Breeding biology during the nestling period at a Black-crowned Pitta *Erythropitta ussheri* nest

by Eric R. Gulson-Castillo, R. Andrew Dreelin, Facundo Fernandez-Duque, Emma I. Greig, Justin M. Hite, Sophia C. Orzechowski, Lauren K. Smith, Rachel T. Wallace & David W. Winkler

Received 30 March 2017; revised 3 July 2017; published 15 September 2017

http://zoobank.org/urn:lsid:zoobank.org:pub:8F5C236B-0C84-402A-8F73-A56090F59F56

Summary.—The natural history of most Pittidae is understudied, but the breeding biology of the genus *Erythropitta*, a recently recognised grouping of red-bellied pittas, is especially poorly known. We monitored and video-recorded a Black-crowned Pitta *E. ussheri* nest in Sabah, Malaysian Borneo, during the nestling period and found that the male had a higher visitation rate and the female was the sole adult that brooded. We clarify this species' nestling development and describe two vocalisations: (1) the first instance of a fledgling-specific song in Pittidae and (2) a soft grunt-like sound given by adults arriving at the nest early in the nestling period. We analysed the structure of each visit, finding that the longest segment of most parental visits was the period between food delivery and parental departure. We hypothesise that adults linger to await the production of faecal sacs and aid nestlings to process food.

The pittas (Pittidae) are a colourful group of Old World understorey birds that were recently split into three genera: *Pitta*, *Hydrornis* and *Erythropitta* (Irestedt *et al*. 2006). This classification is supported by morphology and occurrence of sexual dimorphism (Irestedt *et al*. 2006), but further comparisons are difficult because data on much of the pittas' natural history are lacking. Only the breeding biology of Gurney's *Hydrornis gurneyi*, Giant *H. caerulea*, Rainbow *Pitta iris* and Fairy Pittas *P. nympha* have been fully documented (Round & Treesucon 1986, Round *et al*. 1989, Gretton 1988 *in* Lambert & Woodcock 1996, Zimmermann & Noske 2003, Lin *et al*. 2007b, Donald *et al*. 2009, Kim *et al*. 2012), while sporadic quantitative data have been reported for a handful of other species (Lambert & Woodcock 1996, Erritzoe & Erritzoe 1998). The nests and clutch sizes of most *Erythropitta* are known, but virtually no detailed observations have been made on the nesting behaviour of any species in this genus.

Black-crowned Pitta *Erythropitta ussheri* is endemic to northern Borneo. There are eight published breeding records (Gibson-Hill 1950; summarised in Lambert & Woodcock 1996, Mann 2008; excluding one with a 'yellow chick', see Discussion), which show that—like many other Bornean birds—the species usually nests just after the north-east monsoon (February–July; Fogden 1972). Its nest is a domed structure of sticks, bark, fine roots and leaves, and it lays two white eggs with dark red and black spots forming a ring at the broader end (Lambert & Woodcock 1996). This taxon is sometimes treated as a subspecies of Garnet Pitta *E. granatina* due to certain plumage similarities and 1–2 apparently hybrid specimens (the number varies according to the authority; Stresemann 1938 *in* Voous 1961, Erritzoe & Erritzoe 1998). Regardless, detailed observations on the nests of either taxon would be novel (Lambert & Woodcock 1996).

Based on a nest of Black-crowned Pitta, we present the first detailed documentation of the nestling period in an *Erythropitta* species. We partitioned each provisioning visit into

 ISSN-2513-9894 (Online)

time periods around the beginning and end of feedings, and present hypotheses as to the selection factors affecting the length of each visit segment and visit duration as a whole.

Methods

Study area.—The study took place in Tawau Hills Park (04.399°N, 117.889°E), a reserve managed by the state agency, Sabah Parks, in southern Sabah, Malaysia, in northern Borneo. The park is *c*.72 km from the border with Kalimantan, Indonesia, and protects 280 km^2 of lowland dipterocarp forest, lower montane forest and patches of other habitat (Omar & Nais 1995). We concentrated our efforts in the lowlands, surveying our study site near the park headquarters daily for pitta activity between 26 February and 20 May 2013, covering an area of *c*.1.5 km^2. We regularly scouted ridges and swamps near the Tawau River, monitoring pitta territories and nesting activities.

Nest observations.—The Black-crowned Pitta nest was found midday on 2 March 2013, when three of us (JMH, DWW, SCO) following the base of a gully inadvertently stepped on a log adjacent to the nest, causing the bird to flush. Prior to this, the same observers had been performing Black-crowned Pitta playback nearby at half-hour intervals with no vocal response. At the time of discovery, the nest was complete and held two eggs. We did not visit again until 4 March, when we erected a hide *c*.7 m from the nest, opposite the stream running through the gully. The hide was sited behind the intersection of a fallen log and a large buttressed stump, and consisted of two curtains of camouflage cloth hung over parallel lines of parachute-cord, so that a lens could be placed between the two curtains and a person could sit comfortably behind the log. The fallen log concealed us from the nest as we entered the hide. We monitored the nest using our cameras and continually recorded events around it. Videos were made using Canon 5D Mark II, 5D Mark III or 7D camera bodies with 70–200 mm, 400 mm or 500 mm lenses, often with 1.4× or 2× teleconverters. A subset of our videos is archived at the Macaulay Library of Natural Sounds, Cornell University (www.macaulaylibrary.org) and are referred to here using their ML catalogue numbers.

Our initial nest watch lasted 154 minutes on 4 March. We then did not visit the nest until 6 March, allowing the birds to acclimatise to disturbance before we began a nest-watching routine that spanned, maximally, 07.00–18.00 h daily. Over the 15-day nestling period, we summed on average 8.67 observation hours per day and completed five full-day nest watches. Our videos from 6 March showed the mostly obscured bird on the nest consuming both eggshells (ML 479789), indicating the nestlings hatched that day. We numbered days thereafter using this date as day 0.

On 16 March (day 10) at 13.20 h we extracted the chicks while wearing nitrile gloves to prevent predator-attracting scents and took them 50 m away to be banded, measured and photographed. During this time, SCO remained near the nest to ensure that the birds did not return before the nestlings had been replaced. We excluded post-banding events in our behavioural analysis for 16 March. On 18 March at 12.00 h we set mist-nets around the gully, blocking flyways to the nest. The mist-nets were 3–8 m long and 3–5 trammels tall, with 30 mm mesh. We kept them open during our watches until we had caught both adults, the female on 19 March and the male on 20 March. We excluded these 2.5 days from our analysis of parental care. We collected *c*.70 μl of blood using brachial venipuncture from all four birds (adults and nestlings) that we later used for DNA sexing. The birds were released without harm. We placed bands in unique combinations on the birds' legs and covered the bands with thin pieces of coloured electric tape, replicating colour bands, to ease identification of individuals in the field (Table 1).

The chicks fledged on 21 March (day 15) with the nest still intact. However, when we returned to collect the nest five days later, it had been dismantled, apparently by a predator.

 ISSN-2513-9894 (Online)

TABLE 1
Individual measurements with their colour band combinations.

Bird	Band colour (leg)	Mass (g)	Flat wing (mm)	Tarsus (mm)	Tail (mm)	Culmen (mm)	Bill depth (mm)	Bill width (mm)	Head + bill (mm)
Nestling, day 10	Blue (L), yellow (L)	44.0	61.0	39.0	11.0	7.1	4.2	4.3	36.8
Nestling, day 10	Red (R), blue (R)	40.2	59.0	38.0	11.0	7.0	4.1	5.1	35.2
Female	Orange (R), yellow (L)	59.5	90.0	39.9	38.7	14.3	8.0	6.8	48.8
Male	Yellow (R)	58.5	93.0	42.75	36.1	15.15	7.85	6.3	51.5

This prevented direct measurements of nest dimensions in the field, but we reconstructed these measurements from photographs. We collected and photographed the nest material, sorted by size and type.

Video analysis.—We took the following data for each nest visit recorded on video: sex of the visiting adult, time of arrival, time when the adult started feeding (a 'feeding' occurred when food was visibly placed or manipulated inside a nestling's gape, which could be recognised at a distance by the quick bobbing or shaking of the adult's head), time when the adult gave the last 'feed', number of feeds per visit, time of departure, extraction of faecal sacs, and exit direction from the nest. Arrival and departure times were based on the moment an adult's feet touched or left the nest entrance and were used to calculate visit duration, feeding latency (time between arrival and the first feed; *sensu* Pugesek 1990, Siegel *et al*. 1990) and departure latency (time between the last feed and departure). Time spent feeding was the period between the first and last feeds. We counted the number of times the birds fed nestlings as a proxy for the amount and / or handling time of the food delivered. Direct measurements of food quantity from videos were impossible because of variable image quality. Brooding visits were easily recognised, as they involved an adult entering the nest and remaining there for at least an hour and often much longer.

Sexing the adults.—From observations of the adults in the field and in the hand, we determined that they differed slightly but reliably in plumage, with the male being generally subtly brighter than the female. This dimorphism enabled us to identify them in the videos. Although lighting could influence field marks, the most reliable separator was the shade and extent of blue on the wing-coverts (Fig. 1A–B), bright sky-blue in the male, while the female had desaturated darker blue coverts. However, in poor light the lesser extent of blue on the female's coverts was a better indicator because she showed a broader area of grey between the two rows of blue feathers. While the following marks were less consistent, we used them as supporting evidence: the male had a shaggier and more distinct supercilium, a brighter purple mantle, and a darker black head than the female. On visits for which we lacked video, we designated the visiting adult's sex as 'unknown' due to the difficulty of reliably sexing birds in the field without a video record.

