

# Breeding biology and vocalisations of the Blue-grey Robin *Peneothello cyanus* and its reproductive traits compared with those of other montane New Guinean robins

Richard H. Donaghey<sup>1, 2\*</sup>, Donna J. Belder<sup>3</sup> and Tony Baylis<sup>4</sup>

<sup>1</sup>Centre for Planetary Health and Food Security, Griffith University, Nathan 4111 QLD, Australia

<sup>2</sup>80 Sawards Road, Myalla TAS 7325, Australia

<sup>3</sup>2A Sylvan Way, Glenalta SA 5052, Australia

<sup>4</sup>628 Utopia Road, Brooweena QLD 4621, Australia

\*Corresponding author. Email: ricardo@southernphone.com.au

**Abstract.** We monitored a nest of the Blue-grey Robin *Peneothello cyanus* (Petroicidae) while in the Yopno Urawa Som Conservation Area, Huon Peninsula, Papua New Guinea, from 23 October to 6 December 2014. The nest was watched for 24 hours during incubation of the single egg, and for 25.9 hours during the first 11 days of the nestling period. Vocalisations were recorded. Female daylight incubation constancy was 68%, the mean duration of on-bouts was 5.05 minutes and of off-bouts was 2.32 minutes. The daily number of incubation bouts was 98, and the mean number of incubation bouts per hour was 8.2. Feeding of the female by the male during incubation occurred at and away from the nest. Mean brooding constancy by the female was 51.4% and mean number of brooding bouts per hour 8.9. Mean number of food-delivery trips by the male and female combined was 4.4 per hour, and the mean number of their nest visits was 12.7 per hour. The fate of the nestling was unknown but the high number of incubation bouts and nest visits during the first 11 days of the nestling period suggests that the risk of nest predation was low. At 10 days of age, a nestling weighed 18 g (72% of mean adult weight). The reproductive traits of the Blue-grey Robin are compared with those of three other montane New Guinean robin species. Male Blue-grey Robins had a repertoire of seven song types near the nest, females sang five song types at the nest, and two song types were sung by both the male and the female.

## Introduction

Diamond (1972) conducted extensive field surveys along an elevational gradient on Mt Karimui, Eastern Highlands, Papua New Guinea (PNG), to document and analyse the altitudinal ranges of congeneric pairs of bird species. He discovered that altitude was the most important ecological sorting mechanism and that more congeneric pairs segregated by altitude than by any other features such as habitat and vertical foraging niches. On Mt Karimui, the Blue-grey Robin *Peneothello cyanus* occupied a zone from 1580 to 2130 m above sea level (asl) but was replaced by the White-winged Robin *P. sigillata* at higher altitudes. Freeman & Class Freeman (2014) resurveyed Diamond's transects to investigate if montane birds have shifted upslope in response to global warming. They discovered that the White-winged Robin has moved upslope >100 m and now occurs only above 2330 m asl near the summit of Mt Karimui (2520 m).

The Blue-grey Robin is sexually monomorphic and measures 14–15 cm in length (Boles 2007). Mean weight of males is 26.9 g (range 24–30 g,  $n = 10$ ) and of females 23.2 g (range 20.7–26.0 g,  $n = 10$ ) (Diamond 1972). The adult is blue-grey with blackish wings and tail. The immature is mottled blue-grey and streaked brown (Figure 1). The species is distributed along the Eastern and Western Central Ranges and on outlying ranges including the Bird's Head, Huon Peninsula and Adelbert Mountains. It is a shy and elusive robin that inhabits the understorey of mid-montane forest from 900 to 2750 m (mainly 1500–2500 m asl) (Coates 1990; Boles 2007; Beehler & Pratt 2016). Throughout most of its range, the Blue-grey



**Figure 1.** Immature Blue-grey Robin, Camp 12, YUS CA, Huon Peninsula, Papua New Guinea. Photo: David Bryden

Robin is replaced by the White-winged Robin at higher altitudes. However, on the Bird's Head, West Papua, where the White-winged Robin is absent, the Smoky Robin *P. cryptoleuca* occurs at higher elevations than the Blue-grey Robin (Diamond 1972; Coates 1990; Boles 2007). Near Kwau village in the Arfak Mountains, West Papua, the Blue-grey Robin co-exists with the Green-backed Robin *Pachycephalopsis hattamensis* from 1580 m to at least 1700 m asl but is replaced by the Smoky Robin above 1800 m asl (Donaghey & Donaghey 2019; RHD unpubl. data). The Blue-grey Robin is sedentary, territorial, and presumably socially monogamous (Coates 1990; Boles 2007). It is a typical 'thicket-flycatcher' that spends most of its time (~70% of observations) sally-striking arthropod prey from understorey foliage and ~25% of observations



**Figure 2.** Wing-flutter display of a brooding Blue-grey Robin on the nest in response to a visiting male with food, YUS CA, Huon Peninsula, PNG. Photo: Donna Belder

gleaning. Of the gleaning observations, ~60% were from understorey vegetation and ~35% were on the ground (Croxall 1977; Boles 2007).

Beehler & Pratt (2016) recognised two subspecies: the nominate *cyanus* of the Bird's Head, and *subcyanea* of the Eastern Central Ranges, South-east Peninsula and the Huon Peninsula. Benz (2011) studied the phylogeography of the Blue-grey Robin throughout New Guinea. Using mitochondrial sequence data, phylogeographic analyses recovered three primary clades whose distributions corresponded to biogeographic boundaries such as the Bird's Head, and the Strickland Gorge west along the Western Central Range, and east throughout the Eastern Central Range to the South-east Peninsula. Gill *et al.* (2024) recognised a third subspecies, *atricapilla*, of the Border Ranges and Western Central Ranges based on Benz (2011). The first subclade of the subfamily Eopsaltriinae includes the genera *Melanodryas*, *Peneothello*, *Gennaeodryas*, *Eopsaltria*, *Quoyornis* and *Tregellasia*. The second subclade contains *Heteromyias*, *Plesiodryas* and *Poecilodryas* (Christidis *et al.* 2011).

At our mid-mountain study site in the Yopno Urawa Som Conservation Area (YUS CA), the Blue-grey Robin co-existed with the Black-capped Robin *Heteromyias armiti* and Lesser Ground Robin *Amalocichla incerta* but at higher elevations it was replaced by the congeneric White-winged Robin (Donaghey 2022). All of these robins forage and nest low in the understorey (Diamond 1972; Croxall 1977; Coates 1990; Boles 2007; Pratt & Beehler 2015). In New Guinean robins, clutch size is generally one in montane species and one or two in lowland species but is unknown in most lowland species (Coates 1990; Donaghey 2015a). Clutch size is one in the upper-montane White-winged Robin (Donaghey 2022) and in the Blue-grey Robin (Harrison 1971; Coates 1990; Boles 2007). Food limitation and nest predation are two interacting factors that influence clutch size and reproductive strategies (Martin 1992). Skutch (1949) proposed that greater parental activity at the nest increases nest predation and favours small clutch sizes. We studied the breeding biology of the Blue-grey Robin to elucidate its reproductive strategy and to compare its reproductive traits with those of the White-winged Robin, and co-existing mid-montane robins in the YUS CA, Huon Peninsula.

The nest and egg of the Blue-grey Robin have been described (Harrison 1971; Coates 1990; Boles 2007). However, nothing is known about aspects of this species' breeding biology such as incubation and nestling periods, parental incubation behaviour and care of young. Our main objectives were to document: (1) nest-site and nest characteristics; (2) clutch size, incubation period, daylight incubation constancy, the number of nest visits, and the length of on- and off-bouts during incubation; (3) nestling period, brooding constancy, the number of food-delivery trips and visits to the nest throughout the nestling period, and nestling diet; and (4) to compare these with other New Guinean montane robins, especially closely related species.

## Study site and methods

### Study area

RHD and David Bryden conducted a 6-week exploratory trip that included the Huon Peninsula in July–August 2014 (Donaghey 2015b). Soon after, TB, DJB and RHD flew into Sapmanga, Yopno Urawa Som Conservation Area (YUS CA, named after the Yopno, Urawa and Som Rivers), Huon Peninsula, elevation 900 m asl. We arranged porters and guides at Gomdan village and walked up to Camp 12 (6°01'S, 146°50'E; 2300 m asl), where we studied mid-montane robins (Petroicidae) from 23 October to 6 December 2014. The vegetation above Camp 12, at 2400 m asl, is described by Inaho (2012) and Donaghey *et al.* (2019a).

### Observations at nest

A Blue-grey Robin nest with an egg was found near Camp 12 on the morning of 10 November. We watched this nest from a portable hide during the incubation period and for the first 11 days of the nestling period (Day 1 of the nestling period represents the day that the nestling hatched), using a 25× telescope mounted on a tripod. Only the female incubated and brooded, and she was identified by her behaviour and food solicitation (see Figure 2).

To determine the time that the female spent incubating, we watched the nest during all daylight hours on the afternoon of 13 November and the following morning. The durations of all bouts on and off the nest were timed to the nearest second with a lap/split stop watch. An incubation session or 'on-bout' is the time (minutes and seconds) spent incubating; an absence or 'off-bout' is the time that an incubating female spent away from the nest. Incubation and brooding constancy are the percentage of daylight hours spent in incubation and brooding, respectively. The time that a female spent brooding, and the numbers of feeding trips, nest visits, and faecal sacs removed per hour were determined by watching the nest for the first 11 days of the nestling period, for a total of 25.9 hours. We measured the height of the nest above the ground and recorded characteristics of the nest and nest site. The fate of the nest was not determined because we were committed to returning to Sapmanga village on 7 December.



