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Breeding biology of the Black-capped Robin *Heteromyias armiti* compared with the Grey-headed Robin *H. cinereifrons* and other tropical-rainforest Australasian robins

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Abstract. We studied the breeding biology of the mid-montane Black-capped Robin *Heteromyias armiti* (Petroicidae) in the Yopno Urawa Som Conservation Area, Huon Peninsula, Papua New Guinea, from 23 October to 6 December 2014. All three nests found were attended by a breeding pair. We watched one nest during the incubation stage for 12 hours. Clutch size was one. Female daylight incubation constancy was 77.5%, the mean duration of incubation on-bouts was 7.66 minutes and of off-bouts 2.32 minutes. The daily number of incubation bouts was 72, thus the mean number of visits by the female to the nest was six per hour. Feeding of the incubating female at the nest by the male was not observed. The nestling period was 22 days. The female brooded the nestling and delivered most of the meals to the nestling. Male care of the nestling was primarily delivering food to the female off the nest. Mean brooding constancy by the female was 57.7% for the whole nestling period. Mean number of food-delivery trips by the female over the entire nestling period was 4.4/hour, and the mean number of nest visits by both the male and female was 9.3/hour. The high nest success coupled with the high nest-visitation rates during the nestling period suggests that the risk of nest predation is low. Peak nestling growth (to 84–85% of adult weight) occurred at 19 days of age. By comparing reproductive traits in the congeneric Grey-headed Robin *H. cinereifrons* and other tropical-rainforest Australasian robins the reproductive strategy of the Black-capped Robin appears to have evolved more in response to food availability than to a high risk of nest predation.

Introduction

Comparisons of breeding biology among south-temperate and tropical Australasian robins (Petroicidae) contribute to an understanding of the selective forces that shape variation in reproductive strategies. Australasian robins have life-history traits, such as long nesting seasons, low clutch size, relatively short nestling periods, high nest predation, renesting and high adult survival, that are more typical of tropical than north-temperate birds. Mean clutch size of landbirds varies globally from 4.5 eggs in northern latitudes to just over 2.0 in the tropics and most southern latitudes in Australasia, the Afrotropics and Oceania (Jetz *et al*. 2008). New Guinean forest passerines lay much smaller clutches (mean 1.5 eggs) than other tropical birds (Freeman & Mason 2014). Clutch size declines with elevation in tropical birds in the Venezuelan Andes, Malaysian Borneo and New Guinea (Boyce *et al*. 2015). Among New Guinean robins, clutch size is generally one in montane species and one or two in lowland species but is unknown for most lowland species (Coates 1990; Donaghey 2015a).

The evolution of clutch size in passerine birds traditionally has been attributed mainly to food limitation in north-temperate birds (Lack 1947, 1948, 1954), and to nest predation in neotropical birds (Skutch 1949, 1985) or an interaction between these two selective mechanisms (Martin 1992). Nest failure of passerines is high in wet, humid neotropical forests, mostly as a consequence of high nest predation (Skutch 1949, 1985; Willis 1972; Snow & Snow 1979; Morton & Stutchbury 2000; Robinson *et al*. 2000). In contrast, North American passerines generally have lower nest predation (Nice 1957; Ricklefs 1969; Martin 1993; Conway & Martin 2000; Thompson 2007). The hypothesis of Skutch (1949) that parental activity at the nest increases nest predation and favours small clutch sizes was tested by Martin *et al*. (2000a) by comparing wood warblers (Parulidae) in Argentina with those from North America. Martin *et al*. (2000a) found more numerous nest visits were correlated with higher nest predation. After removing poor-quality nest sites from an analysis in Arizona, USA, Martin *et al.* (2000b) found that more nests were depredated during the nestling phase when parental activity was greatest. High risk of nest predation should select for parental behaviour that reduces nest visitation through a higher incubation constancy, longer incubation on-bouts and shorter off-bouts, and fewer food-delivery trips.