We later confirmed adult sex by amplification of W- and Z-specific alleles using the 2550F/2718R sexing protocol (Fridolfsson & Ellegren 1999). In our amplification of the W- and Z-specific alleles, we used as a reference the DNA of a Black-crowned Pitta specimen, which we collected during the same expedition (CUMV 55593). We stained this specimen with a 1% Lugol's (IKI) solution (Metscher 2009) and inspected a 50 μm CT scan obtained on an GE eXplore CT-120 micro CT (General Electric, Fairfield, CT) taken at the Cornell Imaging Facility (http://www.biotech.cornell.edu/brc/imaging-facility). The specimen showed ova in its ovary, so we definitively sexed the reference pitta as female. Molecular sexing confirmed our visual identifications of the video records.

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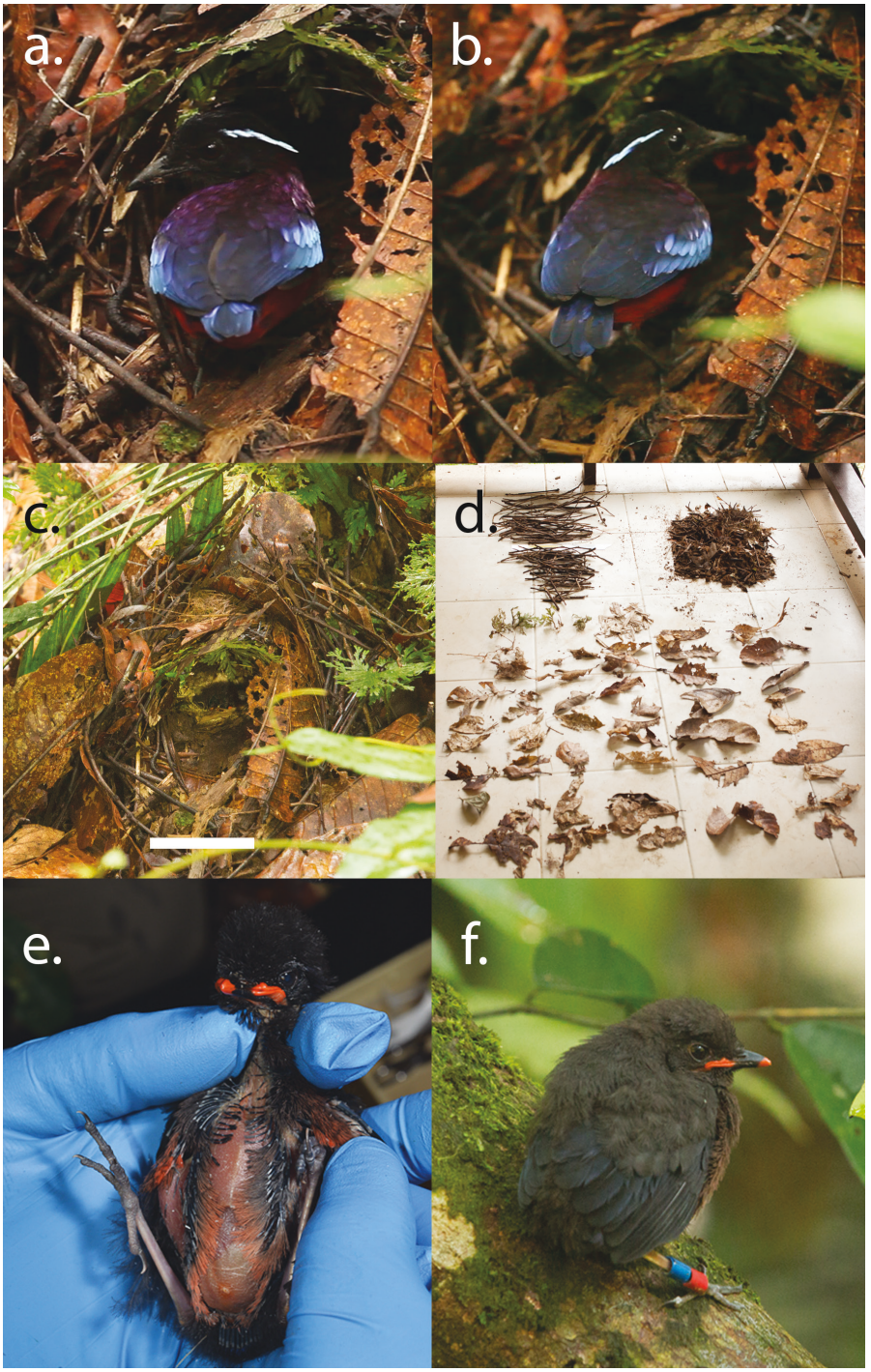

Figure 1. Various aspects of the nesting biology of Black-crowned Pitta *Erythropitta ussheri*. (A) Adult male at the nest entrance (Justin M. Hite). (B) Adult female showing duller wing-coverts and mantle coloration, plus greyer face (Emma I. Grieg). (C) The intact nest and immediate surroundings, with orange bill tips of the nestlings just visible in the nest; the white bar measures *c.*10 cm (David W. Winkler). (D) The nest components disassembled. (E) A nestling on day 10 (© J. Ryan Shipley). (F) A juvenile an hour after fledging on Day 15 (Sophia C. Orzechowski).

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Linear measurements.—We used ImageJ 1.49 (Schneider *et al*. 2012) to measure nest dimensions, nest components, and faecal sacs from photographs and video screenshots. We aligned nest components next to a ruler so that we could convert measured pixels into mm. We excluded sticks not entirely visible in the photographs. We measured the nest's general dimensions (e.g. height and width) by taking a video screenshot when an adult had its bill perpendicular to the camera so that we could use bill length as a scale. Similarly, we used screenshots of the birds holding faecal sacs to calculate sac width and length using known bill dimensions (see Table 1).

Sound analysis.—We used Raven Pro 1.4 (Bioacoustics Research Program 2011) for all acoustic measurements. When measuring upper and lower frequencies of a vocalisation, we used the functions Frequency 95% and Frequency 5%, which give intervals containing 90% of the energy of a selection. This helped maintain consistency across measurements.

Statistical analysis.—We performed all statistical analyses in R version 3.1.0 (R Core Team 2014). We used linear models (function 'lm') to understand which factors affected aspects of visit length or visitation rate. In all cases, we tested for behavioural differences between the sexes and for trends across the nestling season by date. Dependent variables are listed in Table 2. Sex and date are predictors for all models; other predictors (explained below) are context-specific and attempt to explain variation in our measurements and their effects on visit structure. We used hour of the day to test for circadian patterns in visitation rate. We noticed that feeding latency decreased rapidly during the first three days of observation, so we included both date squared and a dichotomous variable indicating whether or not the nestlings were being brooded (because the male often visited to feed while the female was brooding and the female sometimes fed nestlings before entering the

TABLE 2
Linear model (function 'lm') outputs for tests of the strength of the relationship between each dependent variable and the listed independent variables. (*) indicates statistical significance at $P = 0.05$.

Dependent variable	Independent variables	Estimate	Standard error	*t* value	*P* value
(a) visitation rate	(Intercept)*	11.82	2.36	5.02	<0.001*
	date*	-0.15	0.03	-4.48	<0.001*
	sex—female*	-13.07	4.56	-2.87	0.005*
	hour of day	0.002	0.03	0.06	0.95
	date:sex—female*	0.17	0.06	2.71	0.008*
(b) visit duration	(Intercept)	4.59	38.09	0.12	0.90
	date	0.37	0.55	0.66	0.51
	sex—female	-4.97	4.80	-1.04	0.30
	sex—unknown	-1.95	21.39	-0.09	0.93
(c) feeding latency	(Intercept)	400.71	263.71	1.52	0.13
	sex—female	1.05	0.99	1.06	0.29
	date	-9.13	7.76	-1.18	0.24
	I(date^2)	0.04	0.06	0.85	0.40
	brooding - no*	-139.87	39.39	-3.55	<0.001*
	date:brooding - no*	2.01	0.58	3.48	0.001*
(d) log (feeding duration)	(Intercept)*	3.43	1.19	2.89	0.005*
	sex—female	-0.16	0.14	-1.18	0.24
	date*	-0.05	0.02	-3.06	0.003*
	no. of feeds*	0.68	0.04	18.49	<0.001*
(e) departure latency	(Intercept)*	62.90	22.21	2.83	0.005*
	date	-0.63	0.32	-1.95	0.05
	faecal sac—yes*	8.96	2.77	3.23	0.002*
	sex—female	1.30	2.56	0.51	0.61

 ISSN-2513-9894 (Online)

nest to brood) as a predictor for the feeding latency of each visit. To evaluate the relationship between feeding duration and the amount of food delivered, we used number of feeds as a predictor for feeding duration. We also included a dichotomous variable testing the effect of faecal sac removal on the departure latency. All models are summarised in Table 2.

Finally, we used a Fisher's exact test (function 'fisher.test') for count data to determine: (1) if there was a statistical relationship in exit direction from the nest with or without a faecal sac (excluding the 9.8% of visits for which exit direction could not be determined), and (2) if the difference between the number of faecal sacs extracted by each sex was due to a difference in the number of visits to the nest by each parent.

