probably the second or third report of a possible hybrid Black-crowned × Garnet Pitta (Erritzøe & Erritzøe 1998), matching the description of one collected in 1935 by V. von Plessen at Peleben on the Kayan River, North Kalimantan (Erritzøe & Erritzøe 1998). Another potential hybrid was collected by Lumholtz at Kaburau, also on the Kayan River—it has much more extensive red than the other birds, resembling Garnet Pitta with limited black tips to some crown feathers, and not all authors accept this as a record of hybridisation (Voous 1961, Lambert & Woodcock 1996). These other hybrids were collected c.150–250 km from Tawau Hills Park. We found no other evidence of Garnet Pitta at Tawau Hills and observed no evidence of hybridisation in the other individuals we trapped.

Nine individuals were trapped, of which two were subsequently recaptured. The only bird caught in 2012 was radio-tagged with a c.0.4 g beeper radio-tag. The night after its capture, we tracked the bird to its roost site, c.2 m above ground on a branch with its plumage fluffed extensively, as in previous reports (L. Emmons *in* Lambert & Woodcock 1996). The following night, the tag was found in low shrubbery, evidently removed by the pitta.

BLUE-BANDED PITTA *Erythropitta arquata*

Uncommon, but regularly distributed in appropriate habitat and reliably encountered in their territories. We found two territories in the lowlands, at c.345 and 290 m (the former shown in Fig. 11, red points) and two in the highlands at 850 and 1082 m. All birds appeared to favour the steep slopes of ridges, in accord with previous habitat assessments (Lambert & Woodcock 1996).

We observed the use of sonations, or non-vocal sounds, similar to those in Black-crowned Pitta (Pegan *et al.* 2013). These sonations sound like a soft knock on wood and appear to be produced using the wings. In one video (ML 479573), after the bird had been singing from a perch for a couple of minutes, it lifted its wings without extending them and puffed its belly feathers. It then brought its wings down quickly as its belly is deflated, with a soft *tok* recorded just as its wings hit its sides, before they bounced back up. The quality of the sound was similar in both species. Further studies are required to determine whether they use the sonation in the same context as Black-crowned Pitta (Pegan *et al.* 2013, see above). Although other pittas make sonations, their context appears somewhat different. Those of African Pitta *angolensis* and Green-breasted Pittas *P. reichenowi* sound different and are associated with displays (summarised in Erritzøe & Erritzøe 1998). Eared Pitta *Hydrornis phayrei* makes sonations by flicking their wings toward each other, instead of their flanks (Round 2002); these are made repeatedly prior to calling. Gurney's Pitta *H. gurneyi* makes wing-claps against its flanks together with territorial calls (Well 2007). Giant Pitta *H. caerulea* also makes wing-claps; it is unclear if they use their flanks, but they produce the sounds in flight when alarmed (Lambert & Woodcock 1996).

BORNEAN BANDED PITTA *Hydrornis schwaneri*

Common on steep slopes and ridges leading to Gunung Lucia. Between the hostel and the summit, we observed at least four pairs along the trail at c.950 m on 12 July 2012. On 22 July 2012, we found at least one individual in the lowlands near the park headquarters at c.300 m. It was observed five more times in this area on 24–30 July 2012 (when our visit ended), and was generally easy to find, calling frequently. The bird stayed in a relatively small area (Fig. 11, yellow points). Because this area was within our main study area and well-surveyed throughout the period, we are confident that it was not present and calling before late July.