In temperate-forest and woodland robins of eastern Australia, rates of nest predation vary with geographical regions, habitat and elevation. In south-eastern temperate-woodland robins, nest predation is 50–73% in the Eastern Yellow Robin *Eopsaltria australis* (Marchant 1985; Zanette & Jenkins 2000; Debus 2006a,b), 65% in the Hooded Robin *Melanodryas cucullata* (Fitri & Ford 2003), 86% in the Scarlet Robin *Petroica boodang* (Debus 2006b), and 62.5% in the Flame Robin *P. phoenicea* (Robinson 1990). In contrast, in south-western Australian woodlands, nest predation is low (15.2%) in the White-breasted Robin *Quoyornis georgianus* (Russell *et al*. 2004), and nest failure is 25–40% in the Western Yellow Robin *Eopsaltria griseogularis* (Donaghey & Donaghey 2022). In upland tropical rainforest in north-eastern Australia, the Grey-headed Robin *Heteromyias cinereifrons* has moderate nest predation (42.5%) and a short nestling period (12–13 days), suggesting that risk of nest predation is an important selection pressure (Frith & Frith 2000; Donaghey 2022). Contrary to the generalisation that nest predation is higher in tropical than in temperate birds, the high-elevation montane White-winged Robin *Peneothello sigillata* has high nest success and high nest visitation in both the incubation and nestling periods, which is indicative of a low risk of nest predation (Donaghey 2022). Australian robins with a high loss of eggs and nestlings compensate by high survival of adults (Brown *et al*. 1990; Rowley & Russell 1991; Russell *et al*. 2004; Coleman *et al*. 2012), and renesting after nest failure. Frequent renesting occurs in the Jacky Winter *Microeca fascinans* (Wood *et al.* 2008), Eastern Yellow Robin and Scarlet Robin (Debus 2006a), Red-capped Robin *Petroica goodenovii* (Dowling 2003), White-breasted Robin (Russell *et al*. 2004) and Southern Scrub-robin *Drymodes brunneopygia* (RHD unpubl. data). We studied the breeding biology of the New Guinean Black-capped Robin *Heteromyias armiti* in mid-montane rainforest, to elucidate its reproductive strategy and compare its reproductive traits with those of other tropical-rainforest robins of Australia and New Guinea.

Molecular phylogenetic analysis of the Petroicidae revealed that the subfamily Eopsaltriinae comprises two subclades, the first of which includes the genera *Tregellasia*, *Quoyornis*, *Eopsaltria*, *Gennaeodryas*, *Melanodryas* and *Peneothello* (Christidis *et al.* 2011). The second subclade contains *Poecilodryas*, *Plesiodryas* and *Heteromyias*. Christidis *et al.* (2011) recognised that the Grey-headed Robin of north-eastern Australia and the New Guinean Ashy Robin *H. albispecularis* are separate species, and that the latter probably consists of at least two species. Beehler & Pratt (2016) and Gill & Donsker (2021) recognised two species of *Heteromyias* endemic to New Guinea, the Ashy Robin *H. albispecularis* and Black-capped Robin *H. armiti*. The Black-capped Robin consists of two subspecies, *rothschildi* of the Western, Border and Eastern Ranges, and *armiti* of the South-eastern and Huon Peninsulas and the Adelbert Mountains (Beehler & Pratt 2016). We studied subspecies *armiti* on the Huon Peninsula.

The sexually monomorphic, adult Black-capped Robin has a distinctive black cap and ear-patch, with a broad white eyebrow extending from above the eye to the nape, and a white throat that extends to the eye. The back is olive, underparts greyish, legs pale pink and the bill is blackish with a pale tip (Coates 1990; Boles 2007; Pratt & Beehler 2015; Figure 1). Adults are 15–18 cm long and weigh 31–36 g (mean 33 g, n = 3: Diamond 1972). The Black-capped Robin is sedentary, territorial, presumably socially monogamous and insectivorous (Croxall 1977; Coates 1990; Boles 2007). It is a shy and elusive robin that inhabits mid-montane forests, from 1400 to 2600 m above sea level (asl), mainly 1700–2400 m asl (Coates 1990). It commonly perches sideways on vertical stems, with its body more or less horizontal. Foraging manoeuvres include pouncing to the ground from a perch, snatching and gleaning arthropod prey from understorey vegetation and the ground (Croxall 1977; Boles 2007). In our study area, the Black-capped Robin coexisted with the Blue-grey Robin *Peneothello cyanus*, Lesser Ground Robin *Amalocichla incerta* and Canary Flyrobin *Devioeca papuana.*

The nest of the Black-capped Robin has been described (Harrison & Frith 1970; Coates 1990; Boles 2007), and colour and dimensions of the egg documented (Harrison & Frith 1970). However, nothing is known about incubation and nestling periods, incubation behaviour and parental care of young. The main objectives of our study 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 to the nest throughout the nestling period, and nestling diet; (4) nest success, nest failure, anti-predator behaviour of adults and young, and any potential nest predators; and (5) to compare these reproductive traits with those of the closely related Grey-headed Robin and other tropical-rainforest Australasian robins.

Study site and methods

Study area

RHD and David Bryden conducted a 6-week exploratory trip that included the Huon Peninsula, Papua New Guinea (PNG), during 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, elevation 2300 m (06°01′S, 146°50′E), where we studied mid-montane robins from 23 October to 6 December 2014 (Donaghey *et al.* 2019a). The vegetation above Camp 12 (2400 m asl) has been described by Inaho (2012) and Donaghey *et al*. (2019a).