Results

The nest and its environs.—The small gully harbouring the nest was carved into the steep and densely vegetated lower slopes of a ridge. A trickling stream along its bottom widened into larger puddles immediately before emptying into a swamp in the flat lowland below the ridge. The nest was constructed *c*.0.5 m above the stream on the side of the gully. It was dome-shaped and consisted largely of dead leaves, leaf skeletons and small twigs, plus several small spike mosses (*Selaginella* sp.; Fig. 1C–D; Table 3). Its entrance had a layer of rotting wood chips that the adults landed on when visiting the nest. The entire nest was 24 cm wide and 22 cm tall, and the entrance was 10 × 11 cm. The birds integrated surrounding vegetation into the nest, including some *Selaginella* and the lower end of a rattan (*Calamus* sp.) frond. The birds bent the rattan so that its leaves were woven into the back of the dome and the frond shaded the nest from above. The frond sprang back up when we collected the nest.

Activity at the nest.—On 4 March, our only nest watch during incubation, we observed the male bring a stick to the nest and arrange it inside the main cavity at 06.14 h. He was still inside the nest when the watch ended 2.25 hours later. There was no sign of other birds in this period.

During the nestling period, we observed a total of 241 nest visits over 114.8 hours of observation and recorded 174 of these visits on video. More than half of the total visits were made by the male (64%; 155 visits) and 20% (48 visits) were made by the female, with 16% (38 visits) by an adult we were unable to sex. Excluding hours associated with prolonged human disturbance at the nest, we remain with 209 visits made over 96.2 hours of observation, with a mean 2.17 visits/hour. When calculating sex-specific visitation rates, we further excluded hours in which we observed the nest for <0.8 hours and during which the adult could not be sexed, as when there was no camera recording. This left 154 visits over 74.3 hours, of which the male made 127 (82%). The male visited the nest more frequently but his visitation rate declined steadily over the course of the nestling period (Fig. 2, Table 2). The female progressively increased her visitation rate throughout the season, with her visitation rate converging with that of the male by the end of the season. Time of day did not affect visitation patterns for either sex. Over the nestling period, the male made a mean

TABLE 3
Summary of nest component dimensions by type.

Component type	Mean length	Mean width	Max. length	Max. width	% composition
Stick (n = 71)	205 mm	5 mm	663 mm	9 mm	57%
Leaf (n = 51)	117 mm	41 mm	267 mm	89 mm	41%
Selaginella sp. (n = 3)	108 mm	85 mm	161 mm	157 mm	2%

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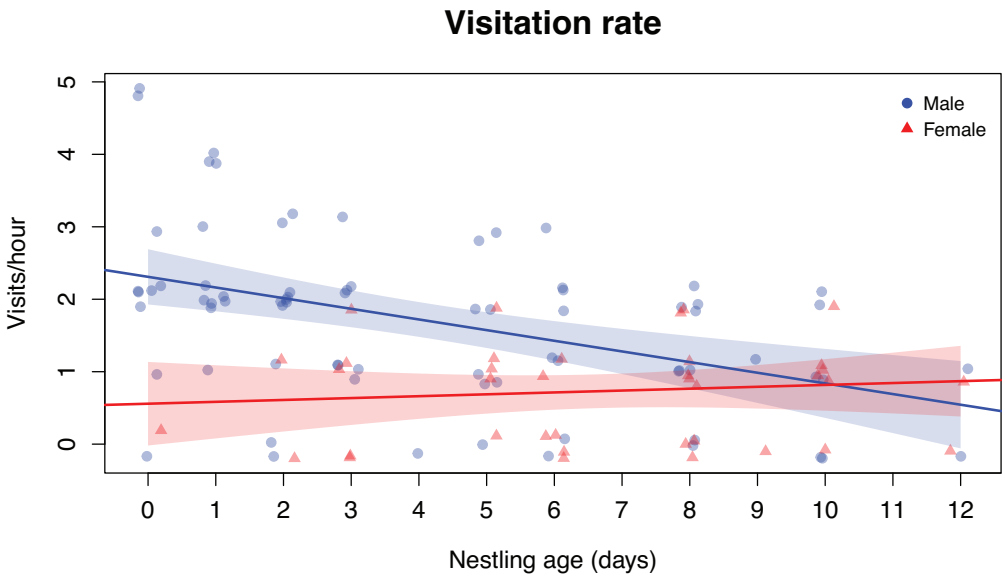

Figure 2. Visitation rate by sex throughout the nestling season. Day 0 = the day the nestlings hatched. Each point represents the number of visits that we witnessed over the course of an hour by sex—the axis ends on day 12 because we excluded all hours in which we caused disturbances or did not observe the nest for ≥0.8 hours (including days 13–15). This excludes visits for which the sex of the bird was unclear. There are few female visits or absences during the first three days because she was brooding. Red triangles = female visits, blue circles = male visits. The lines are linear regressions representing the interaction value on our linear model (see Table 2).

1.69 visits / hour and the female 0.72 visits / hour. Day 1 witnessed the highest visitation rates, when the male made a mean 2.55 visits / hour (the female spent the day brooding). The most visits in an hour we witnessed were five, associated with the rejection of food by the female (see Brooding).

A typical visit began with the adult approaching the nest from the opposite side of the gully (ML 479313) or the bottom of the gully (ML 479977), sometimes perching *c*.3 m away for several seconds before moving to the nest. It then would fly directly to the entrance, land on it, and sometimes look around or in the nest. Then stepping onto the edge of the cup, it would stretch to shove its bill into the begging mouths, shaking its head as it relinquished food. The bird then waited for several seconds before leaving, sometimes departing with a faecal sac (ML 484393). Visits lasted a mean 28.9 seconds, with no effect of sex or date on visit duration (Table 2).

Brooding.—Only the female was observed brooding and we noted eight brooding periods. In counting these bouts, we assumed that a female that was in the nest when we left in the evening and there when we returned next morning, had spent the night brooding (Fig. 3). The female spent almost the entirety of days 0 and 1 brooding, but she gradually brooded less, departing around 10.00 until day 6, when she left the nest at 08.01. We did not record any more instances of brooding and do not know if the female continued roosting in the nest after the evening of day 5. The hours during which the female brooded did not factor into calculating her visitation rate, but the decrease in brooding activity correlated with an increase in provisioning rates.

When arriving at the nest to commence brooding, the female would pause and look around as during a typical provisioning visit. She would then enter, and settle down out of sight except for her red underparts, visible in the dome's shadows (ML 487400). We

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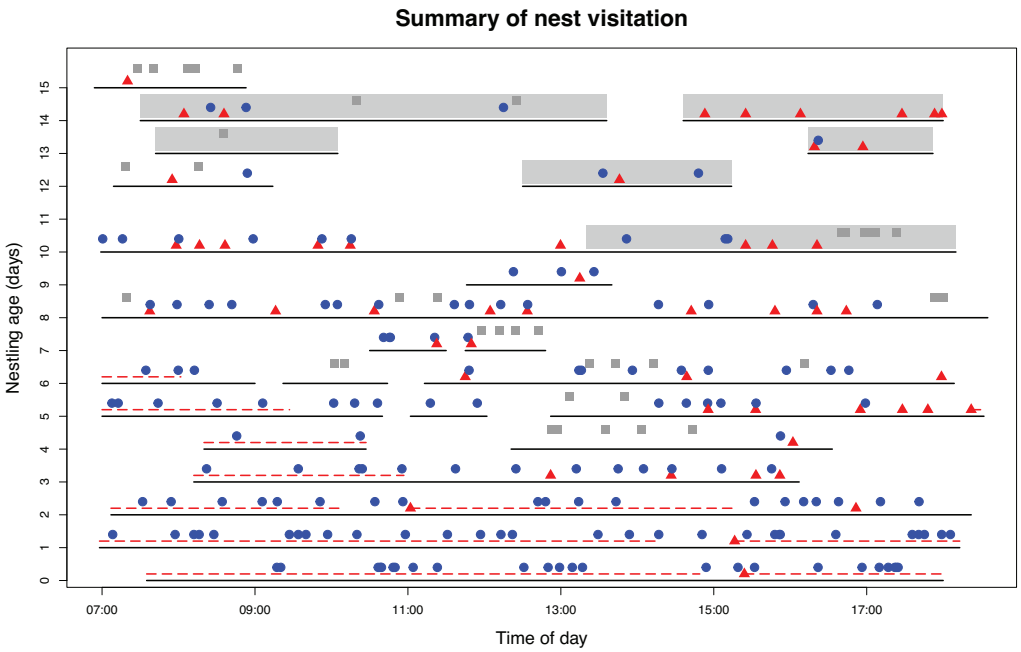

Figure 3. Graphical representation of the visits we witnessed at the nest. Red triangles = female activity, blue circles = male activity, and pale grey squares = visits we could not attribute to either sex, usually because they were not captured on video. Dashed red lines = periods during which the female was brooding, and the female was already on the nest when they do not begin with a point. Solid black lines = our presence at the hide, i.e. sampled period. Periods during which mist-nets were set around the nest and those following an anthropogenic disturbance (either mist-netting or banding of nestlings) are shaded pale grey; we excluded data collected during those periods from most analyses because the disturbances probably affected the birds' behaviour.

recorded her feeding the nestlings before entering the nest twice, but on her first brooding visit she carried the food into the nest with her. When departing, she walked to the edge of the nest head-first and flew away immediately, without pausing (ML 487402).