## Vocalisations

Vocalisations by the male, female and nestling were recorded at the nest. Song bouts by the male near this nest were recorded on 19 November from 0600 to 0800 h while RHD simultaneously observed female incubation behaviour from a hide. In addition, on 29 November, TB recorded a sequence of male song bouts at Camp Parotia, YUS CA, elevation 1950 m asl (6°00'S, 146°49'E), although no nests were found there. On 2 December, TB recorded male, female and nestling vocalisations at and near a Blue-grey Robin nest with a 6-day-old nestling near Camp 12 by using a Nagra LB recorder (wav file 48 Hz/24bit) and Sennheiser MKH40 cardioid microphone placed close to the nest site and an Olympus LS11 (wav file 48 Hz/24bit) and Sennheiser ME62 cardioid microphone placed ~1 m directly under the nest. Vocalisations were recorded at the nest from 0634 to 1046 h. RHD observed Blue-grey Robin behaviour at the Camp 12 nest with a single nestling between 0800 and 1000 h on 2, 3 and 5 December, and from 1500 to 1700 h on 4 December, and simultaneously recorded vocalisations near the nest for each 2-hour nest watch using an Olympus Linear PCM recorder LS-20M and a Sennheiser ME66 microphone. On 6 December, RHD documented robin behaviour at the nest from 0800 to 1000 h, and recorded vocalisations from 0719 to 0930 h using a Sennheiser ME66 microphone, placed below the nest. Spectrograms from these recordings were produced by TB using Raven Pro 1.6, with a value of DFT1024. In a spectrogram selection, e.g. sel014657 denotes recording time of 1 hour, 46 minutes and 57 seconds. Frequency measurements were calculated using peak frequency; this measurement indicates the frequency with the most energy for the selection and is expressed in Hz. Where bandwidth is measured, e.g. BW90%, this depicts the bandwidth of the difference between 5% and 95% frequencies within the selection box.

## Results

### *Characteristics of nest and nest site*

The deep, cup-shaped nest was covered externally by a thick layer of bright-green moss that also hung below the nest base (Figure 2), except for a narrow band at the



**Figure 3.** Egg-cup materials and egg of the Blue-grey Robin, YUS CA, Huon Peninsula, PNG. Photo: Tony Baylis

top which was composed of rootlets and fern fronds. The egg-cup was lined with fine rootlets and a profuse layer of dried fern fronds (Figure 3). The internal nest diameter was 55 mm, external diameter 70 mm, and external depth 105 mm, and pendulous green moss extended below the nest base for ~300 mm. The nest was built 2.5 m above the ground, on a thin sloping branch of an understory sapling next to an embankment above a stream.

### *Clutch size, egg, incubation behaviour and incubation period*

Clutch size was one. The egg was olive-green with a ring of diffuse reddish-brown blotches around the larger end (Figure 3). It weighed 3.8 g at 1600 h on 10 November and measured 23.1×17.8 mm.

Diurnal incubation constancy for a 12-h day was 68% during the last week of the incubation period (Table 1). Incubation constancy averaged 68% from 0600 to 1000 h, 70% from 1000 to 1400 h, and 67% from 1400 to 1800 h. Hourly incubation constancy ranged from 52% to 82% (Table 1). For 24 observation hours over all daylight hours, the mean length of incubation on-bouts was 5.05 minutes (range 0.02–30.57 min.,  $n = 196$ ), and the mean length of incubation off-bouts was 2.32 minutes (range 0.10–9.65 min.,  $n = 195$ ). The mean number of incubation on-bouts was 8.2 per hour (range 2–16,  $n = 196$ ), and 98 for a 12-h day.

During the incubation period, the male fed the female, mostly off the nest. The rate of incubation feeding at the nest was 1–2 times per hour. In response to the male approaching the nest with food, the incubating female solicited food by quivering and elevating her wings and emitting short whistles and squeaks (Figure 2).

### *Hatching, nestling period and parental care of the young*

Hatching of the single nestling occurred at 0822 h on 26 November. Nestling care (brooding of young and food-delivery trips) was quantified at this nest. Time spent brooding varied with time of day and nestling age. Figure 4 shows a significant negative linear relationship between time spent brooding and nestling age. Time spent brooding declined from 42.5 min./h on Day 1 of the nestling period to 15.6 min./h on Day 11 (Table 2). Brooding constancy declined from a mean of 69.7% on Day 1 of the nestling period to 26% on Day 11. Mean brooding constancy for the first 11 days of the nestling period was 51% (Table 2) and was extrapolated to be zero on Day 18 of the nestling period (Figure 4). The mean length of brooding bouts was 3.52 minutes (range 0.07–36.72 min,  $n = 227$ ).

The male brought food for the brooding female. As in the incubation period, when he approached the nest she solicited food, which she either consumed or fed to the young.

Both adults also fed the young directly and flew off with faecal sacs. Of 114 provisioning trips to the nest, the female fed the nestling 71 times (62%); the male fed the young directly 36 times and passed food to the female seven times (Appendix 1). There was a significant linear

**Table 1.** Nest attentiveness of a female Blue-grey Robin during the incubation period, YUS CA, Huon Peninsula. PNG, 2014. Date is given as day.month.

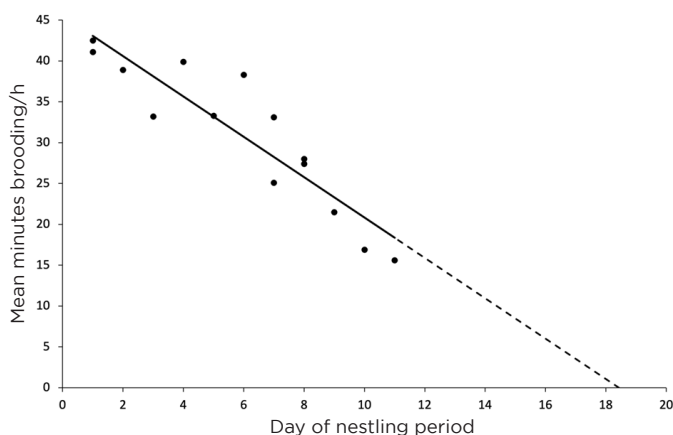
Date	Time (h)	Minutes		Incubation constancy (%)	No. Incubation on-bouts/h
		On nest	Off nest		
14.11	0600–0700	44.77	15.23	74.6	8
14.11	0700–0800	49.36	10.64	82.3	3
14.11	0800–0900	35.48	24.52	59.1	9
14.11	0900–1000	32.92	27.08	54.9	8
14.11	1000–1100	46.80	13.20	78.0	10
13.11	1100–1200	47.76	12.24	79.6	5
13.11	1200–1300	38.47	21.53	64.1	6
13.11	1300–1400	34.09	25.91	56.8	9
13.11	1400–1500	37.82	22.18	63.0	7
13.11	1500–1600	30.99	29.01	51.7	2
13.11	1600–1700	45.87	14.13	76.5	6
13.11	1700–1800	46.23	13.77	77.1	8
<b>Daily incubation on-bouts</b>					<b>81</b>
<b>Mean incubation on-bouts/h</b>					<b>6.8</b>

relationship between number of feeding trips and nestling age (Figure 5). The number of feeding trips ranged from 1.5/h on Day 1 to a maximum of 8.0/h and 7.5/h on Days 8 and 9 of the nestling period, respectively. High feeding rates of 6/h were recorded on morning watches on Days 10 and 11 (Figure 5, Appendix 1). Mean number of feeding trips to the nest was 4.4/h for Days 1–11. Mean total number of nest visits by male and female combined was 12.7/h for Days 1–11. On Day 6, the number of brooding bouts was 16.5/h and the number of nest visits was also highest (20.5/h), with 35 visits by the female and 6 visits by the male during a 2-h morning nest watch. Of 330 nest visits, 257 (78%) were by the female and 73 (22%) by the male. Of the 257 female nest visits, 230 (89.5%) were brooding visits (Appendix 1).

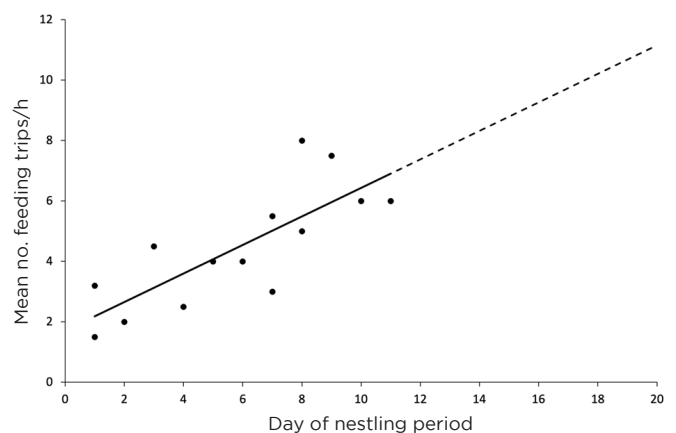
During Days 5–11 of the nestling period, nestling meals identified were earthworms (Annelida), tree crickets (Orthoptera), flies (Diptera), larvae of beetles (Coleoptera), larvae of moths (Lepidoptera) and portions of small lizards (Scincidae). For Days 3–11 of the nestling period, both adults flew off with faecal sacs, at a rate 1–2/h, mostly 1/h.