Observations of the nest

We found three Black-capped Robin nests. Nest 1, when first inspected on 30 October, contained a feathered nestling that weighed 26.9 g. By back-dating from the fledging day and assuming a nestling period of 22 days, this nestling was estimated to be 16 days of age on 30 October. Nest 3 had an egg when found but the nestling was depredated 2 days after hatching. Nest 2, from which the nestling fledged, was watched during the incubation period and throughout the entire nestling period using a 25× telescope mounted on a tripod. The female that attended Nest 2 was identified by a white spot on the crown (see Figure 1), not present in the male, and by her brooding and food-solicitation behaviour.

To determine the time that a female Black-capped Robin spent incubating, we watched Nest 2 for a total of 12 daylight hours throughout an afternoon and the following morning during the last half of the incubation period. 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 duration of time in minutes and seconds spent at the nest in incubation. An absence or ‘off-bout’ is the time spent away from the nest by an incubating female. Incubation constancy is the percentage of daylight hours spent on incubation. Brooding constancy is the percentage of time spent brooding.

Figure 1. Female Black-capped Robin brooding nestling, Nest 2, YUS CA, Huon Peninsula, Papua New Guinea. Photo: Donna J. Belder

Figure 2. Black-capped Robin Nest 2 adorned with long white orchid aerial roots, YUS CA, Huon Peninsula, PNG. Photo: Richard H. Donaghey

Nest 2 was watched for 64 hours during the entire nestling period to determine the amount of time that a female spent brooding, and the number of feeding trips, nest visits per hour, and faecal sacs removed. We recorded anti-predator behaviour such as nest defence and agonistic behaviour directed against interspecific avian species during watches at and away from nests. We measured the height of each nest above the ground and recorded nest-site characteristics after nesting had ended. Nest success (fledging of young) was determined for the three nests where the outcome was known.

Vocalisations

On 2 November, TB recorded the male advertisement piping song of a Black-capped Robin approaching Nest 1, which had a well-feathered chick, by using a Nagra LB recorder (wav file 48 Hz/24bit) and a Sennheiser MKH40 cardiode microphone placed close to the nest site. At Nest 2 on 22 November, TB recorded vocalisations of the female and nestling using an Olympus LS11 recorder (wav file 48 Hz/24bit) and a DPA4060 omnidirectional microphone placed ~15 cm below the nest. The recorder was set to run continuously from 1204 to 1756 h but heavy rain occurred in the mid–late afternoon. Spectrograms from the recordings were produced by TB using Raven Pro 1.64, with a value of DFT2064. Frequency measurements were calculated using Max Frequency; this measurement indicates the frequency with the most energy for the selection and is expressed in kHz. Where bandwidth (BW) is measured, for example BW 50%, this depicts the bandwidth of the selection where >50% of the energy within the call occurs. On 21 November, RHD observed Robin behaviour at Nest 2 from 0915 to 1100 h and simultaneously recorded vocalisations in the vicinity using an Olympus Linear PCM recorder LS–20M and a Sennheiser ME66 microphone.

Results

Figures 1–3 show two of the Black-capped Robin nests. Table 1 presents information on nesting chronology and nest outcome for the three nests. Detailed observations of incubation behaviour and parental care at Nest 2 are quantified below.

Nest site, dimensions and materials and height of nest above the ground

The outer layer of the shallow cup-shaped nest was composed of twigs, tendrils, roots, stems and leaves with a little moss round the rim (see also Harrison & Frith 1970). Nest 2 was adorned externally with long hanging strands of white orchid aerial roots (Figure 2), and Nest 3 had white orchid roots draped below the rim and around the exterior (Figure 3). The cup was lined with fine rootlets (Figure 3; see also Harrison & Frith 1970; Coates 1990). Nest 2 was built in the vertical fork of a slender understorey sapling (Figure 2). Nests 1 and 3 were both built in an unidentified species of a low, dense understorey shrub (Figures 3–4). The nest-site characteristics and dimensions of three nests in the YUS CA are presented in Table 2. The mean height of these three nests above the ground was 1.6 m (range 1.1–2.2 m: Table 2). The distance between Nests 1 and 2 was 467 m, and between Nests 2 and 3 was 581 m. Mean distance of a nest to its nearest neighbour was 524 m.

Clutch size, egg, and incubation behaviour

Two nests (Nests 2 and 3) had one egg, and the third (Nest 1) had one nestling when found. Ground colour of the egg was ivory with brown and purplish blotches all over the surface (Nest 2) or pale olive-cream with brown blotches (Nest 3: Figure 3). The egg in Nest 2 weighed 3.9 g on 4 November, 3 days before it hatched, and measured 23.7 × 17.9 mm. That in Nest 3 weighed 4.1 g 5 days before it hatched and measured 26.2 × 17.9 mm. Diurnal incubation constancy was 77.5% for the female at Nest 2,

Table 1. Nesting chronology of Black-capped Robins at YUS CA, PNG, 2014. Dates are given as day.month; nest outcome: F = failure, S = success.