The male visited the nest during each of the female's diurnal brooding bouts. Early in the season, the male would wait for her to move sideways in the nest chamber, the nestlings would beg, and the male fed them directly. Subsequently, the female brooded so that the nestlings' bills were already visible when the male arrived. The male fed the female at least once, but in most circumstances there was insufficient light to determine if this was a regular occurrence. The feeding latencies for both adults, especially the male, were particularly long on days 0–2 but decreased rapidly with time. The model that best fits these data suggested that the female's presence at the nest caused the male to delay food delivery early in the season, but the interaction between date and the female's brooding behaviour reveals that feeding latency was never very long when the female was not brooding (Fig. 4, Table 2). Mean feeding latency during a visit associated with brooding was 7.8 seconds and that without brooding 1.4 seconds; sex was not a significant predictor in the model (Table 2) probably because the female fed the nestlings from outside the nest before entering it to brood on a couple of occasions meaning that there was still a feeding latency attached to her visits to brood.

Occasionally on days 0–1, the female did not respond to the arrival of the male while she was brooding and the male would depart the nest still carrying the food it had brought. This included the first five visits the male made on day 0, despite these being spread over

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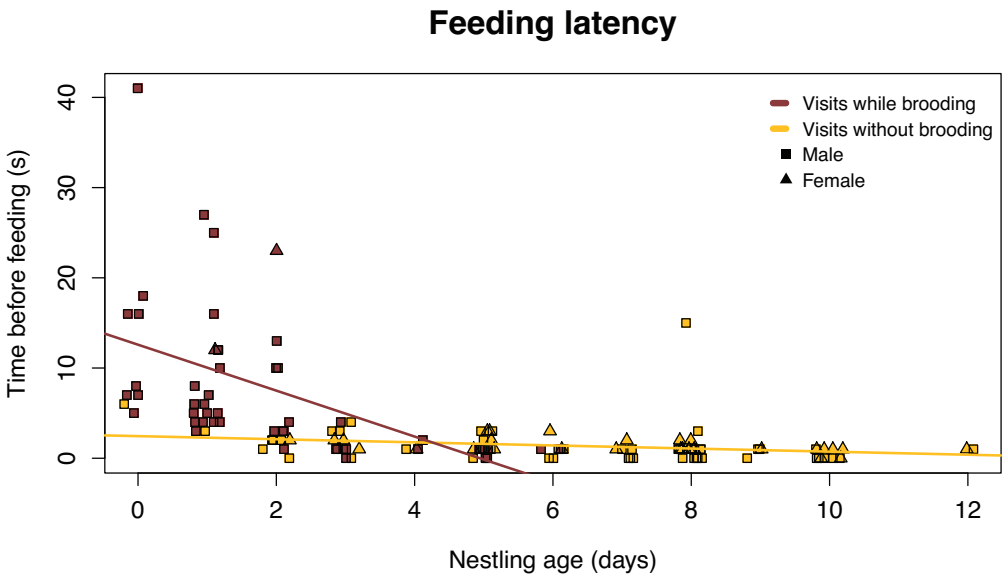

Figure 4. Time between arrival and feeding (feeding latency) declined sharply during the first three days of observation. Feeding latency was longest when the female arrived to brood or the male arrived while the female was brooding. Squares = male visits, triangles = female visits, red points = the female was brooding during the visit, and yellow points = visits when the female was not brooding. The lines are linear regressions representing the interaction value on our linear model (see Table 2).

1.5 hours. On five occasions, the male made up to four consecutive visits before being able to feed the nestlings (e.g. ML 484392). During one of these series of repeated visits, JMH noticed that the male was perched at the edge of the fallen log at the base of the gully, waiting before flying back to the nest again. These repeated visits may have influenced the overall high visitation rates we recorded during these two days (Figs. 2–3).

Additionally, the male hopped by the nest twice without going onto the nest entrance early on day 0 at 07.45 h and 08.52 h. The second time, he perched upright and flicked his wings several times before departing. This latter occasion occurred 30 minutes before we noticed the female eating the eggshells.

Nestling diet and feeding.—The quality of video was generally insufficient to identify the items the adults brought to the nestlings, but it was possible to identify a large diversity of invertebrates, such as orthopterans, lepidopterans (both adults and caterpillars), arachnids, annelids and grubs. We also saw them bring what appeared to be a small colubrid snake (*sensu lato*). When we caught the female in a mist-net coming to the nest, she was carrying a large spider. When we caught the male a day later, he was bringing a 2–3 cm caterpillar and a 2–3 cm cricket. On 26 March, we also saw an adult in the neighbouring territory bring a large spider to its fledgling.

Adults did not differ in the amount of time they spent feeding the nestlings during each provisioning visit; this was correlated with the number of times the bird inserted its head in the nest to feed or move food items ('feeds') during each visit (Fig. 5, Table 2). The male stayed at the nest longest when bringing the small snake, repositioning the prey several times. The mean time the adults spent feeding the nestlings within provisioning visits was 7.0 seconds.

Faecal sacs.—The adults routinely removed faecal sacs from day 2 until the nestlings fledged on day 15. Faecal sacs were large and white, except a clump of dark material at one end (Fig. 6A). When ejecting a faecal sac, a nestling would turn its vent toward the nest

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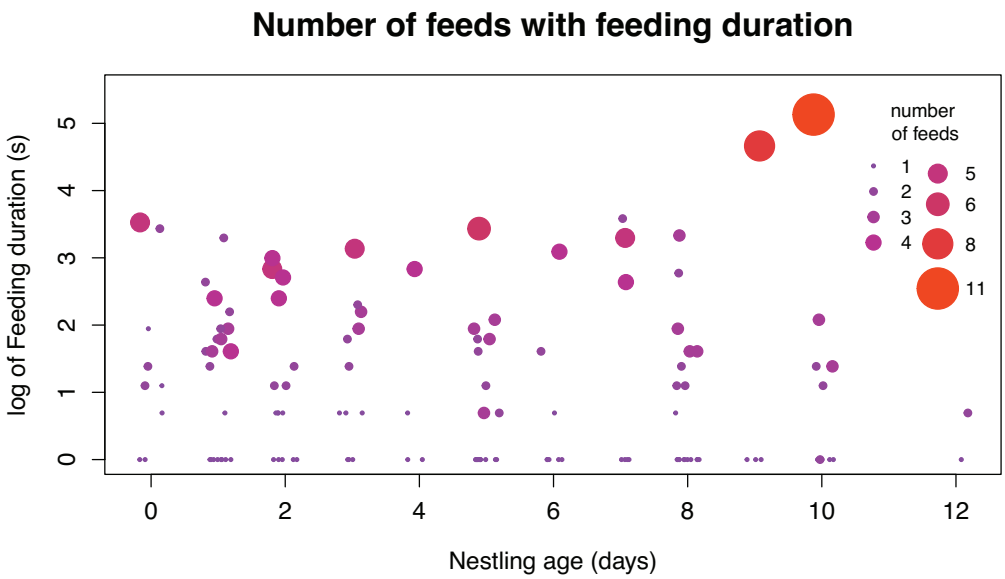

Figure 5. Feeding duration declined somewhat with time but increased noticeably with the number of 'feeds', i.e. the number of times an adult inserted food into the nestlings' mouths. Number of feedings is a proxy for number of food items and effort spent feeding, as we could not distinguish between either possibility on video.

Figure 6A. Adult male Black-crowned Pitta *Erythropitta ussheri* exiting the nest with a faecal sac; the clump of darker matter is visible at the end of the faecal sac furthest from the bird (Emma I. Greig). B. Male looking out of the nest during the departure latency (Justin M. Hite).

entrance and permit an adult to take the sac directly from the cloaca—when the nestlings were older this occurred while its sibling continued to beg. The adults almost always

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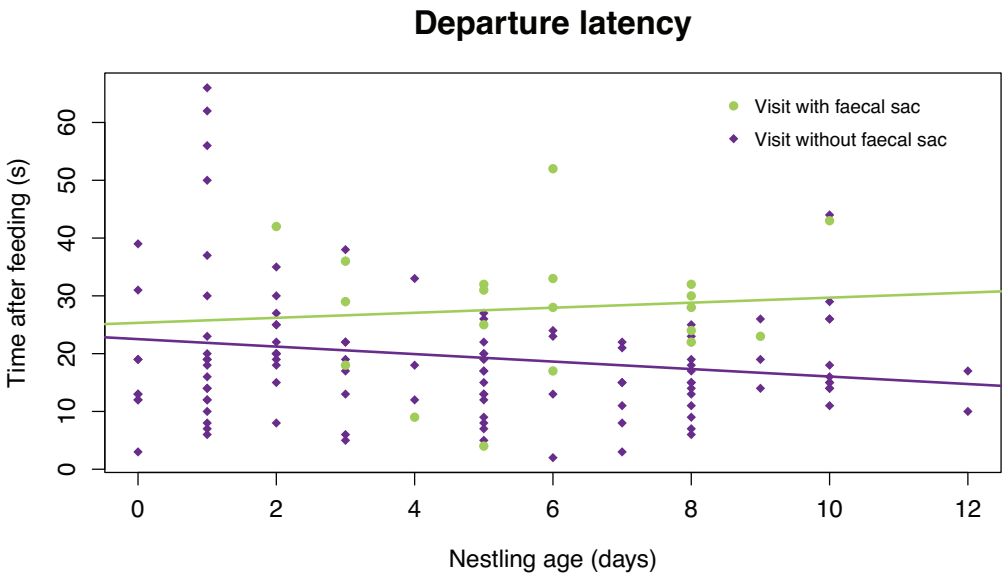

Figure 7. Time spent at the nest after feeding but before departing (departure latency) tended to be longer when an adult extracted a faecal sac. Purple diamonds = visits in which adults did not extract a faecal sac and green diamonds = visits in which they did extract a faecal sac. The lines are linear regressions representing the interaction value on our linear model (see Table 2).

stayed at the nest after they finished feeding the chicks—the departure latency—and the production of faecal sacs significantly increased this length of time (Fig. 7, Table 2) from a mean 19.3 seconds to one of 27.9 seconds. The adults never lingered after receiving a faecal sac, and once when a chick had left a faecal sac on the nest edge without an adult present, the adult promptly removed the sac after feeding the nestlings and its departure latency was only four seconds.