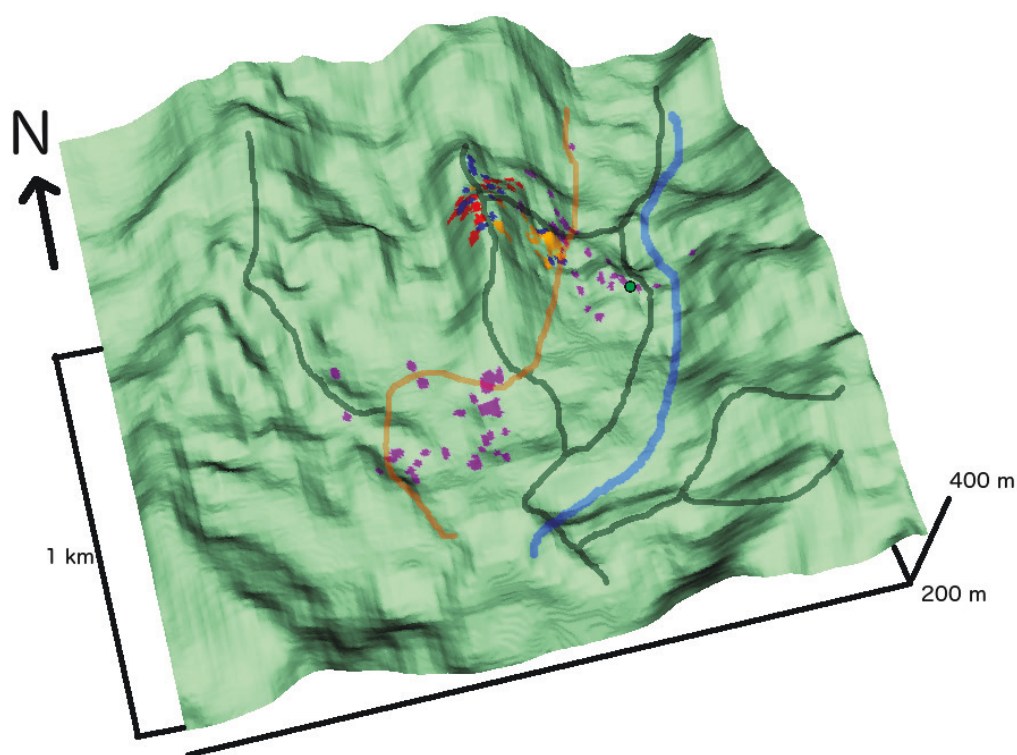


Figure 11. Map of the topography of our study area showing sightings of four species of pittas during the 2012 field work: Black-crowned Pitta *Erythropitta ussheri* (purple), Blue-headed Pitta *Hydrornis baudii* (blue), Bornean Banded Pitta *H. schwaneri* (yellow) and Blue-banded Pitta *Erythropitta arquata* (red). Each point represents a sighting. Variation in point size and shape is an artefact of 3D plotting. The map demonstrates that the areas occupied by each species overlapped considerably, especially on the ridge in the centre, where all four species occurred in close proximity. Black-crowned Pitta was seen more commonly in low swampy areas, whereas the other three species occurred mainly on this ridge and its slopes. A fifth species, Hooded Pitta *Pitta sordida*, was heard infrequently and seen just once, a juvenile, at the green point. Grey lines represent trails, the brown line a water pipeline, and the blue line the Tawau River. 3D map courtesy of JAXA (2015).

Although Lambert & Woodcock (1996) observed that Bornean Banded and Blue-headed Pittas *Hydrornis baudii* are never found in the same area of forest at Danum Valley, at Tawau Hills that which the *H. schwaneri* occupied in 2012 overlapped with a Blue-headed Pitta territory (Fig. 11). In fact, the former was first observed within the lowland study area on 24 July 2012 in precisely the same location as a pair Blue-headed Pittas had been present *c.*1 hour prior. On 30 July, JMH spent several hours observing a female Blue-headed Pitta with a juvenile (see below). Once the female hopped out of view behind a tangle and JMH heard and saw a 'scuffle', with branches in the tangle moving. After this, a Bornean Banded Pitta emerged from the same area the female had disappeared, suggesting that an interaction between the two species had occurred (although contact between them could not be confirmed). Lambert & Woodcock (1996) suggest that habitat preferences are responsible for the apparent segregation of Bornean Banded and Blue-headed Pittas in Danum, but the potential interspecific interaction we observed suggests that competition could play a role as well.

Bornean Banded Pittas were present on the slopes of Gunung Lucia again in 2013, but none was observed in the lowlands near the park headquarters. It is possible that

their occurrence in this area is seasonal, or that the sightings in 2012 in the lowlands were unusual—perhaps a dispersing individual that eventually moved elsewhere permanently.