	Nest number		
	1	*2*	*3*
Date found	30.10	2.11	5.11
Contents when found	1 young	1 egg	1 egg
Date egg hatched		5.11	10.11
Date nestling fledged	5.11	27.11	
Nestling period		22 days	
Nest outcome	S	S	F

observed for 12 hours in the last week of the incubation period. Incubation constancy averaged 78.5% from 0600 to 1000 h, 76.1% from 1000 to 1400 h, and 77.9% from 1400 to 1800 h. Hourly incubation constancy ranged from 58.1% to 92.8% (Table 3). The mean length of incubation on-bouts was 7.66 minutes (range 0.10–47.80 min., $n = 72$), and of off-bouts was 2.32 minutes (range 0.10–9.65 min., $n = 70$). Mean number of female incubation on-bouts was 6/hour (range 2–8/h, $n = 72$), 6.3 bouts/hour in the morning sample and 5.7/hour in the afternoon sample (Table 3). The daily number of incubation on-bouts was 72. In response to the male approaching the nest with food, the incubating female performed a wing-flutter display (quivering and elevating the wings) on the nest accompanied by piping vocalisations to solicit food from the male. The male was not observed to feed the incubating female on the nest; instead, the female descended below the nest to be fed by him. Over 6 hours, the rate of incubation feeding of the female by the male off the nest was 3–4 times/hour.

Nestling period and parental care of the young

Nestling care (brooding of young and food-delivery trips) was quantified throughout the nestling period at Nest 2. Only the female brooded the single young. The male mostly fed the female off the nest, and she either consumed the food or fed the young. Time spent brooding declined significantly ($P < 0.05$) as the nestling grew older, from 51.1 minutes/hour on Day 1 to 5.3 minutes/hour on Day 22 of the nestling period (Appendix 1, Figure 5). Brooding constancy declined from 85.2% on Day 1 of the nestling period to 8.8% on Day 22. Mean brooding constancy was 73.1% for Days 1–11, 35.3% for Days 12–22 and 57.7% for the entire nestling period (Appendix 1). The mean length of brooding bouts at Nest 2 was 4.60 minutes (range 0.05–43.22 min., $n = 482$).

In addition to time spent brooding, the female was almost entirely responsible for feeding the young and removing faecal sacs. The male assisted in nestling care by feeding

Figure 3. Site of Black-capped Robin Nest 3 with an egg in an unidentified shrub species, YUS CA, Huon Peninsula, PNG. Photo: Tony Baylis

Figure 4. Nineteen-day-old nestling Black-capped Robin, Nest 1, YUS CA, Huon Peninsula, PNG. Photo: Tony Baylis

Table 2. Characteristics and dimensions of Black-capped Robin nests, one at Boneno, South-eastern Peninsula (Harrison & Frith 1970) and three at YUS CA, Huon Peninsula, PNG (this study).

Locality	*Year*	*Altitude (m asl)*	*Site*	*Height above ground (m)*	*Dimensions (mm)*			
					External		*Internal*	
					Diameter	*Depth*	*Diameter*	*Depth*
Boneno	1940	1500	Fork of branch	~1.2	~140	~50	~70 × 80	~25
YUS CA								
Nest 1	2014	2365	Forks of low shrub	1.1	110	85	70	45
Nest 2	2014	2320	Vertical fork of small understory sapling	2.2	115	65-70	105	43
Nest 3	2014	2290	Forks of low shrub	1.5	112	80	75	40

Table 3. Nest attentiveness of a female Black-capped Robin (Nest 2) during the incubation period, YUS CA, PNG, 2014. Dates are given as day.month.

Date	*Time (h)*	*Minutes*		*Incubation*	*No. incubation*
		On nest	*Off nest*	*constancy (%)*	*on-bouts/h*
4.11	0600–0700	44.95	15.05	74.9	8
4.11	0700–0800	48.21	11.79	80.4	5
4.11	0800–0900	45.03	14.97	75.1	7
4.11	0900–1000	50.17	9.83	83.6	4
4.11	1000–1100	37.32	22.68	62.2	6
4.11	1100–1200	34.86	25.14	58.1	8
3.11	1200–1300	54.85	5.15	91.4	5
3.11	1300–1400	55.68	4.32	92.8	2
3.11	1400–1500	42.57	17.43	71.0	7
3.11	1500–1600	55.28	4.72	92.1	7
3.11	1600–1700	44.80	15.20	74.7	7
3.11	1700–1800	44.23	15.77	73.7	6
Daily incubation on-bouts					**72**
Mean incubation on-bouts/h					**6**
12-h totals		**557.95**	**162.05**		
12-h mean				**77.5**	