### Nestling growth and development

On the day of hatching, the nestling weighed 3.0 g at 1125 h. At 4 days of age (Day 5 of the nestling period), nestling weight was 8.1 g (32.4% of mean adult weight of 25 g). At 10 days of age, the nestling weighed 18.0 g (72% of mean adult weight). The wing-length of the nestling was



**Figure 4.** Relationship between Blue-grey Robin daytime brooding and nestling age for a brood of one at one nest. Each dot represents the mean minutes brooding per hour for each of 14 nest watches (mean duration 120 min.  $n = 11$ ; 60 min.  $n = 2$ ; and 113 min.  $n = 1$ ). Day 1 of the nestling period represents the day the nestling hatched. The linear regression equation is  $Y = 2.47 + 45.52 X$ ;  $r^2 = 0.83$ ,  $P < 0.0001$ ; significance level = 95%.



**Figure 5.** Relationship between Blue-grey Robin mean number of feeding trips per hour and nestling age for a brood of one at one nest. Each dot represents the number of feeding trips per hour for each of 14 nest watches (mean duration 120 min.  $n = 11$ ; 60 min.  $n = 2$ ; and 113 min.  $n = 1$ ). Day 1 of the nestling period represents the day the nestling hatched. The linear regression equation is  $Y = 0.472 + 1.713 X$ ;  $r^2 = 0.614$ ,  $P < 0.0001$ ; significance level = 95%.



**Table 2.** Brooding by a female Blue-grey Robin at one nest, YUS CA, Huon Peninsula, PNG, 2014. Day = day of nestling period; date is given as day.month; obs. min. = observation minutes; C = brooding constancy.

Day	Date	Time h	Obs. min.	Brooding by female				No. times male fed female
				No. bouts	Total (min.)	Min./h	C (%)	
1	26.11	0822–1015	113	19	77.39	41.10	68.5	12
1	27.11	0700–0900	120	17	85.08	42.50	70.9	9
2	28.11	0700–0800	60	7	38.85	38.85	64.8	4
3	28.11	1500–1700	120	23	66.42	33.21	55.4	6
4	29.11	0800–1000	120	25	79.86	39.93	66.6	16
5	30.11	1500–1700	120	17	66.67	33.34	55.6	10
6	1.12	0800–1000	120	33	76.64	38.32	63.9	13
7	2.12	0800–1000	120	17	66.28	33.14	55.2	2
7	2.12	1500–1700	120	13	50.19	25.10	41.8	3
8	3.12	0800–1000	120	19	55.96	27.98	46.6	1
8	3.12	1500–1600	60	8	27.40	27.4	45.7	
9	4.12	1500–1700	120	13	43.01	21.55	35.8	2
10	5.12	0800–1000	120	12	33.78	16.89	28.2	3
11	6.12	0800–1000	120	7	31.25	15.63	26.0	
<b>Brooding</b>								
<b>Days 1–11</b>				<b>1553</b>	<b>230</b>	<b>798.78</b>	<b>51.4</b>	

15 mm at 6 days of age and 28 mm at 10 days (31% of mean adult wing-length of 91 mm: Diamond 1972).

On the day of hatching, the nestling was naked and pink. The 6-day-old nestling had short feathers emerging from pins on the dorsal tract and its eyes were closed (Figure 6). At 8 days, the eyes were closed and feathers were erupting from the head, back and wing-covert pins (Figure 7).

### *Vocalisations of adults near and at nest and of nestling*

Spectrograms of ten different song types (A–J) by male and female Blue-grey Robins near and at the Camp 12 nest were identified by matching recorded vocalisations with observations during the nest watches (Figure 8). Song type J (Figure 8) was given by a male upslope from the Camp 12 nest. The frequency and other parameters of definitive song types A–J are presented in Appendix 2.

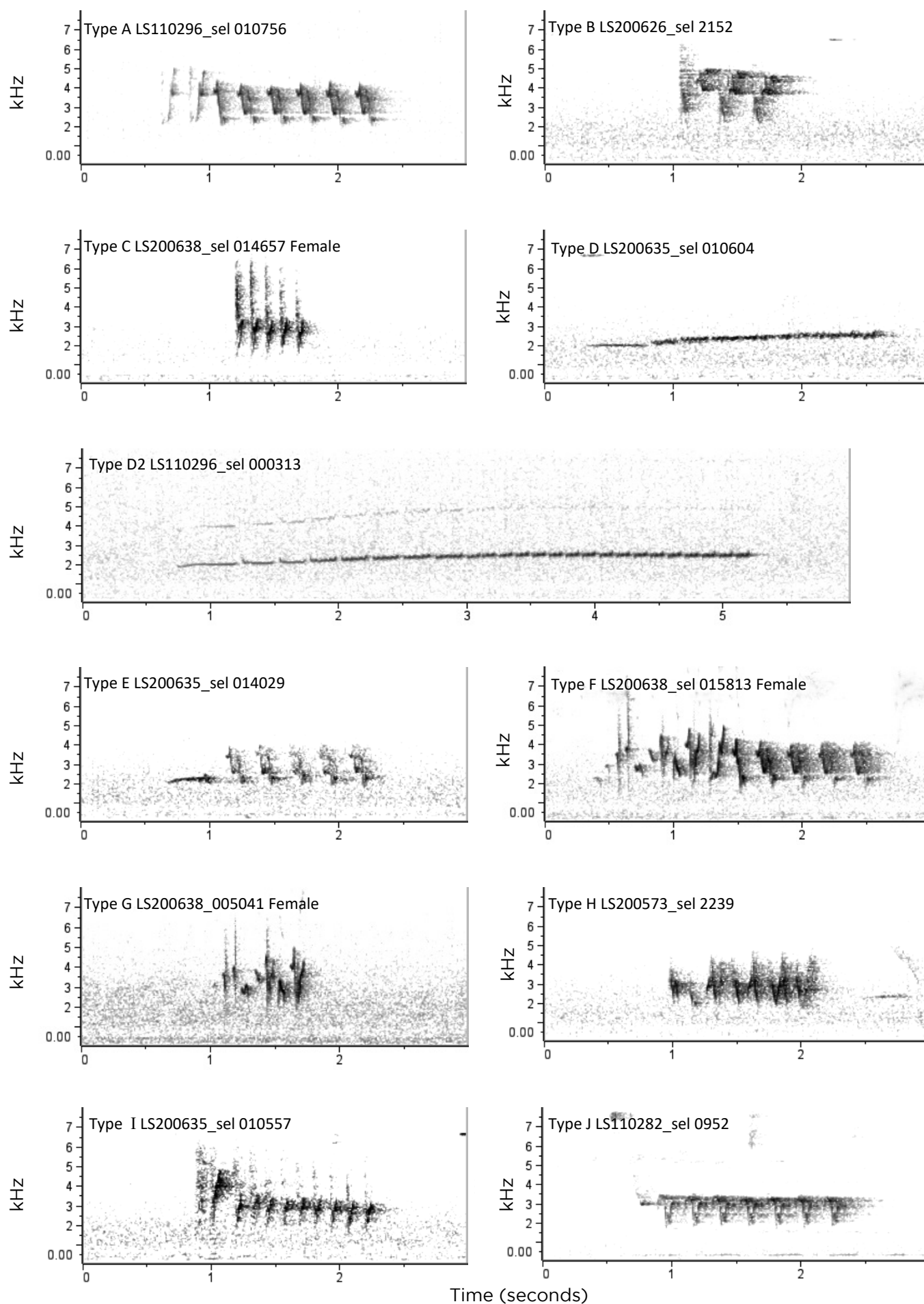
Songs A, B, C, D, H, I and J were given in male song bouts near the Camp 12 nest; thus the male there had a repertoire of seven song types. Song J was sung also by two counter-singing males at Camp Parotia on 29 November, during a 1-minute 30-second sequence (LS110282\_sel 0920–1050) of 14 male songs. Song J was produced nine times and Song C five times. In Figure 8, Songs C, D, E, F and G were sung by the female, and Songs C and D were given by both the male and female. Song D varied in length and structure (Figure 8). The longer Song D2, presumed to be given by the female, was only recorded close to the nest. Male song bouts at Camp 12 and the sequence and number of song types are presented in Figures 9, 10 and 11. Figure 9 depicts a 2-minute sequence of song types and calls (LS200573\_sel 2207–2407) from 0623 to 0625 h on 19 November while the female was incubating. In general, songs tend to be long, complex vocalisations given by males in the breeding season, especially in north-temperate passerine songbirds, to advertise territory