Birds exiting the nest with a faecal sac tended to fly downstream along the gully (92% of visits with a faecal sac, in the remaining 8% exit direction could not be determined from the videos and were excluded from analysis). The birds occasionally dropped faecal sacs in a small pool in the gully, 15–20 m from the nest. With a Fisher's exact test, we found that the adults were significantly more likely to fly upstream or across the gully, to nearby cover, when they left without a faecal sac (72% of visits without a faecal sac, $P < 0.001$).

We observed the pittas remove 35 faecal sacs over the course of the nestling period. Of those that we could measure digitally, mean faecal sac length was 30.3 mm and mean width 22.6 mm ($n = 18$). Unfortunately, the measurements we took were insufficiently precise to detect changes in faecal sac size over time. Excluding the first two days with no faecal sacs, the adults removed a mean 0.40 sacs / observation hour, or one sac about every 2.5 hours. The male removed more faecal sacs than the female, 16 vs. nine, but a Fisher's exact test showed that this was driven by his higher visitation rate, not a difference in the rate of faecal sac removal by sex per visit ($P = 0.31$).

Visit structure.—To compare the relative length and importance of each visit segment across the nestling period, we plotted them as a proportion of their corresponding visit (Fig. 8). Feeding latency represented a large proportion of each visit during the first three days, but subsequently was consistently short. Feeding duration tended to be short, but showed more variation throughout the season. Otherwise, departure latency consistently comprised the bulk of each visit: the adults spent most of their time on the nest after they had finished feeding the nestlings.

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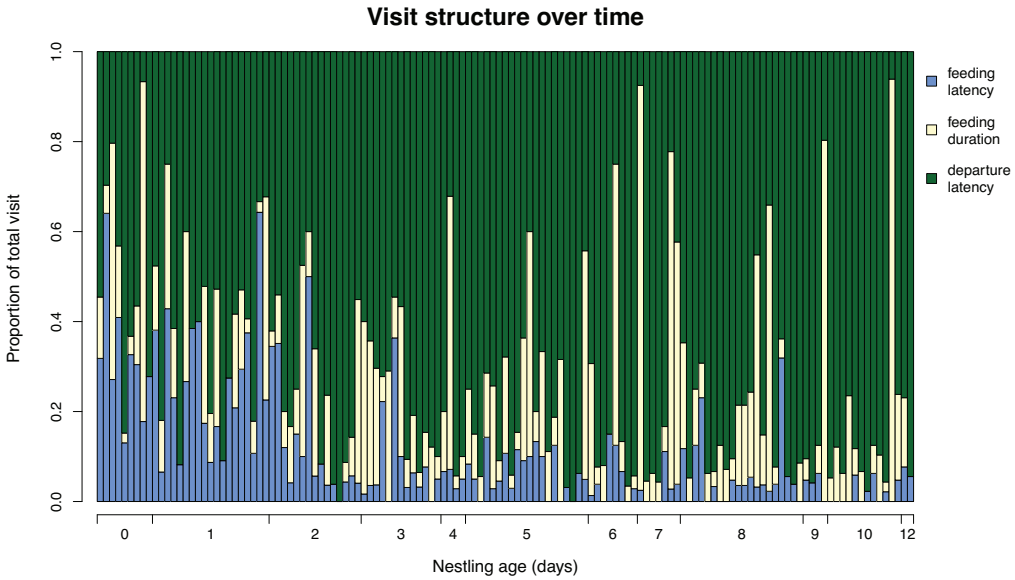

Figure 8. The proportion of a visit taken by each visit segment: pale blue segments = feeding latency, yellow segments = time spent feeding, and dark green segments = departure latency. Note the predominance of departure latency on most visits. All visits plotted included all three visit segments, but if any visit segment duration was <1 second it does not appear on this plot. Therefore, it appears as if certain visit segments are missing from some of these visits.

Vocalisations at the nest.—The birds seldom vocalised during the incubation and nestling periods, making it almost impossible to locate them away from the nest. They failed to respond to playback and only gave their principal song, a plaintive whistle, sporadically while we were in the hide. We heard this vocalisation no more than five times per day and did not hear it after day 10.

We observed two undescribed vocalisations associated with nesting. The vocalisation given by a fledgling is discussed below (see Nestling development and fledging). The other vocalisation was heard regularly only until day 2, although we heard it once each on days 3 and 4. This was a soft grunt- or cluck-like noise accompanied by a quick deflation of the body cavity and a downward pulse of the tail (ML 484302; Fig. 9). Calls were almost always given in short series; the longest series was 31 calls and the mean 5.1 calls. The male generally gave this call at the nest before feeding the nestlings while the female was brooding. Once, the male gave a call between feeds, while holding food in his bill. We heard the male give this call on 21 of 43 visits while the female was brooding and calls could be detected. We could not hear the call when conditions were unfavourable (such as when many cicadas were singing or during heavy rain). The male only gave this call once when the female was absent from the nest, on day 2. The female gave it once when she was returning to brood on days 1 and 2, and once before flying to the nest during a provisioning visit on day 3. The female's call was higher in pitch (ML 487400–401; Fig. 9).

The vocalisation we heard most frequently around the nest was the Blue-headed Pitta *Hydrornis baudii*-like call described by Pegan *et al*. (2013), which we transcribed as a slurred *hyiaaar* (ML 212068). We heard this twice for the first time on day 2, again on day 6 and regularly afterwards, with daily occurrences except on days with fewer than two hours of observation. On many occasions, the circumstances prompting the call were not apparent to us—the birds sometimes uttered the call 2–4 times and were then silent, but

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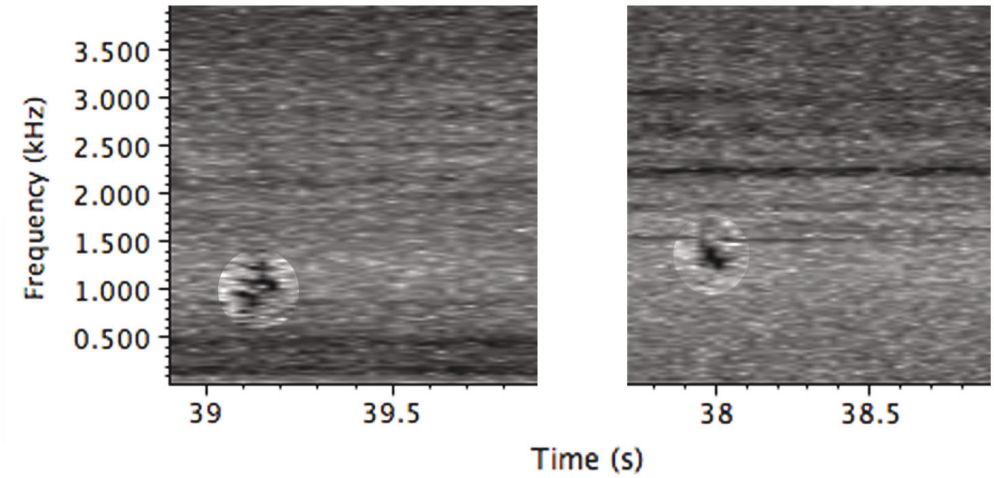

Figure 9. Sonograms of male (left) and female (right) grunt-like sounds given at the nest entrance. Mean low frequency of male grunt vocalisations was 0.865 kHz and mean high frequency 1.180 kHz. Mean duration of the call was 0.13 seconds (n = 8 vocalisations). Mean low frequency of female vocalisations was 1.207 kHz and mean high frequency 1.417 kHz. Mean duration of the call was 0.08 seconds (n = 3). Circles were artificially enhanced using Photoshop to make the vocalisations obvious. Sonogram parameters: Hann type, window size of 2,561 samples, hop size of 1,281 samples, overlap of 50%, DFT of 4,096 samples.