the female off the nest throughout the entire nestling period but, in 64 hours of observation, visited the nest only three times to feed the female, which then fed the young (once), and once he fed the young directly (Appendix 2). The number of feeding trips per hour increased linearly (P <0.001), ranging from 0.5/hour on Day 2 to a maximum of 7.5/hour on Day 11 of the nestling period (Figure 6, Appendix 2). High feeding rates of ≥6/hour were recorded on morning watches on Day 9 (7.0), Day 11 (6.5 and 7.5), Day 14 (6.5), Day 19 (6.0), Day 20 (6.5) and Day 21 (6.5) but also on Day 3 (6.0) (Appendix 2). Throughout the nestling period, the number of feeding trips per hour was mostly higher in the early morning (0700–0900 h) than in mid–late morning (0900–1100 h). Mean number of feeding trips to the nest per hour was 4.1 for Days 1–11, 5.0 for Days 12–22, and 4.4 for the entire nestling period. Mean number of nest visits per hour by both the male and female was 10.6 (Days 1–11), 7.4 (Days 12–22) and 9.3 for the whole nestling period (Appendix 2). Nest visits included all feeding trips and all other non-feeding visits such as female brooding. The number of nest visits was highest in the first half of the nestling period because brooding bouts (9.3/h) were almost twice that in the second half (5.0/h).

Diet of nestling and nest-sanitation behaviour

During the last two-thirds of the nestling period, most of the identified food items were large earthworms (Annelida). Smaller prey identified included centipedes (Chilopoda), spiders (Arachnida), cicadas and bugs (Hemiptera), crickets (Orthoptera), flies (Diptera), beetle larvae and pupae (Coleoptera), moth larvae and adults (Lepidoptera), and wasps (Hymenoptera).

On Day 2 of the nestling period, the female consumed all the faecal sacs but on Day 3 one faecal sac was consumed and one was removed from the nest. Every day after Day 3 the female carried all faecal sacs away from the nest. The mean rate of disposal of faecal sacs was 1.25/hour (range 1.0–2.0/h) for the first half of the nestling period, and 1.7/hour (range 1.0–2.0/h, mostly 1.5 or 2.0/h) during the last half of the nestling period.

Nestling growth and development

On the day of hatching, the nestlings in Nests 2 and 3 weighed 3.1 g and 3.2 g, respectively. At 10 days of age (Day 11 of nestling period), the nestling in Nest 2 weighed 17.5 g (53% of mean adult weight of 33 g). At 15 days, the nestling in Nest 2 weighed 21.1 g (64% of mean adult weight), and at 19 days, 2 days before fledging, it weighed 27.6 g (84% of mean adult weight). At 18 days, the nestling in Nest 1 weighed 28 g (85% of mean adult weight). The wing-length of the 16-day-old nestling in Nest 1 was 46 mm (47% of mean adult wing-length of 97 mm: Diamond 1972), and of the 19-day-old nestling in Nest 2, 2 days before fledging, was 54 mm (56% of mean adult wing-length of 97 mm: Diamond 1972).

On the day of hatching, nestlings were naked with pink-coloured skin. The 6-day-old nestling in Nest 2 had short pins on the wing-coverts and dorsal tract. At 9 days, the eyes were still closed and some feathers were erupting from the wing-covert pins (Figure 7). At 13 days, the eyes were open, the nestling had chestnut-brown scapulars, mantle and back, and the primaries and secondaries had erupted. At 15 days, the upperparts and underparts were well-feathered, the crown dark brown, breast pale brown and abdomen brownish grey. At 19 days, the upperparts were brown, breast rufous-brown and abdomen pale tan (Figure 4).

The comfort movements of nestlings aged 15–21 days included preening, and stretching the body forward and up. Wing flapping occurred at 19 days. Nestling begging was

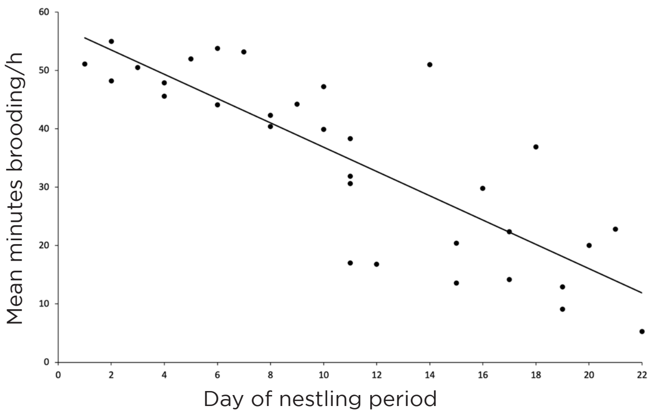

Figure 5. Relationship between nestling age and brooding by a female Black-capped Robin, Nest 2, YUS CA, Huon Peninsula, PNG.