BLUE-HEADED PITTA *Hydrornis baudii*

Shy, quiet and difficult to observe during both visits; however, they were more reliably found and regularly heard during 2012. One pair was observed regularly that year (Fig. 11, blue points). The birds seemed to favour a particular rattan *Calamus* sp. clump and were often seen together. They were seen nearly every evening on 19–28 July, at 16.30–17.30 h, atop a west to east-running ridge, but also frequented in a swampy area at its base. When moving together, they sometimes called every 15–30 seconds. More frequently, one of the pair would call once or twice, then disappear. This pair vocalised after playback only if they had been calling previously. On 28 July 2012, just before 17.00 h, one gave several of the ‘alarm note[s] of the female’ (Lambert & Woodcock 1996), then an upslurred *porrrrwuh?*, perhaps similar to what has been described as a possible alarm call (B. Gee *in litt.* in Erritzøe & Erritzøe 1998). Lambert & Woodcock (1996) and Bruce (2003) suggested that the first-mentioned call, the loud and nasal *kwee-ouu*, is a ‘female alarm call’ but we observed both sexes give a call matching this onomatopoeic description (ML 479549).

Although we never found a nest, JMH discovered a young bird on 30 July 2012, within the same territory (Fig. 12). It followed its female parent closely, generally standing silently next to her as she foraged, but occasionally begging emphatically as she ate or moved onward (ML 479513); we never saw it being fed. The young was a male, identified by its bright white throat (similar to that of an adult male). Given that no pitta is known to be dependent for more than two months (Erritzøe & Erritzøe 1998), and that the bird showed remnants of gape flanges and of the orange bill tip shown by many nestling pittas, we consider that this was a juvenile (younger than two months) in pre-formative moult to immature plumage. This plumage does not precisely match the description for juvenile or immature plumage given by Lambert & Woodcock (1996) and Erritzøe & Erritzøe (1998), as neither source mentions a bright white throat. However, it is difficult to believe this bird



Figure 12. Two frames from a video of an immature male Blue-headed Pitta *Hydrornis baudii* (top) showing a white throat, patches of blue in the underparts, and reddish wing-coverts, with an adult female Blue-headed Pitta (bottom). Frames from video ML 479513 (Justin Hite)

was old enough to be moulting to adult plumage (given its gape and begging behaviour), and we suggest that previous descriptions of immature male plumage, based on two specimens (Erritzøe & Erritzøe 1998), may not represent the complete range of pre-adult variation.

See Bornean Banded Pitta account for description of a possible interaction between that species and a Blue-headed Pitta.

During the drier season in 2013, birds sang less and were observed less frequently. However, whenever they sang they did so in long series, repeated every few seconds as they moved through the understorey. We detected the birds across a larger area than in 2012, sometimes in different areas on the same day (e.g., 9 March, when we had three birds 442, 324 and 285 m away from each other, respectively) and across the Tawau River. This leads us to suspect that at least three territories were established, although there could have been more.

One pair, which may have been the same as that observed in 2012, spent several days around 7–20 April 2013 near one segment of the Tawau River, on the main trail. They were often flushed from the trail as they foraged in the strip of forest between the river, the trail and the nearby swamp, although we never saw them leave drier ground. The birds disappeared as suddenly as they arrived in the area, and we suspect that they departed (rather than became less detectable), because we regularly walked this trail throughout the season.

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References:

- Bruce, M. D. 2003. Family Eurylaimidae (broadbills). Pp. 54–93 in del Hoyo, J., Elliott, A. & Christie, D. A. (eds.) *Handbook of the birds of the world*, vol. 8. Lynx Edicions, Barcelona.
- Berg, M. L., Beintema, N. H., Welbergen, J. A. & Komdeur, J. 2006. The functional significance of multiple nest-building in the Australian Reed Warbler *Acrocephalus australis*. *Ibis* 148: 395–404.
- Clements, J. F., Schulenberg, T. S., Iliff, M., Roberson, J. D., Fredericks, T. A., Sullivan, B. L. & Wood, C. L. 2018. The eBird/Clements checklist of birds of the world: v. 2018. <http://www.birds.cornell.edu/clementschecklist/download/> (accessed 19 December 2018).
- Erritzøe, J. & Erritzøe, H. B. 1998. *Pittas of the world: a monograph on the pitta family*. Lutterworth Press, Cambridge, UK.
- Dial, R., Mifsud, B., Karolus, A., Greenwood, T., Aldred, J., Prudente, C. & Hatcher, B. 2005. Finding and climbing the world's tallest tropical trees. Expeditions Council of the National Geographic Society. Unpubl.
- Fogden, M. P. L. 1972. The seasonality and population dynamics of equatorial forest birds in Sarawak. *Ibis* 114: 307–342.
- Fogden, M. P. L. 1976. A census of a bird community in tropical rainforest in Sarawak. *Sarawak Mus. J.* 24: 251–267.
- Gulson-Castillo, E. R., Dreelin, A. R., Fernandez-Duque, F., Greig, E. I., Hite, J. M., Orzechowski, S. C., Smith, L. K., Wallace, R. T. & Winkler, D. W. 2017. Breeding biology during the nestling period at a Black-crowned Pitta *Erythropitta ussheri* nest. *Bull. Brit. Orn. Cl.* 137: 173–194.
- JAXA (Japan Aerospace Exploration Agency). 2015. Advanced land observing satellite global digital surface model. <http://global.jaxa.jp/projects/sat/alos/> (accessed 8 June 2015).