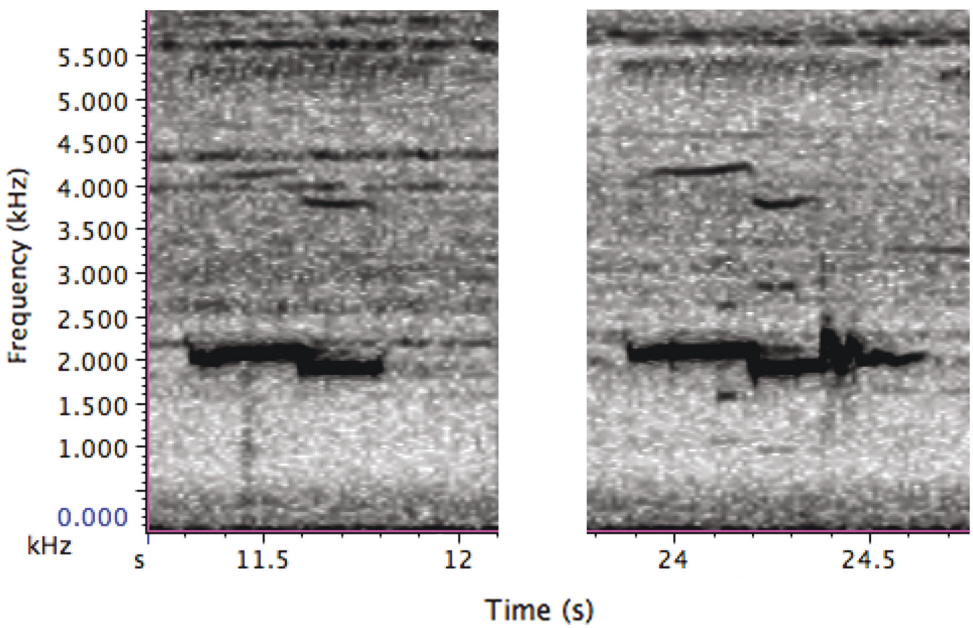

Figure 10. Two variants of the fledgling-specific vocalisation. Mean low frequency was 1.870 kHz and mean high frequency 2.095 kHz. Mean duration of the call was 0.59 seconds (n = 10 vocalisations). Both main notes have a harmonic with a frequency between 3.800 and 4.200 kHz. Sonogram parameters as Fig. 9.

on days 6 and 8 they repeated it >80 times over 15 minutes. However, there were instances in which the birds appeared to call in response to activity at the nest. One bird called >10 times as SCO placed a microphone in front of the hide on day 8. On day 10, the birds gave this call four times just before a White-crowned Hornbill *Berenicornis comatus*—a known

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nest predator that had been calling *c*.10 minutes earlier—flew low through the midstorey. Other birds began alarm-calling as soon as the hornbill came into view. Later on day 10, the birds gave this call in conjunction with a flurry of calls from a Scaly-crowned Babbler *Malacopteron cinereum*, 1.5 hours before a small monitor (Varanidae) crawled into the gully in the direction of their calls. The male gave this call once from the nest on day 12, while facing the hide, two days after we banded the chicks—this was also the only occasion we witnessed the adults give a loud vocalisation from the nest. One bird gave this call just after hitting, and before escaping from, a mist-net near the nest on day 13.

Two other instances during which the birds used the *hyiaaar* call were particularly noteworthy: (1) while we banded the nestlings and (2) when the nestlings fledged. (1) SCO heard the birds calling the entire time she was in front of the nest while we banded the nestlings on day 10, starting just after she arrived and ceasing just after the nestlings had been replaced, 23 minutes later, and she had returned to the hide. (2) On day 15, two hours before the nestlings fledged, the parents made *c*.13 calls per minute for 24 minutes, amounting to 250–350 renditions of the call. They then gave the call five times from behind the hide, the last time a mere six minutes before the chicks fledged. Afterwards, the adults called continuously while we located the fledglings and filmed them; the adults stopped calling when we left the vicinity (see Nestling development and fledging).

Throughout our nest-watch period, the birds in a nearby territory to the north-east where we had searched unsuccessfully for a nest were also silent. This territory was separated from our focal nest by *c*.140 m in which we never saw or heard pittas. However, on 26 March, both neighbouring adults started vocalising, one singing and one giving *hyiaaar* calls, in a gully on a ridge slope (ML 177987). They eventually led us to a fledgling. After the high calling activity of the fledging day, the birds in both territories behaved differently. Our focal birds remained silent and went unrecorded between 21 March and 26 April, when we finally heard and saw the colour-banded male singing again. The adults in the neighbouring territory never stopped singing regularly after we found their fledgling.

Nestling development and fledging.—The nestlings were not visible on days 0 and 1, mostly because the female spent most of the day brooding. On day 2 they began to lean their heads forward to receive food and, over the next few days, gradually begged more vigorously. After day 2, the nestlings started to vocalise as soon as they could see an adult perched on the other side of the gully. Their begging was a frantic, rapid twittering repeated by both nestlings continually (unless they had just received food, in which case they resumed begging soon afterwards). Earlier in the season their begging had subsided by the time the adult departed (e.g. ML 484319), but from day 8 the begging continued until the adult had disappeared (e.g. ML 484393).

Nestlings were similarly sized when we banded them on day 10 (Table 1) and had comparable feather growth (Fig. 1E). Their contour feathers were partially in sheath and did not fully cover their underparts or the neck-sides. The barbs of even the fully emerged feathers were loosely attached to each other, affording the feathers a fluffy appearance. The feathers of the upperparts were dark grey but had hints of brown in natural lighting when the birds fledged. The base of the bill and the tip were red-orange; the rest, including the culmen, was black. The throat feathers were mostly still in sheath. The flight feathers were a somewhat darker grey than the upperparts and only one-quarter emerged from their sheaths; the greater coverts looked similar but were only about one-eighth emerged. All of their breast and belly feathers were about half to two-thirds emerged from their sheaths. The breast feathers ranged from dark grey to a paler and warmer brownish grey. The belly feathers were pale carmine with grey bases. The upper flanks were grey quickly transitioning to bright orange-red on the lower flanks. Feathers covered only about half of

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the breast and belly. The tail feathers had only just broken the sheath and were still only 10% emerged. The upper leg was sparsely covered by pin-feathers. The tarsus was pale horn and the toes pale grey.

The nestlings fledged on day 15 at 08.53 h. At this time, the adults seemed particularly wary of the hide, looking at it repeatedly on every visit while the nestlings appeared to move closer to the edge of the nest. Eventually, both nestlings left the nest, one after the other, flying across the gully with no obvious hesitation. We re-found one at 09.22 h, perched 1 m high on a branch *c*.15 m from the nest (ML 479335, Fig. 1F). It was uttering an undescribed vocalisation that we only heard that day. The call was a high-pitched and clearly whistled *whee-ooo* that ended abruptly and had a slightly buzzy ring to the second note (ML 181706; Fig. 10). Unlike the *hyiaaar* call the adults uttered, the fledgling's call comprised two clearly defined notes of similar length. The adults were out of sight as we recorded the fledgling but gave the *hyiaaar* call repeatedly. As soon as we left the area and returned to the hide, the adult calls ceased but not those of the nestling. A few minutes later all birds fell silent. Soon afterwards, we spotted the adult hopping away, followed closely by the fledgling.

The fledgling in the neighbouring territory did not make the novel 'fledgling' sound the day we saw it. It was silent and allowed ERGC to unknowingly set a tripod 2 m away before an adult came to feed it. All three fledglings from both nests were superficially very similar and were probably similarly aged. They retained the orange bill tip and base observed when they were ten-day-old nestlings. The entire body was uniformly covered in contour feathers that still had the ragged or fluffy appearance of day 10. The flight feathers were dark grey, the secondaries tinged blue, and the tail was still only just visible. The grey breast feathers transitioned to red-tinged flank and belly feathers. The tarsi were still dull horn and feet grey. The fledglings probably appeared greyer than they did on day 10 in part due to the morning light. They looked smaller than the adults, as was obvious when they hopped after their parents.

Beyond the two territories discussed above, we detected birds in juvenile plumage twice in two separate territories: on 19 March and 28 April. The former was around adult size but was still in dusky-brown plumage and had an orange bill tip. The latter was accompanied by an adult giving the *hyiaaar* call.

Discussion

This study revealed many important details concerning the breeding biology of Black-crowned Pitta. Below, we discuss these in the same sequence used in the Results.

Distinguishing the sexes, nest placement and incubation.—Black-crowned Pitta is generally considered to be sexually monochromatic (Lambert & Woodcock 1996), although Erritzoe & Erritzoe (1998) suggested that the red belly of females of the closely related Garnet Pitta might be paler than in males. During our nest observations, the underparts were usually not visible but we found the upperparts useful in distinguishing the sexes. Sexual differences in colour intensity have been previously reported for other monochromatic pittas including Hooded *Pitta sordida*, Rainbow, Noisy *P. versicolor*, Superb *P. superba*, Whiskered *Erythropitta kochi* and members of the recently split Red-bellied Pitta complex *E. erythrogaster* (Rothschild & Hartert 1914, Coates 1990, Taylor & Taylor 1995, Erritzoe & Erritzoe 1998, Zimmermann & Noske 2003). It seems probable that this could be true for other apparently monochromatic pitta species. Such detailed colour distinctions should be made with caution and be supported at least by photographs or video. Low *et al*. (2016) appears to be the only other relevant study that used video equipment for this purpose, although they used supercilium shape rather than colour intensity to distinguish

 ISSN-2513-9894 (Online)

the sex of Blue-winged Pittas *P. moluccensis* (the difference in white wing patch size reported by Wells 2007 may not have been visible in their video recordings).