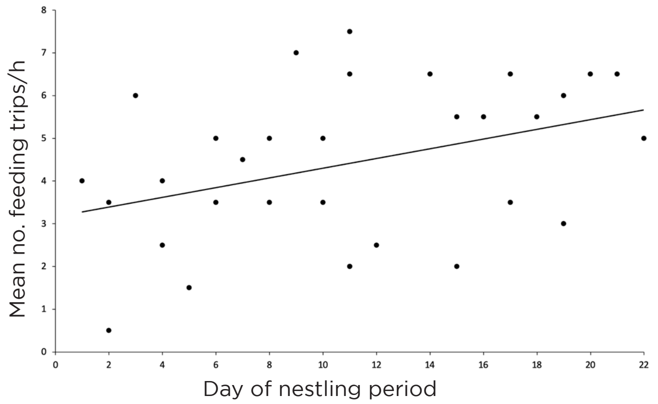

Figure 6. Relationship between Black-capped Robin feeding trips and age of the single nestling, Nest 2, YUS CA, Huon Peninsula, PNG.

Figure 7. Nine-day-old nestling Black-capped Robin, Nest 2, YUS CA, Huon Peninsula, PNG. Photo: Donna J. Belder

inaudible for the first 14 days. At 15–20 days, begging calls mostly consisted of cheeps and chirps.

Nest success

The nestlings in both Nests 1 and 2 fledged. That in Nest 3 hatched by 1115 h on 10 November but was absent, presumably depredated, by 1230 h on 12 November.

Vocalisations of adults and a nestling

The spectrogram in Figure 8a, recorded at 0804 h on 2 November at Nest 1, depicts the typical male advertisement song of longer piping elements (notes) with a frequency of 1.992 kHz delivered at a rate of three elements per second, and a shorter sequence of repeated syllables (a sequence of elements that are consistently recognisable) also at a rate of three/second (Robertson 2013). In this instance, the male was approaching the nest with food to pass to the female to feed the nestling. A nest watch was conducted at Nest 2 on 21 November from 0915 to 1100 h and a simultaneous recording was made to determine behaviour associated with vocalisations. Male advertisement song was recorded at Nest 2 from 1041 to 1046 h. The female was off the nest from 1039 to 1042 h. This behaviour suggests that the male fed her off the nest and that male advertisement song was a signal to the female that he was delivering food.

The spectrogram in Figure 8b, recorded at 1247 h on 22 November at Nest 2, shows the piping song of the female at a frequency of 2.132 kHz, delivered at approximately one element per second. The begging calls of the nestling consisted of two elements, with frequency of 3.796 kHz and 3.281 kHz. A different call, with a broad bandwidth of 3328 Hz (BW 50% – see Methods) and Max Frequency of 2.085 kHz, occurred between 4 and 5 seconds, and might have been from the female.

During the nestling period, the female brooded the nestling and mostly fed it. She performed a wing-flutter display accompanied by vocalisations on and off the nest to solicit food from the male. The watch at Nest 2 at 0915–1100 h on 21 November revealed that while the female brooded the nestling, a low-intensity wing-flutter display consisted of moderate wing quivering and regular single piping notes. A high-intensity wing-flutter display consisted of single and double piping notes that increased in amplitude with more vigorous wing flutters and greater elevation of the wings. The wing-flutter display was also performed off the nest when the female descended from the nest to be fed by the male. The different call with a broad bandwidth (see above) was heard while the female was at the nest feeding the chick so we suggest that this call was from the nestling.

The spectrogram in Figure 8c, recorded at 1257 h, depicts the piping song of the female and a nestling begging call with variable frequency (range 3.187–4.242 kHz) that differed from the chick's call shown in Figure 8b.

Discussion

Breeding season

Records of nesting Black-capped Robins in Papua New Guinea include several nests, each with a single nestling, on Mt Hagen in mid September to early October (Coates 1990), a nest with an egg at Boneno, near Mt Simpson, South-eastern Peninsula, in late December (Harrison &