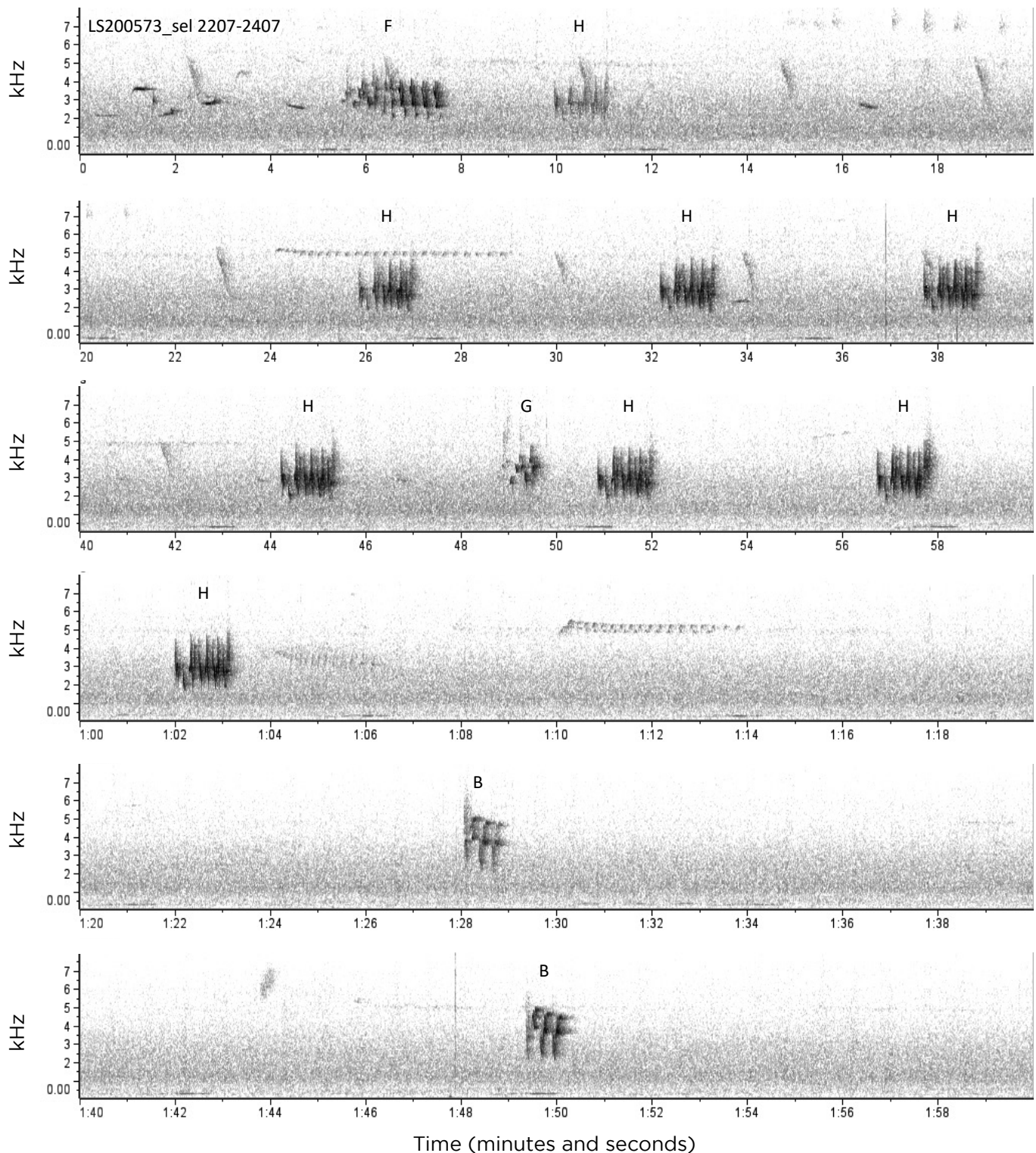
**Figure 6.** Six-day-old nestling Blue-grey Robin, YUS CA, Huon Peninsula, PNG. Photo: Tony Baylis



**Figure 7.** Eight-day-old nestling Blue-grey Robin, YUS CA, Huon Peninsula, PNG. Photo: Tony Baylis



**Figure 8.** Spectrograms of definitive song types A-J by male and female Blue-grey Robins at and near the nest, YUS CA, Huon Peninsula, PNG. Xeno-canto: <https://xeno-canto.org/explore?query=nr:972447>. Spectrograms: Tony Baylis



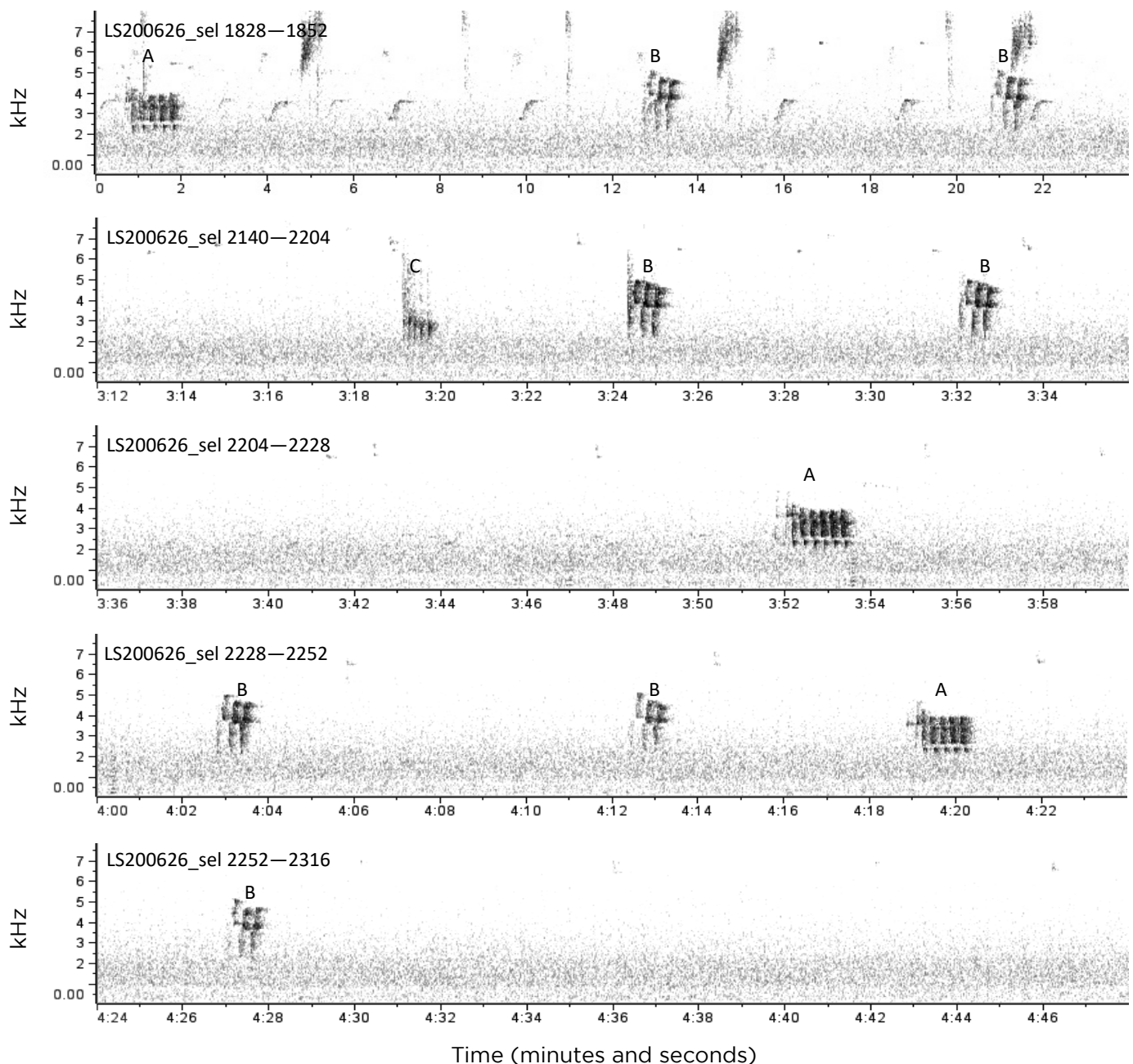
**Figure 9.** Spectrogram of a 2-minute sequence of song types by a male Blue-grey Robin near the nest while the female was incubating, 19 November 2014, YUS CA, Huon Peninsula, PNG. Xeno-canto: <https://xeno-canto.org/explore?query=nr:972452>. Spectrogram: Tony Baylis

and attract mates. Calls tend to be shorter, simpler and produced by both the male and the female throughout the year. Unlike songs, calls have specific functions such as flight, threat and alarm (Catchpole & Slater 1995; Lovette & Fitzpatrick 2016). Figure 9 begins with food-solicitation short whistles by the female at 2 seconds. Song F heralded the start of the song bout 4 seconds later. The male then sang Song H eight times in 52 seconds, followed by a pause of 26 seconds and then two B song types. Song G at 49 seconds, which occurred between two H songs,

is a female song. Male Songs H and B occurred while the incubating female was on the nest.