The nest, its placement on the ground and the clutch of two eggs are consistent with previous descriptions for Black-crowned Pitta and all other *Erythropitta* species, except some members of the Red-bellied Pitta complex (Lambert & Woodcock 1996, Rosell & Ceriban 2012). By using sticks to anchor the rattan frond to the nest dome, the Black-crowned Pittas modified their environment to cover their nest. Other pittas have shown resourcefulness when building their nests or making them cryptic: digging holes in riverbanks (Meyer & Wiglesworth 1989), using soft mud to bind the nest lining (J. Howes *in litt*. *in* Lambert & Woodcock 1996, Low *et al*. 2016), covering their nest with a layer of moss (Coates 1990) and building their nest such that a palm (*Licuala* sp.) grew through it (Eames 1996).

We can make limited statements concerning the incubation period at our Black-crowned Pitta nest. That the male brought a stick to the nest suggests that he participated in nestbuilding (*cf*. Lambert & Woodcock 1996). Furthermore, the addition of a stick two days before the nestlings hatched shows that the species continues construction well into the incubation period. Tarboton *et al*. (2011) also recorded an African Pitta *P. angolensis* bringing nest material during incubation, although the clutch was incomplete. Taylor & Taylor (1995) reported that Noisy Pittas brought soft material to the nest at almost every changeover during incubation. It is impossible to ascertain if the female Black-crowned Pitta also incubated based on our short observation, but those made at a nest in Lambert & Woodcock (1996) and her prominent role in brooding suggest that she probably did.

We discovered this nest by inadvertently flushing an incubating adult. Pittas vary in how resistant they are to flushing from the nest, but several sit tight enough to be caught, including Blue-naped *Hydrornis nipalensis*, New Britain *Erythropitta gazellae* and Papuan Pittas *E. macklotii* (Dahl 1899 *in* Erritzoe & Erritzoe 1998, Gilliard & LeCroy 1967, Erritzoe & Erritzoe 1998). Hooded Pittas appear more willing to flush during incubation but sit tight during brooding (Coates 1990). Our observations and those by Sheldon (in prep. *in* Lambert & Woodcock 1996), who observed an adult remain on its eggs until it was almost touched, suggest that Black-crowned Pittas are typical in their reluctance to leave the nest. During the nestling period, we once stood *c*.5 m from the nest and the brooding female did not flush, but we never moved closer.

Parental provisioning, effort and brooding.—The male and female exhibited differential parental investment: the male provisioned the nestlings more extensively over the course of the nestling season, while the female was the sole bird we recorded brooding. Other species of pitta show various trends in parental division of labour. In Rainbow and Blue-winged Pittas, both sexes appear to contribute almost equally to nestling provisioning (Zimmermann & Noske 2003, Hutchinson & Mears 2006). Male Giant and Hooded Pittas visit the nest somewhat more frequently than females, making *c*.55% of visits (Round *et al*. 1989, Coates 1990). Similar to Black-crowned Pitta, the male Gurney's Pitta at two nests made more visits than the female and at one nest female visitation increased in the second week (Round & Treesucon 1986, Gretton 1988 *in* Lambert & Woodcock 1996). That said, our results show that the relative contributions of each sex changed during the nestling season. Therefore, the results of other studies cannot validly be compared to ours, unless they properly sampled throughout the nestling season. In the studies mentioned above, those of Hooded and Blue-winged Pittas did not span the entire nestling period (although the extent to which this is true is unspecified in the latter; Coates 1990, Hutchinson & Mears 2006). The same was true at one Gurney's Pitta nest (Round & Treesucon 1996). However, the observations at Rainbow, Giant and the other Gurney's Pitta nests all provide a benchmark

 ISSN-2513-9894 (Online)

by which to compare the relative efforts of male and female pittas (Round *et al.* 1989, Zimmermann & Noske 2003; A. Gretton pers. comm.).

Compared to all other relatively well-studied pittas, Black-crowned Pitta had a much lower mean visitation rate—only 2.17 visits / hour and at most averaging 2.55 visits / hour in a day. Gurney's, Hooded and Rainbow Pitta visitation rates range from 6.73 to 9.3 visits / hour (Gretton 1988 *in* Lambert & Woodcock 1996, Coates 1990, Zimmermann & Noske 2003), while those at a Fairy Pitta nest increased from 2.2 to 6.2 visits / hour over the first seven days of the nestling period (Lin *et al*. 2007b). Pairs of Giant and Bar-bellied Pittas *Hydrornis elliotii* made *c*.3.2 visits / hour each (Round *et al*. 1989, Eames 1996), which is more similar to Black-crowned Pitta, albeit still a higher visitation rate. Visitation rates for species for which few observations exist (Hooded and Bar-bellied Pittas) may not be directly comparable to our nest, but it is otherwise clear that the Black-crowned Pittas at this nest had a notably low visitation rate.

Multiple factors could lead to a lower visitation rate but data to discriminate among them are scarce. Compared to the species that occur further north, Black-crowned Pitta has a smaller clutch size (two vs. 3–5) and therefore may require less activity around the nest (Skutch 1949)—the exceptions are Giant and Bar-bellied Pittas, which also lay two eggs (the nest of the latter that Eames 1996 observed had two eggs, but the species can lay 2–4 eggs) and had lower visitation rates. Black-crowned Pitta nestlings might require less food if they receive a higher quality diet (Twining *et al*. 2016) or have a longer nestling period (but see Nestling development and fledging). Our observations of nestling diet appear typical of many pittas (Round *et al*. 1989, Lin *et al*. 2007b, Donald *et al*. 2009, Kim *et al*. 2012). This is not necessarily indicative of nutritional content, though, especially because we have no measure of how prominently earthworms figured in diet relative to other invertebrates.

Data concerning brooding in other pittas is relatively scarce, partially because it can be unclear if observers include brooding under the term 'incubation'. It appears that males have occasionally been observed brooding in Gurney's Pitta (Gretton 1988 *in* Lambert & Woodcock 1996), but in Giant, Blue-rumped *Hydrornis soror* and Noisy Pittas females alone have been noted brooding, as at the Black-crowned Pitta nest we studied (Round *et al*. 1989, Lambert *et al*. 1995, Taylor & Taylor 1995). Interestingly, both sexes at a Black-crowned Pitta nest in Danum Valley, Sabah, incubated the nestlings (Lambert & Woodcock 1996); although the extent to which the male brooded is unclear, this indicates there is some variation to be explored by future studies with larger samples, assuming sexes were always correctly identified. Like Gurney's and Giant Pittas, the Black-crowned Pitta female we observed brooded at night at least until the evening of day 5, although Giant Pittas continue brooding until their nestlings are near fledging (Round *et al*. 1989). We have no direct evidence that the Black-crowned Pitta did not continue brooding at night after day 5, but she began visiting the nest earlier in the morning and was not seen arriving as dusk approached thereafter. Her brooding patterns overall resembled those of a Gurney's Pitta (Gretton 1988 *in* Lambert & Woodcock 1996): early on, she brooded nearly all day and she gradually decreased the number of hours spent at the nest.

Correlations with visit segment durations and visit function.—We found that the pittas spent most of their time on the nest after feeding the nestlings, in the departure latency period. This is initially counter-intuitive because the older nestling begged continually during this period, which increases nest detectability and might attract predators (Haff & Magrath 2011, Ibáñez-Álamo *et al*. 2012), and the adults' presence often seems to serve no parental purpose. We found longer departure latencies associated with visits in which the adults removed faecal sacs. Once a faecal sac was produced the adults departed immediately. One exception to the tendency of longer departure latencies was the single time a faecal sac

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was waiting at the nest entrance when an adult arrived with food. The bird removed the sac immediately after food delivery, resulting in an especially short departure latency. This is similar in Blue-winged Pittas—longer visits are associated with the extraction of faecal sacs (Low *et al*. 2016). This made us suspect that the adults could anticipate the production of a faecal sac and waited for it before departing the nest. A recent study of Red-whiskered Bulbul *Pycnonotus jocosus* reached the same conclusion after experimentally discovering that the timing and mass of faecal sacs was linked to feeding frequency (Quan *et al*. 2015). This suggests that the benefits of nest sanitation (Petit *et al*. 1989, Guigueno & Sealy 2012, Ibáñez-Álamo *et al*. 2016)—especially given the visual conspicuousness of faecal sacs—may oppose selection for reduced auditory exposure to predators (Tarwater *et al*. 2009).

Two other factors might influence the length of the departure latency. First, the adults might be watching for predators from the nest—they frequently looked out of the nest during this period (Fig. 6B) and Lambert *et al*. (1995) reported a Blue-rumped Pitta standing at its nest for more than three hours after it spotted the observers. Second, the birds may have been ensuring that nestlings properly handled the food—they also frequently looked into the nest for extended periods during this period.

Nestling biology associated with faecal sacs was comparable to that in other pittas. Nestlings of other species present the sacs to adults in a similar fashion (Gretton 1988 *in* Lambert & Woodcock 1996, Coates 1990) and the sacs appear to be similarly sized (approximately the length of the head, excluding the bill, of the nestling at day 10, *c*.30 mm, similar to African Pittas; Masterson 1987). Gretton (1988 *in* Lambert & Woodcock 1996) found a Gurney's Pitta 'faecal sac dump' 12–15 m from the nest, like ours. Other species also exhibit sex biases in faecal sac extraction, but it is unclear whether they may have been caused by sex biases in visitation rates as at our nest: Coates (1990) noted that the male Hooded Pitta extracts more faecal sacs while Eames (1996) found that female Bar-bellied Pitta extracts more—although Eames' observation period was limited.