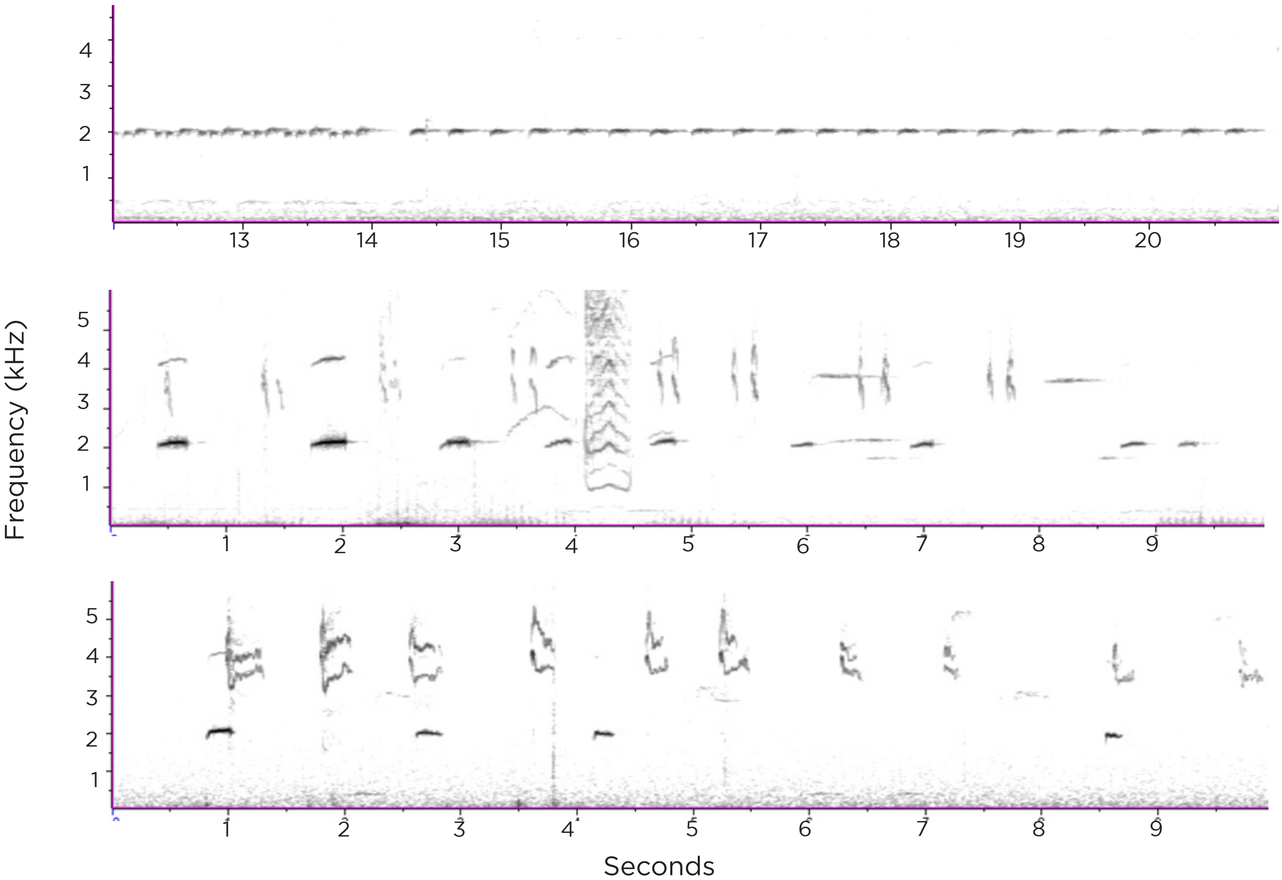

Figure 8. Spectrograms of Black-capped Robin vocalisations. (a) Advertisement song of adult male approaching Nest 1, which had a 19-day-old nestling; (b) Vocalisations of adult female and those of her 17-day-old nestling at Nest 2; (c) Piping vocalisations by adult female and a different call by her 17-day-old nestling at Nest 2. Spectrograms: Tony Baylis

Frith 1970), and three nests each with a nestling in late October to late November in the YUS CA, Huon Peninsula (this study). Assuming a nestling period of 3 weeks, the nesting season (nest building to fledging) of this species extends for nearly 5 months (late August to mid January) in the mid dry to early wet season. This nesting season is similar to that of two other New Guinean montane robins. In the White-winged Robin, the nesting season is at least 5–6 months (early August to mid January: Donaghey 2022), and at least 4 months (October–January) in the Lesser Ground Robin (Donaghey *et al*. 2019b). All three of these montane New Guinean robins and also the Grey-headed Robin breed in the austral spring to early-to-mid summer. The nesting season of most pairs of Grey-headed Robins extends for 4 months from September to December in the mid dry to early wet season. The abundance of arthropods in litter and foliage accelerates in the wet season and coincides with the nestling period and period of post-fledging dependence (Frith & Frith 1985, 1990, 2000). The Ashy Robin, endemic to the Arfak Mountains, Vogelkop Peninsula, West Papua, appears to breed during both the austral winter and summer, suggesting that the climate there differs from that of montane Papua New Guinea (Noske *et al*. 2016).