- Lakim, M. 2008. Comparative behavioral ecology of sympatric *Presbytis rubicunda* and *Macaca fascicularis* in Tawau Hills Park, Sabah, Malaysia. Ph.D. thesis. Univ. of Malaysia Sabah, Kota Kinabalu.
- Lambert, F. R. 1989. Daily ranging behaviour of three tropical forest frugivores. *Forktail* 4: 107–116.
- Lambert, F. R. & Woodcock, M. 1996. *Pittas, broadbills, and asities*. Pica Press, Robertsbridge.
- Medway, L. & Wells, D. R. 1970. Bird report: 1968. *Malay Nat. J.* 23: 47–77.
- Myers, S. D. 1999. An observation of a Banded Broadbill *Eurylaimus javanicus* nest in Pasoh Forest Reserve, Peninsular Malaysia. *Forktail* 15: 101.
- Myers, S. 2009. *Birds of Borneo: Brunei, Sabah, Sarawak, and Kalimantan*. Princeton Univ. Press.
- Norman, M. M. 1964. Bird notes from the Tawau area. *Sabah Soc. J.* 2: 43–78.
- Omar, S. & Nais, J. 1995. Tawau Hills Park: an overview. Pp. 1–7 in Ismail, G., Omar, S. & Din, L. (eds.) *A scientific journey through Borneo: Tawau Hills Park Sabah*. Pelanduk Publications, Subang Jaya.
- Powell, R. A. 2000. Animal home ranges and territories and home range estimators. Pp. 65–110 in Boitani, L. & Fuller, T. K. (eds.) *Research techniques in animal ecology: controversies and consequences*. Columbia Univ. Press, New York.
- Pegan, T. M., Hruska, J. P. & Hite, J. M. 2013. A newly described call and mechanical noise produced by the Black-and-crimson Pitta *Pitta ussheri*. *Forktail* 29: 160–162.
- Pegan, T. M., Gulson-Castillo, E. R., Biun, A., Byington, J. I., Moyle, R. G., Tuh Yit Yu, F., Wood, E. M., Winkler, D. W. & Sheldon, F. H. 2018. An assessment of avifauna in a recovering lowland forest at Kinabalu National Park, Malaysian Borneo. *Raffles Bull. Zool.* 66: 110–131.
- Phillipps, Q. 1970. Some important nesting notes from Sabah. *Sabah Soc. J.* 5: 141–144.
- Phillipps, Q. & Phillipps, K. 2014. *Phillipps' field guide to the birds of Borneo: Sabah, Sarawak, Brunei, and Kalimantan*. Third edn. Princeton Univ. Press.
- Prentice, C. 1988. Observations of the nuptial behaviour of Black and Yellow Broadbill *Eurylaimus ochromalus*. *Enggang (Newsl. MNS Selangor Bird Group, Kuala Lumpur)* 1: 8.
- Prum, R. O. 1993. Phylogeny, biogeography, and evolution of the broadbills (Eurylaimidae) and asities (Philepittidae) based on morphology. *Auk* 110: 304–324.
- Prum, R. O., LaFountain, A. M., Berg, C. J., Tauber, M. J. & Frank, H. A. 2014. Mechanism of carotenoid coloration in the brightly colored plumages of broadbills (Eurylaimidae). *J. Comp. Physiol. B* 184: 651–672.
- R Core Team. 2015. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. <http://www.R-project.org/> (accessed 18 June 2015).
- Raikow, R. J. 1987. *Hindlimb myology and evolution of the Old World suboscine passerine birds (Acanthisittidae, Pittidae, Philepittidae, Eurylaimidae)*. Orn. Monogr. 41. American Ornithologists' Union, Washington DC.
- Round, P. 2002. Systematic notes on Asian birds. 30. An undescribed acoustic display of the eared pitta *Anthocincla phayrei* Blyth, 1863. *Zool. Verhand.* 340: 197–199.
- Sabah Parks. 2018. Tawau Hills Park. <http://www.sabahparks.sabahparks.net/the-parks/tawau-hills-park> (accessed 19 December 2018).
- Scott, D.W. 1992. *Multivariate density estimation: theory, practice, and visualization*. Wiley, New York.
- Seino, T., Kitayama, K. & Lakim, M. 2007. Floristic composition and stand structure of the mixed dipterocarp forest in Tawau Hills Park, Sabah, Malaysia. *Sabah Parks Nature J.* 8: 63–82.
- Smythies, B. E. 1999. *The birds of Borneo*. Fourth edn. Natural History Publications, Kota Kinabalu.
- Tjia, H. D., Komoo, I., Ali, C. A. & Tahir, S. 1992. Geology of Taman Bukit Tawau, Semporna Peninsula, Sabah. *Geol. Soc. Malaysia Bull.* 31: 113–131.
- Venables, W. N. & Ripley, B. D. 2002. *Modern applied statistics with S*. Fourth edn. Springer Verlag, New York.
- Verner, J. & Engelsen, G. J. 1970. Territories, multiple nest building, and polygyny in the long-billed marsh wren. *Auk* 87: 557–567.
- Voous, K. H. 1961. Birds collected by Carl Lumholtz in eastern and central Borneo. *Nytt Mag. Zool.* 10 (Suppl): 127–180.
- Wells, D. R. 2007. *The birds of the Thai-Malay Peninsula*, vol. 2. Christopher Helm, London.
- Winkler, D. W., Pegan, T. M., Gulson-Castillo, E. R., Byington, J. I., Hruska, J. P., Orzechowski, S., Van Doren, B. M., Greig, E. & Wood, E. 2017. Collecting the complete specimen package: student-led expeditions as an educational and collections-building enterprise. Pp. 185–200 in Webster, M. (ed.) *The role of collections in ornithology: the extended specimen*. Stud. Avian Biol. 50. CRC Press, Boca Raton.
- Zimmermann, U. M. & Noske, R. A. 2003. Breeding biology of the Rainbow Pitta, *Pitta iris*, a species endemic to Australian monsoon-tropical rainforests. *Emu* 103: 245–254.
- Zubkova, E. N. 2017. Nesting material and nest building technique in two species of broadbill (*Cymbirhynchus macrorhynchos* and *Corydon sumatranus*, Passeriformes, Eurylaimidae) from southern Vietnam. *Biol. Bull.* 44: 769–786.
- Zubkova, E. N. & Korzun, L. P. 2014. Morphofunctional aspects of the trophic specialization of the frugivorous Green Broadbill *Calypptomena viridis* (Passeriformes, Eurylaimidae): a comparative analysis. *Biol. Bull.* 41: 788–800.

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