Feeding latency (the time between adult arrival and when it feeds the nestlings) decreased dramatically over the first few days and remained low during the rest of the nestling period. Our analysis correlated this segment well with brooding time periods because the male had to wait for the female to move in order to feed the nestlings, which was unnecessary in later brooding periods because the female stopped covering the nestlings' heads. However, this is difficult to disentangle from nestling development—younger chicks may have more difficulty begging and their response to an adult's presence probably takes longer—explaining why the female also deliberated before feeding when she arrived to brood. Our negative trend in latency is consistent with the hypothesis that birds should feed the nestlings as promptly as possible to reduce begging intensity (Tarwater *et al.* 2009), although this did not prevent further begging.

There appear to be no data for other pitta species to compare with our measurements of feeding duration, but their association with quantity of food and handling time are likely to hold true for other members of the family.

Nestling development and fledging.—The nestlings fledged 15 days after hatching, which is comparable to the 12–16 days reported for other pittas (Erritzoe 2003) and the 15–16 days suggested by Lambert & Woodcock (1996) at their Black-crowned Pitta nest. By observing ingestion of both eggshells by the female and the actual fledging by the nestlings, we report an accurate timespan of the nestling period for both offspring. We also present the first detailed description of nestling Black-crowned Pittas. They resembled other described nestling pittas after the pin-feathers have opened (Erritzoe & Erritzoe 1998), with their colours matching those of a juvenile. Our observations of a recently fledged juvenile match descriptions of juveniles / immatures in Lambert & Woodcock (1996). Notably, we

 ISSN-2513-9894 (Online)

saw no yellow feathers in the development of the Black-crowned Pitta nestlings, which contrasts with the description of a 'chick' in Lambert & Woodcock (1996). This supports the scepticism of Erritzoe & Erritzoe (1998) and suggests that the yellow-plumaged chick associated with specimen NHMUK 1956.60.234 at the Natural History Museum, Tring, is not a pitta.

Fledging is poorly understood in pittas. Just before the nestlings fledged, the adults' behaviour, including repeated use of the *hyiaaar* call, appeared to be encouraging the nestlings to leave the nest. Such behaviour in the family has otherwise been recorded only by adult Mangrove Pitta *Pitta megarhyncha*. Choy & Wee (2010) reported that while Mangrove Pittas generally fly from their nest following a provisioning visit, they started hopping for long distances shortly before the nestlings fledged. At their nest, the nestlings also left the nest several times before finally fledging. It was interesting to note how easily the nestlings observed by us flew for the first time.

This is the first report of a fledgling-specific vocalisation for any species of pitta—the closest observation is that of a mournful whistle given by a captive full-grown immature Green-breasted Pitta *Pitta reichenowi* (Lambert & Woodcock 1996). Fledgling oscines are known to exhibit abrupt changes in vocal abilities (Clemmons & Howitz 1990, Sawhney *et al*. 2006). These represent steps in the transition from begging calls to adult vocalisations, and might aid adults to locate dependent fledglings (Sawhney *et al*. 2006).

Vocalisations at the nest.—Our observations permit us to elaborate on the context of the novel *hyiaaar* call described by Pegan *et al.* (2013; referred to as the 'baudii-like call'). We have direct evidence that it serves as an alarm call when the birds perceived danger to themselves or to the nest, but we also consider that it may be used in contact. This is supported by our observations of the fledging event and the frequent use of this call outside the breeding season, although it is then difficult to assess if danger is imminent. Alarm calls have been recorded around Gurney's, Rainbow, Bar-bellied, Mangrove and Blue-winged Pitta nests and were provoked by intraspecific, human and predatory threats (Round & Treesucon 1986, Zimmermann 1995, Eames 1996, Choy & Wee 2010, Low *et al*. 2016). At a broader scale, an 'alarm call' has been noted for almost all species of pitta (Lambert & Woodcock 1996, Erritzoe & Erritzoe 1998). P. D. Round (*in litt. in* Lambert & Woodcock 1996) noted that Eared Pittas *H. phayrei* may use their 'alarm' call as a 'contact' call, so flexibility in context may be more widespread.

Declines in adult vocal activity have been reported in various other pittas at the onset of nesting, including Gurney's, Bar-bellied, Noisy, Rainbow, Fairy and African Pittas (Round & Treesucon 1986, Eames 1996, Woodall 1997, Zimmermann & Noske 2003, Lin *et al*. 2007a, Tarboton *et al*. 2011). This makes pittas difficult to find during these periods, especially as they may not respond to playback as readily as at other times (Lin *et al*. 2007a). The birds in one Black-crowned Pitta territory continued to be silent after their young fledged, while those in the neighbouring territory began singing regularly relatively shortly afterwards. We believe this is probably either because the latter birds lost their fledglings to predators and had no reason to remain silent, or because the former were warier of humans in their territory due to their extended interactions with us and did not want to attract attention.

We consider that the soft grunt- or cluck-like vocalisations the adults made at the nest entrance before feeding were probably to communicate with either the nestlings or the brooding female. Use of this vocalisation is otherwise difficult to interpret, especially why it was sometimes repeated more than ten times. Intriguingly, this vocalisation or one similar was also reported in ordinary provisioning visits by Hooded Pittas (Coates 1990). The male Black-crowned Pitta almost exclusively gave this call while the female was brooding, but not on every visit. He gave the vocalisation only once, and the female

 ISSN-2513-9894 (Online)

twice, when the nestlings alone were present, and the female gave it once before flying to the nest. Its function is unclear, but we believe our observations help clarify the context in which it is used. Gurney's and Bar-bellied Pittas have been reported making similar sounds under different circumstances. Gurney's Pittas utter a *hoo* when adults change-over at the nest (Gretton 1988 *in* Erritzoe & Erritzoe 1998), while Bar-bellied Pittas give a soft *coo* on approaching the nest, which the chicks answer vocally (Eames 1996). The latter case suggests that other pittas communicate with nestlings before feeds, but further studies are needed to reveal if these vocalisations are analogous.

Concluding remarks.—Our observations at a Black-crowned Pitta nest have provided data on the parental roles, rates of provisioning, nestling development, biology associated with faecal sacs and vocal behaviour. This is the first detailed perspective of the nesting biology of any species of *Erythropitta*, permitting initial comparisons with other pitta genera. However, one nest cannot accurately represent the nesting behaviour of an entire genus. Our observations are the first step towards understanding the breeding biology of *Erythropitta* and should be complemented by future studies. Enabled by use of video recordings, we noticed various small behaviours that have otherwise been noted only in one or two species of pitta; given the few detailed studies of the family, we predict that these behaviours are more widespread than have been recorded. We also consider that the manner we subdivided each nest visit enabled interesting insights into the importance of various activities. We hope that others may find this method useful to understand avian biology and eventually to make larger scale comparisons than possible here.

Acknowledgements

We thank our fellow expedition members who joined our nest-watch rotation: Cat Lauck and Kayleigh Chalkowski. The generous support and guidance of Dr Maklarin Bin Lakim, Fred Tuh Yit Yu, and the Sabah Parks staff who accommodated us and helped navigate permit systems made our work in Sabah possible. We thank Charles Dardia and the Cornell University Museum of Vertebrates, Brad Walker, Jay McGowan, Matt Medler and the Macaulay Library of Natural Sounds, Irby Lovette, and other Cornell Lab of Ornithology staff who provided logistical support and equipment loans, including video and audio-recording equipment. Richard Noske and Udo Zimmermann provided invaluable advice concerning the study of pittas as we prepared our expedition, while Adam Gretton kindly responded to subsequent questions. Additional thanks are owed to Kelly Hallinger for her instrumental help with genetic sexing, Teresa Porri for her assistance with CT scans, Ryan Shipley for permitting us to use his photograph of the nestling, Harry Greene for his help in identifying the snake, Teresa Pegan for providing manuscript advice and encouragement, Guy Kirwan for efficient editorial assistance, and three anonymous reviewers who made helpful comments. The undergraduate-led expedition during which this nest was documented was generously funded by the Ivy Expeditions Fund, Cornell Lab of Ornithology and programme support funds from Cornell University to DWW. *Ethics statement*: all of our field work conformed to the approved Cornell IACUC protocol #2001-0051 to D. W. Winkler, an access license from the Sabah Biodiversity Council, and a research permit issued by Sabah Parks.

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Addresses: Dept. of Ecology and Evolutionary Biology, Cornell Univ., Ithaca, NY, 14853, USA. Eric R. Gulson-Castillo, Emma I. Grieg, Justin M. Hite, Sophia C. Orzechowski & David W. Winkler, Cornell Lab of Ornithology, Ithaca, NY, 14850, USA. Eric R. Gulson-Castillo & David W. Winkler, Cornell Univ. Mus. of Vertebrates, Ithaca, NY, 14850, USA. Justin M. Hite, Kaua'i Forest Birds Recovery Project, Hanapepe, HI, 96716, USA. Sophia C. Orzechowski, Dept. of Wildlife Ecology and Conservation, Univ. of Florida, Gainesville, FL, 32611, USA. Corresponding author: Eric R. Gulson-Castillo, e-mail: erg57@cornell.edu

 ISSN-2513-9894 (Online)