The spectrogram in Figure 10 (LS200626), recorded from 0815 to 0819 h on 2 December near the nest, is a 2-minute sequence (five 24-second segments; segments showing no songs are not shown) from a 4-minute 48-second sequence of male Songs A, B and C. In the first spectrogram row, three songs (types A, B, B) occurred in 24 seconds. In the next four rows, the song sequence





**Figure 10.** Spectrogram of song types by a male Blue-grey Robin near the nest with a 6-day-old nestling, 2 December 2014, YUS CA, Huon Peninsula, PNG. The spectrogram shows five 24-second segments from a 4-minute 48-second sequence (segments showing no songs are not shown). Xeno-canto: <https://xeno-canto.org/explore?query=nr:972453>. Spectrogram: Tony Baylis

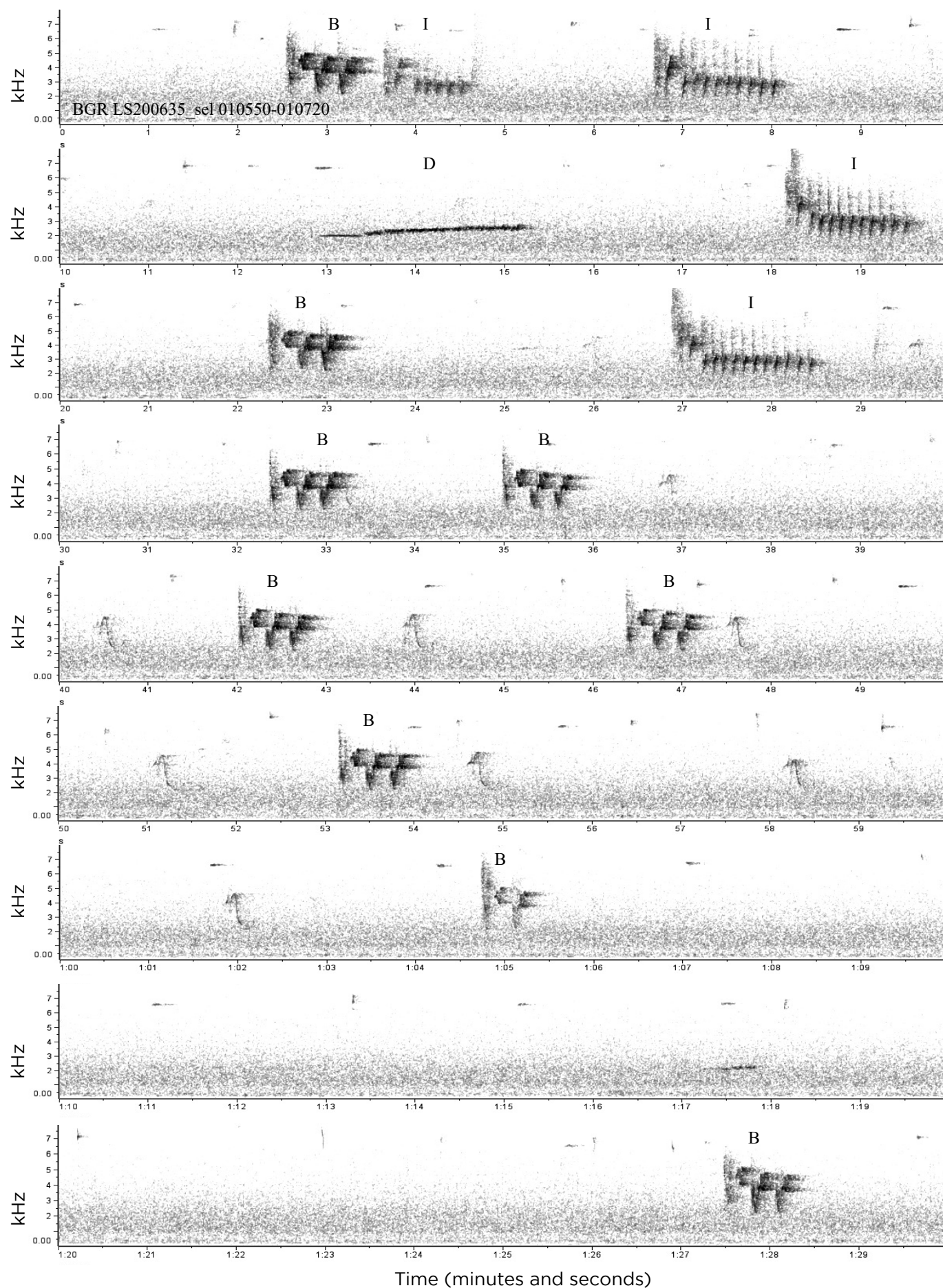
was C, B, B, A, B, B, A, B in 1 minute 36 seconds. In the Figure 10 spectrogram, Song B occurs seven times, Song A three times and Song C once. The spectrogram in Figure 11 (LS200635\_sel 010550-010720), recorded from 0853 to 0854 h on 3 December while the female was brooding a 7-day-old nestling, depicts a 1-minute 30-second sequence of 14 male songs, B, D and I. Song B occurs nine times, I four times and D once.

The spectrograms in Figure 8 depict three female song types, E, F and G, given at and near the nest. Song E (LS200635\_sel 014029) was delivered by the female on the nest at 0930 h on 3 December. In the Video 6586, the female gave Song E as she left the nest. In Video 6297, the female sang Song E as she returned to the nest and brooded the young. Figure 8 presents an example of Song F (LS200638\_sel 015813) by the female on 6 December. Another example of female Song F (LS200635\_sel 014039) at the nest occurred at 0930 h on 3 December. The example

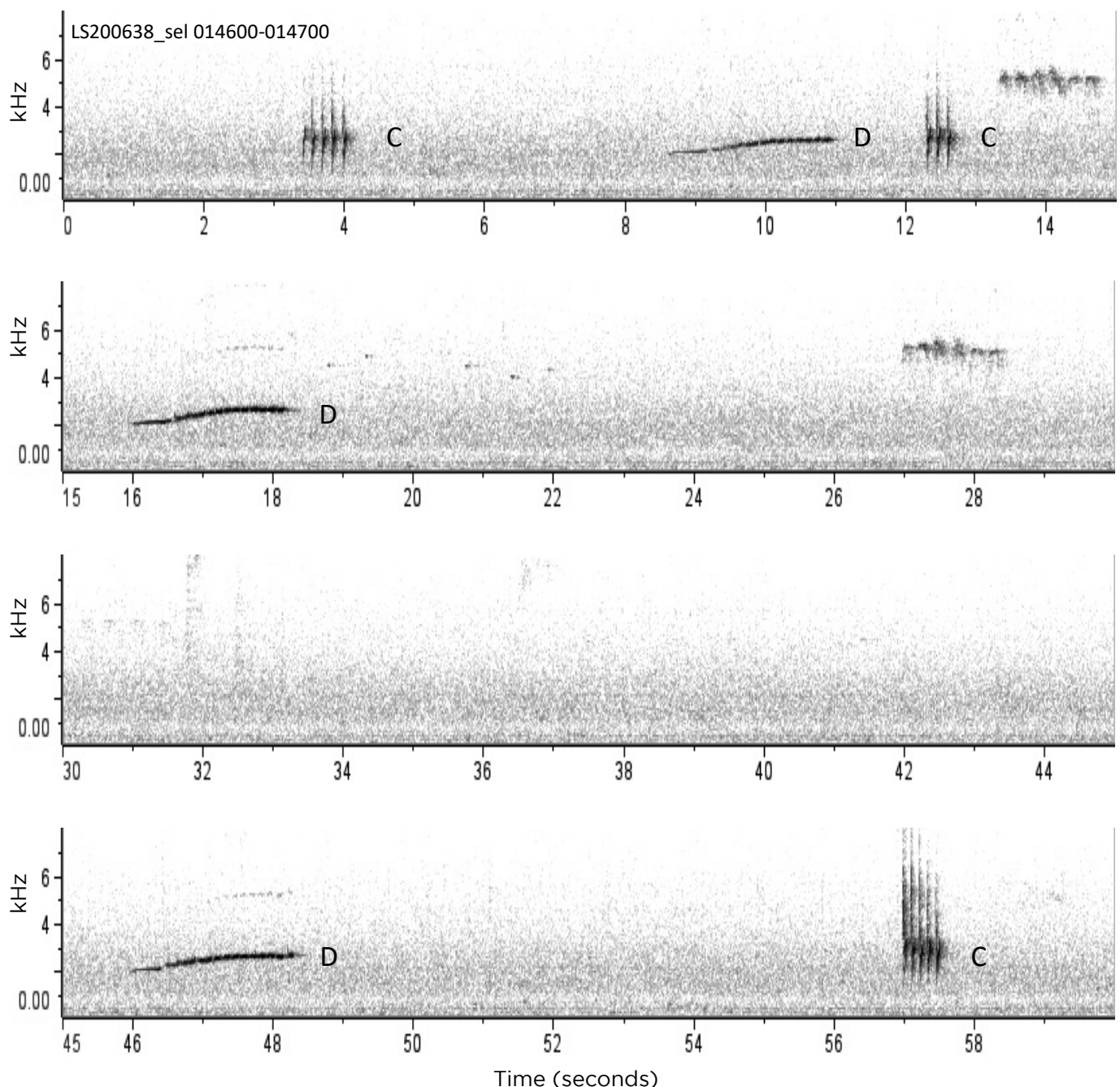
in Figure 8 of Song G (LS200638\_sel 005041) occurred at 0815 h while the female was at the nest during a nest watch from 0800 to 1000 h on 6 December. A second example of Song G (LS200635\_sel 014022) occurred at 0930 h during a nest watch from 0800 to 1000 h on 3 December.

The spectrogram in Figure 12 (LS200638\_sel 014600-014700), recorded for 1 minute at 0911 h on 6 December, depicts a sequence of songs by the female on the nest while brooding a 10-day-old nestling. The sequence consists of Songs C, D, C and D followed by a pause of 28 seconds, and then Song D and Song C. Toward the end of the sequence, the male flew to the nest and fed the young while the female remained on the nest. The louder Song D at 46 seconds possibly suggests that the male also sang at the nest but this seems unlikely since male song was not observed. In this sequence, Song D by the female on the nest occurred three times.





**Figure 11.** Spectrogram of a 1-minute 30-second sequence of song types by a male Blue-grey Robin near the nest with a 7-day-old nestling, 3 December 2014, YUS CA, Huon Peninsula, PNG. Xeno-canto: <https://xeno-canto.org/explore?query=nr:972454>. Spectrogram: Tony Baylis

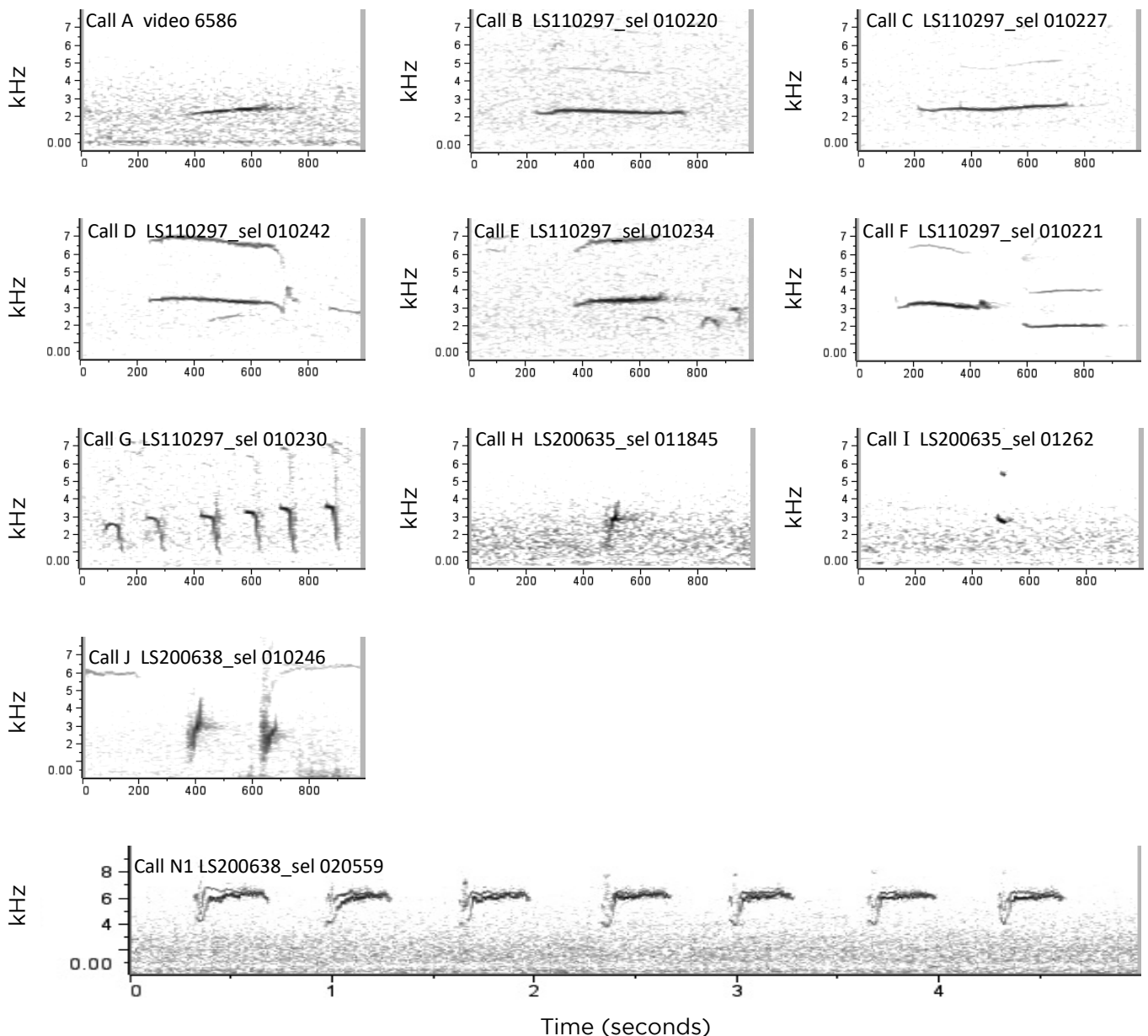


**Figure 12.** Spectrogram of a 1-minute sequence of song types by a female Blue-grey Robin brooding a 10-day-old nestling, 6 December 2014, YUS CA, Huon Peninsula, PNG. Xeno-canto: <https://xeno-canto.org/explore?query=nr:972455>. Spectrogram: Tony Baylis

Both the male and the female sing the whistle Song D. In Figure 11, a male sang Song D once in a bout of 14 songs on 3 December. Once a male was observed to sing Song D at the nest. In a song bout by the female at the nest on 6 December, she sang Song D three times (at 10 seconds, between 16 and 18 seconds, and between 46 and 48 seconds: Figure 12). From 0826 to 0827 h during a nest watch from 0800 to 1000 h on 6 December, she sang Song D five times, followed by Song C and another whistle (Song D). These observations of a female singing Song D suggest that the female sings Song D at the nest more frequently than does the male. This whistle (Song D) occurs in about one-third (18 of 60) of all recordings catalogued in *Birds of the World* (Boles 2020). Song C is also used by both the male (Figure 10) and female (Figure 12). In Figure 12, the female sang Song C twice in the first 13 seconds, and once at the end of the sequence.

Figure 13 depicts spectrograms of ten definitive adult call types and a nestling begging call (Call N1). The frequency and other parameters of definitive call types A–J and nestling begging calls are presented in Appendix 3.

Call A, taken from a video (Video 6585), was given by the female as she left the nest and, at first glance, seems very similar to Calls B, C, D and E. Calls A and E were very similar in length, as were Calls B, C and D (B, C and D were longer than A and E) but other values were not so similar. Calls A, B and C had similar peak frequency. Calls A, C and D shared a similar bandwidth. Call F appeared to be a phrase consisting of two elements (see Appendix 3). We recorded two examples of this call and one is shown in Figure 13. We have collectively called A–F ‘short whistle’, although its function was undetermined. Short whistles were heard and identified close to the nest but, because of their short length and usually low energy, identification



**Figure 13.** Spectrograms of definitive adult call types A–J by Blue-grey Robins at and near the nest, and nestling begging calls (N1), YUS CA, Huon Peninsula, PNG. See text for further details. Time is in milliseconds for Calls A–J and seconds for nestling calls. Xeno-canto: <https://xeno-canto.org/explore?query=nr:972456>. Spectrograms: Tony Baylis

away from the nest was problematical. Call G, a rapid repetition of a single element, was given with different numbers of repetitions. It was only heard at or close to the nest. Call H was a very short element and may be the call described by Coates (1990) and Pratt & Beehler (2015) as *chwink*. Call H was given by individuals in the vicinity of the nest; it had relatively high energy, and is probably more easily identified in the field than the short whistles or Call G. Call I was the shortest of all types described, and was recorded on only one occasion. Call J was given by the female on the nest to solicit food from the male.

Seven of these ten adult calls (A, B, C, D, E, H and I) have a single element. Three calls (F, G and J) have multiple elements. The N1 calls are given by a 10-day-old nestling begging. Repetitive begging calls are typical of nestlings and are usually given in response to adults arriving with food. Appendix 3 shows the repetitive nature of nestling calls, and the spectrograms in Figure 13 show a rate of ~14 nestling calls in 10 seconds. Nestling begging calls have high energy and typically cease after nestlings

are fed or shortly after an adult departs from the nest. Appendix 4 (28-second sequence of calls and songs by a pair of Blue-grey Robins at and near the nest with a 6-day-old nestling, 6 December) depicts spectrograms during a long song sequence.

## Discussion

Australasian temperate and tropical robins have life-history traits (e.g. long nesting season, low clutch size, high nest predation, re-nesting attempts, extended parental care and high adult survival) that are more typical of tropical than north-temperate songbirds (see references in Donaghey 2022). New Guinean forest passerines lay much smaller clutches (mean 1.5 eggs) than other tropical birds (Freeman & Mason 2014). Clutch size declines with altitude in tropical birds (Boyle 2008; Boyce *et al.* 2015; Donaghey 2015b). The evolution of clutch size in north-temperate songbirds has been attributed mainly to food limitation



(Lack 1954), and to nest predation in neotropical birds (Skutch 1949, 1985). Martin *et al.* (2000) tested the Skutch hypothesis and found that more nests were depredated during the nestling period when parental activity was greatest. Conway & Martin (2000) suggested that, for North American passerines in which only the female incubates, nest predation is a major selective pressure in shaping reproductive traits such as high nest attentiveness and fewer nest visits and that these traits have evolved more in response to nest predation than food availability. Martin *et al.* (2011) reported that, for passerines in temperate and tropical regions, risk of nest predation is more dominant than food limitation in the evolution of nestling growth rates and parental provisioning strategies that minimise nest predation. High risk of nest predation should select for reduced nest visitation by fewer and longer incubation on-bouts and fewer food-delivery trips.

### *Breeding season*

In the Blue-grey Robin, the nesting season (nests with an egg or a nestling) is November and December on Mt Missim, Morobe Province, PNG (Coates 1990), and in the YUS CA, Huon Peninsula (this study). In the Eastern Central Ranges in the Kubor Range and Mt Hagen, nesting records include nests, each with a single nestling, in mid and late September and late April. At Telofomin in the Border Ranges, a nest contained an egg in late September. In the South-east Peninsula at Efogi, Central Province, nesting records include a nest with an egg, in late December, and at Boneno, north-west of Mt Simpson, several nests had an egg or nestling, in late December to early January. These records (see references in Coates 1990) suggest that the nesting season of the Blue-grey Robin extends for 5–8 months (early September–late April) in the mid dry to late wet season (Coates 1990).

The nesting season extends for at least 5–6 months (early August–late April) in the late dry to mid wet season in the White-winged Robin (Coates 1990; Donaghey 2022), for at least 5 months (late August–mid January) in the Black-capped Robin (Coates 1990; Donaghey *et al.* 2023), and at least 4 months (October–January) from the late dry to early wet season in the Lesser Ground Robin (Coates 1990; Donaghey *et al.* 2019b). All four of these species of montane New Guinean robins breed in the austral spring to mid summer. Many nest records over a nesting season are required to more accurately determine the nesting season length of robin species at different localities.

### *Nest, egg, clutch size, incubation and nestling periods*

Like the Blue-grey Robin, the Lesser Ground Robin, White-winged Robin and Arfak Robin *Heteromyias albispecularis* build bulky nests composed externally of bright-green moss (Coates 1990; Noske *et al.* 2016; Donaghey *et al.* 2019b; Donaghey 2022; this study). The Black-capped Robin constructs a substantially smaller nest, externally composed of twigs, roots and stems with some moss (Donaghey *et al.* 2023). All five species construct nests in understorey vegetation at heights of 1–2.2 m above ground.

A clutch size of one has been documented for all five of these montane New Guinean robins. The incubation period is at least 16 days in the White-winged Robin (Donaghey 2022) and Blue-grey Robin (this study) but is unknown in other New Guinean robins. For 17 Australian robin species, the mean incubation period is 16 days (range 14–19 days: Russell *et al.* 2004). The mean nestling period of 21 Australasian robins (including those of New Zealand) is also 16 days (range 9–23 days: Donaghey 2022), but is longer (17–22 days) in three of the above four montane robins endemic to New Guinea.

### *Comparison of reproductive traits with other montane New Guinean robins*

Table 3 compares the reproductive traits and strategies of four montane New Guinean robins. Incubation constancy was higher in the congeneric White-winged Robin (73.2%) than in the Blue-grey Robin (68.0%). Mean incubation bouts were 1.7 minutes shorter and mean off-bouts 1.0 minute shorter in the White-winged Robin than in the Blue-grey Robin. However, number of incubation bouts/hour and the daily number of bouts/12 hours were 1.5 times more in the White-winged Robin than in the Blue-grey Robin (Table 3). For Days 1–11 of the nestling period, the mean number of feeding trips/nestling/h was similar for both these species but mean nest visits/h were 1.7 times lower in the Blue-grey Robin than in the White-winged Robin (Table 3). The fewer incubation bouts and nest visits per hour during the nestling period by the Blue-grey Robin than by the White-winged Robin suggest that the risk of nest predation is greater in the former (Conway & Martin 2000; Martin *et al.* 2000; Donaghey 2022; Table 3).

Incubation constancy was lower in the Blue-grey Robin (68.0%) than in the Black-capped Robin (77.5%). Mean incubation bouts were 2.6 minutes shorter in the former but mean off-bout length was the same in both species. The number of incubation bouts/hour and bouts/12 hours were 1.4 times greater in the Blue-grey Robin than in the Black-capped Robin (Table 3). For Days 1–11 of the nestling period, mean brooding constancy and mean number of brooding bouts/h were similar in both these species (Table 3). Mean number of feeding trips/nestling/h was also similar for both species. Mean number of nest visits/h was 1.2 times higher in the Blue-grey Robin than in the Black-capped Robin, which suggests that the risk of nest predation is lower in the former according to Martin's hypothesis. Nest success appears to be high in the Black-capped Robin but sample sizes were small (Donaghey *et al.* 2023). The extent of nest predation was unknown in the Blue-grey Robin and needs further study.

The mean number of feeding trips to nestlings per hour (feeding trips/nestling/h) was 1.7 times higher in the Lesser Ground Robin than in the Black-capped Robin for a 22-day nestling period (Table 3). In contrast, for Days 1–11 of the nestling period, the number of feeding trips/hour was similar in the Blue-grey Robin and Black-capped Robin (Table 3). For Days 1–11 of the nestling period, mean number of nest visits per hour was lower in the Black-capped Robin (10.6/h) than in the Blue-grey Robin (12.7/h) and White-winged Robin (21.7/h) (Table 3). The White-winged Robin has short incubation on- and off-bouts, a high nest-visit rate during the incubation and nestling periods,

**Table 3.** Comparison of reproductive traits of four montane endemic New Guinean robins. F = female, M = male, \* = incubation feeding off the nest. Mean adult weight of White-winged Robin is from Frith & Frith (1993) and for the three other robin species is from Diamond (1972).

Species	Blue-grey Robin	White-winged Robin	Black-capped Robin	Lesser Ground Robin
Mean adult weight (g)	25	23	33	31.6
Clutch size	1	1	1	1
Incubation period (days)	16+	16+		
F incubation constancy (%)	68.0	73.2	77.5	
Incubation on-bout length (min.)	5.05	3.35	7.66	
Incubation off-bout length (min.)	2.32	1.33	2.32	
Number incubation bouts/h	8.2	12.5	6	
Number incubation bouts/12 h	98	150	72	
M incubation feeding/h	1–2	4.6	3.0*	
Mean M and F incubation visits/h	9.7	17.1	6	
Nestling period (days)		19 (17–21)	22	22
<b>Days 1–11 of nestling period</b>				
F nestling brooding (%)	51.4	43.3	57.7	
Mean brooding bouts/h	8.9	13.4	9.3	
Mean feeding trips/nestling/h	4.4	5.5	4.1	7.5
Mean nest visits/h	12.7	21.7	10.6	7.5
<b>Days 1–22 of nestling period</b>				
Mean brooding bouts/h		8.8	7.5	
Mean feeding trips/nestling/h		7.2	4.4	7.5
Mean nest visits/h		17.6	9.3	7.5
Nestling/fledgling weight as % of adult weight		93	84	87
Nestling/fledgling wing-length as % of adult wing-length		57.0	55.7	81.6
Reference	This study	Donaghey 2022	Donaghey <i>et al.</i> 2023	Donaghey <i>et al.</i> 2019b

a long nestling period and apparently high nest success, all of which are indicative of a low risk of nest predation (Donaghey 2022). In contrast, the mid-montane Black-capped Robin has a similar long nestling period and high nest success but has fewer incubation on-bouts and far fewer nest visits than the White-winged Robin, suggesting that the risk of nest predation is higher for the former species (Donaghey *et al.* 2023).

### Nestling growth and development

There are few data on nestling growth rates for tropical New Guinean robins. On the day before fledging, a Lesser Ground Robin weighed 27.4 g (86.7% of mean adult weight) (Donaghey *et al.* 2019b; Table 3). Nestling growth to 21 g (91–93% of mean adult weight) occurred at 10–13 days of age in the White-winged Robin (Donaghey 2022) whereas nestling growth and development were slower in the Black-capped Robin (84% of mean adult weight attained at 19 days of age: Donaghey *et al.* 2023). Near fledging, wing-length was 56% of mean adult wing-length in the Black-capped Robin (Donaghey *et al.* 2023), 57% in the White-winged Robin, and 82% in the Lesser Ground Robin (Donaghey *et al.* 2019b; Table 3). These

comparisons suggest that in three New Guinean montane robins with low risk of nest predation, nestling periods of 19–22 days allow nestlings to fledge with longer wings and attain heavier weights by fledging.

### Male and female vocalisations

Both male and female Blue-grey Robins sing. Males have at least seven song types, females at least five, and at least two are sung by both the male and the female. At Mt Hagen, the male White-winged Robin has a repertoire of six song types but their sequence in the dawn song is far more complex, and song bouts are much longer than in the Blue-grey Robin (RHD & TB unpubl. data). In the mid-montane YUS CA, the Blue-grey Robin co-exists with the Lesser Ground Robin, which has a distinct complex musical song (Donaghey *et al.* 2019b) compared with the simple repetitive piping advertisement song with the same frequency by the Black-capped Robin (Donaghey *et al.* 2023). Both the Blue-grey Robin and White-winged Robin share a song type (in structure, not frequency) that has been recorded close to nest sites. In the former, this song type is D2, a series of short whistling elements that form an extended long whistle. The White-winged Robin nest

whistle is also a series of short whistled elements forming a long whistle (unpubl. data). This long whistle of the Blue-grey Robin is a fairly flat whistle with a peak frequency of 2437 Hz whereas the White-winged Robin whistle descends in frequency and has a peak frequency of 5203 Hz. The function of these whistle songs is unknown. However, male song bouts of the Blue-grey Robin occur throughout the day and probably function as territorial advertisement but may also function to synchronise parental-care behaviour at and near the nest. A brooding female Blue-grey Robin on the nest sang a bout of Songs C and D (which are used by both the male and the female). This female song may function in coordinating male parental-care nest visits, and provide information to the male when nest predation risk is low. Female song in songbirds has been considered rare in north-temperate birds (Catchpole & Slater 1995) but more common in tropical birds (Slater & Mann 2004). Odom *et al.* (2014) found that female song is widespread in Australasia and phylogenetically globally widespread and ancestral in songbirds.

### Risk of nest predation

Risk of nest predation appears to be lower in the high-elevation White-winged Robin than in the Black-capped Robin based on various indicators, such as a higher daily number of incubation bouts, and higher nest-visitation rates of the former (Donaghey 2022; Donaghey *et al.* 2023). In the mid-mountains of the YUS CA (elevation 2200–2500 m asl), where the Black-capped Robin co-exists with the Blue-grey Robin, risk of nest predation appears to be low in the former, based on its relatively high nest success (67%) but the number of incubation bouts/h was higher in the Blue-grey Robin (8.2) than in the Black-capped Robin (6.0) and mean number of nest visits/h for Days 1–11 of the nestling period was also higher in the Blue-grey Robin (12.7) compared with that in the Black-capped Robin (10.6), suggesting that nest predation risk is also low in the Blue-grey Robin. However, nest visits/h were 1.7 times more frequent in the White-winged Robin than in the Blue-grey Robin (Table 3). This suggests that risk of nest predation is lowest in the White-winged Robin but comparatively low in the mid-montane Blue-grey Robin and Black-capped Robin, but this needs verification.

There are very few data on nest predation for lowland rainforest birds of New Guinea. Nest predation appears to be very high in lowland rainforest in south-eastern PNG (Bell 1982). Using data from Skutch (1985) and Robinson *et al.* (2000) for sites in Central America from lowland Panama to highland Guatemala, Boyle (2008) showed that nest predation declined with elevation. Robinson *et al.* (2000) found that nest success was lower (29%) for understorey passerines in lowland central Panama compared with a mean nest success of 53% in open-cup-nesting temperate birds in North America.

### Breeding strategy

The female Blue-grey Robin incubates the single egg but the male contributes by feeding the female on and off the nest. Incubation constancy is 68%, and mean length of on-bouts is 5.05 minutes and off-bouts is

2.32 minutes. Parental nestling care in the Blue-grey Robin for Days 1–11 of the nestling period is characterised by a high incidence of female brooding (51%) and high mean number of brooding bouts (8.9/h). Food-delivery rates per nestling of 4.4/h were lower than in the White-winged Robin (5.5/h) (Table 3). Martin (2015) found that the small clutch sizes of tropical birds allow adults to increase food-delivery rates per young, and reduce nest visits to reduce mortality risk to adults and juveniles. A Black-capped Robin nestling attained 84% of adult weight at 19 days of age; thus nestlings can fledge with longer wings than robins with shorter nestling periods. Assuming that the Blue-grey Robin has a long nestling period similar to that in the White-winged Robin and Black-capped Robin, a low risk of nest predation allows nestlings to fledge with longer wings to escape from predators and reduce mortality (Martin *et al.* 2011; Martin 2015). Our observations that low risk of nest predation shapes the reproductive strategies of White-winged and Black-capped Robins is consistent with Martin's theory, but more conclusive data are needed for the Blue-grey Robin.

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**Appendix 1.** Blue-grey Robin nestling care (brooding and feeding young) at one nest, YUS CA, Huon Peninsula, PNG, 2014. Day = day of nestling period; date is given as day.month; obs. min. = observation minutes; F = female, M = male, Y = young.

Day	Date	Time	Obs. min.	Nest visits									
				By F		By M				No. feeding trips		No. nest visits	
				No. brooding bouts	F fed Y and brooded	F fed Y and off	F fed Y Total	M fed F at nest	M fed F fed Y directly	Total	No./h	Total	No./h
1	26.11	0822–1015	113	19	2	1	20	4	2	1	6	27	14.3
1	27.11	0700–0900	120	17	2		17	6	1		3	24	12.0
2	28.11	0700–0800	60	7	2		7				2	7	7.0
3	28.11	1500–1700	120	23	6	3	26	5			9	31	15.5
4	29.11	0800–1000	120	25		2	27	3	2	1	5	33	16.5
5	30.11	1500–1700	120	17	4	2	19	2		2	8	23	11.5
6	1.12	0800–1000	120	33	4	2	35	5		1	7	41	20.5
7	2.12	0800–1000	120	17	1	3	20	2		2	6	24	12.0
7	2.12	1500–1700	120	13	3	1	14		1	6	11	21	10.5
8	3.12	0800–1000	120	19	5	2	21	2		3	10	26	13.0
8	3.12	1500–1600	60	8	3	2	10		1	2	8	13	13.0
9	4.12	1500–1700	120	13	5	6	19	1		4	15	24	12.0
10	5.12	0800–1000	120	12	4	2	14			6	12	20	10.0
11	6.12	0800–1000	120	7	3	1	8			8	12	16	8.0
<b>Totals</b>			<b>1553</b>	<b>230</b>	<b>44</b>	<b>27</b>	<b>257</b>	<b>30</b>	<b>7</b>	<b>36</b>	<b>114</b>	<b>330</b>	
<b>Mean feeding trips/h and nest visits/h</b>													
<b>Days 1–11</b>											<b>4.4</b>	<b>12.7</b>	

**Appendix 2.** Measurements of frequency and other parameters of Blue-grey Robin definitive song types A–J, YUS CA, Huon Peninsula, PNG. Delta time (seconds) = length of time for the selection; low freq (Hz) = lower frequency bound of selection; high freq (Hz) = upper frequency bound of selection; peak freq (Hz) = frequency that peak power/energy occurs within selection; delta freq (Hz) = difference between upper and lower frequency limits of selection; BW 90% (Hz) = bandwidth of the difference between 5% and 95% frequencies within selection box.

<i>Song type</i>	<i>Delta time</i>	<i>Low freq</i>	<i>High freq</i>	<i>Peak freq</i>	<i>Delta freq</i>	<i>BW 90%</i>
A	1.68	1945	5033	3656	3088	1218
B	0.82	1972	5950	4500	3978	2015
C	0.55	1611	6112	2718	4501	2343
D	2.26	1817	2792	2343	974	515
D2	4.5	1767	2675	2437	907	281
E	1.62	1716	4004	2250	2288	1406
F	2.16	1445	5007	2578	3561	1687
G	0.72	1739	4987	2812	3247	1593
H	1.18	1668	4726	2859	3058	1125
I	1.61	1586	3518	3140	1931	890
J	1.43	1825	5945	2671	4120	2390

**Appendix 3.** Measurements of frequency and other parameters of Blue-grey Robin definitive call types A–J, and nestling begging calls, YUS CA, Huon Peninsula, PNG. Delta time (seconds) = length of time for the selection; low freq (Hz) = lower frequency bound of selection; high freq (Hz) = upper frequency bound of selection; peak freq (Hz) = frequency that peak power/energy occurs within selection; delta freq (Hz) = difference between upper and lower frequency limits of selection; BW 90% (Hz) = bandwidth of the difference between 5% and 95% frequencies within selection box.

<i>Call type</i>	<i>Delta time</i>	<i>Low freq</i>	<i>High freq</i>	<i>Peak freq</i>	<i>Delta freq</i>	<i>BW 90%</i>
<b>Adult calls</b>						
A	0.280	1952	2515	2343	563	234
B	0.569	1912	2550	2343	637	140
C	0.546	2040	2787	2390	747	234
D	0.489	2512	3723	3281	1211	281
E	0.314	2929	3666	3375	736	140
F (1)	0.749	1660	3551	3093	1891	1265
F (2)	0.339	2721	3505	3093	784	234
F (3)	0.315	1660	2260	1968	599	93
G (1)	0.067	965	2878	2484	1913	1125
G (2)	0.077	965	3100	2859	2134	1453
G (3)	0.077	762	3252	2906	2490	1500
G (4)	0.069	965	3405	3187	2439	1031
G (5)	0.062	1067	3761	3375	2693	1687
G (6)	0.048	1474	3862	3515	2388	1406
H	0.054	1467	3913	2812	2445	1125
I	0.048	2423	3170	2718	746	234
J (1)	0.049	1452	4666	2906	3214	1125
J (2)	0.066	888	4694	2250	3806	1078
J (3)	0.311	888	4709	2906	3820	1265
<b>Nestling calls</b>						
N1 (1)	0.381	4020	6821	5906	2801	937
N1 (2)	0.346	3855	6623	5953	2768	1078
N1 (3)	0.374	3690	7217	5859	3526	890
N1 (4)	0.368	3592	7711	5953	4119	890
N1 (5)	0.340	3625	7777	5906	4152	1265
N1 (6)	0.346	3592	7942	5906	4350	984
N1 (7)	0.340	3789	6821	5906	3031	984



**Appendix 4.** Spectrogram of 28-second Long Song sequence of calls and songs (LS 297\_01 sel 010218) by a pair of Blue-grey Robins at and near the nest with a 6-day-old nestling, recorded at 0940 h on 2 December 2014, YUS CA, Huon Peninsula, PNG. This sequence has Songs D and F and Calls B, D, E, F and G. A short whistle (Call B) is given at 0.5 seconds, Call F at 2 seconds, and a longer whistle (Song D) between 3.5 and 5.5 seconds and at 23–26.5 seconds. Call G occurs at 10–11 and 13.5 seconds. Song D overlaps with Call G at 13.0–13.5 seconds, suggesting that these two vocalisations are given by two birds, presumably the male and female of a pair. In this Long Song sequence, we attribute the short whistle, Song D and Call G to the female but possibly also the male. During this sequence, the female was at the nest but the male visited the nest, presumably at 13 seconds. Song F, presumably by the female, can also be heard at 15 seconds. ♀ = female, ♂ = male.