Nest, clutch size, and incubation and nestling periods

Two tropical-rainforest robins, the Lesser Ground Robin and White-winged Robin, build bulky nests composed externally of bright-green moss (Coates 1990; Donaghey *et al*. 2019b; Donaghey 2022). The Grey-headed Robin and Black-capped Robin build substantial smaller nests constructed externally of twigs, roots and stems with some moss (Harrison & Frith 1970; Coates 1990; Frith & Frith 2000; Higgins & Peter 2002; this study).

A clutch size of one has been documented for three of these New Guinean robins: Lesser Ground Robin (Donaghey *et al*. 2019b), White-winged Robin (Donaghey 2022) and Black-capped Robin (Table 4; this study). For other montane New Guinean robins, clutch size is also one in the Blue-grey Robin, White-eyed Robin *Pachycephalopsis poliosoma*, Green-backed Robin *P. hattamensis* and Ashy Robin (Coates 1990; Boles 2007; Noske *et al*. 2016; Donaghey & Donaghey 2019). Clutch size is one or two (mostly two) in the Grey-headed Robin, and two in the White-faced Robin *Tregellasia leucops* on lowland Cape York Peninsula, Australia. Median clutch size is two (range 1–4) in 18 species of Australian robins (Russell *et al*. 2004).

The incubation period is at least 16 days in the White-winged Robin (Donaghey 2022) and 17–19 days in the Grey-headed Robin (Frith & Frith 2000) but is unknown in other New Guinean robins. The mean incubation period of Australian robins is 16 days (range 14–19 days, n =17: Russell *et al*. 2004) and mean nestling period is also 16 days (range 9–23 days, n = 21: Donaghey unpubl. data). For tropical-rainforest robin species, the nestling period is shorter in the Grey-headed Robin (mean 12–13

Table 4. Comparison of reproductive traits of five tropical-rainforest Australasian robins. F = female, M = male; * = incubation feeding off the nest. References: F & F 2000 = Frith & Frith (2000); D 2022 = Donaghey (2022); D *et al.* 2019 = Donaghey *et al.* (2019); D unpubl. = RD unpubl. data. Mean adult weight of Lesser Ground Robin is from Diamond (1972).

Species	*Grey-headed Robin*	*Black-capped Robin*	*White-winged Robin*	*Lesser Ground Robin*	*White-faced Robin*
Mean adult weight (g)	35	33	23	31.6	15.2
Nest height (m) (and range)	2.2. (0.5–4.0)	1.6 (1.1–2.2)	2.2 (2.0–2.3)	1.4 (1.0–2.1)	
Mean egg weight (g)	4–5	4	3.95		
Egg weight as % of adult weight	11.4–14.7	12.1	17.2		
Clutch size (and range)	1.6 (1–2)	1	1	1	2
Incubation period (days)	17–18		16+		
F incubation constancy (%)	66.0	77.5	73.2		55.0
Incubation on-bout length (min.)	6.8	7.66	3.35		6.96
Incubation off-bout length (min.)	3.9	2.32	1.33		5.77
No. incubation bouts/h	5.8	6	12.5		4.8
No. incubation bouts/12h	70	72	150		58
No. M incubation feeding trips/h	1.3	3.0*	4.6		
Mean no. M & F incubation visits/h	7.1	6	17.1		
Nestling period (days) (and range)	12–13 (10–14)	22	19 (17–21)	22	11–13
F brooding nestling (%) (and range)	28.5 (Days 4–12)	57.7	43.3		
Mean no. brooding bouts/h	8.1	7.5	8.8		
Mean no. feeding trips/nestling/h	4.8	4.4	7.2	7.5	
Mean no. nest visits/h	11.8	9.3	17.6	7.5	
Nestling/fledgling weight as % of adult weight	77	84	93	87	
Nestling/fledgling wing-length as % of adult wing-length	49.0	55.7	57.0	81.6	
Reference	F & F 2000	This study	D 2022	D *et al.* 2019	D unpubl.

days) and White-faced Robin (11–13 days: Donaghey unpubl. data) in north-eastern Australia but longer (17–22 days) in three montane robins endemic to New Guinea, the Lesser Ground Robin, White-winged Robin and Black-capped Robin (Donaghey *et al*. 2019b; Donaghey 2022; this study).

Comparison with Grey-headed Robin

Overall, the reproductive traits and strategies of two congeneric *Heteromyias* robins are remarkably similar (Table 4). During the incubation and nestling periods, in both the Black-capped Robin and Grey-headed Robin the sitting female performs a wing-flutter display on the nest in response to the male's approach. The male rarely visits the nest with food but regularly feeds the female off the nest. At one Grey-headed Robin nest that was video-recorded for 4 hours, the male twice fed the brooding female on the nest (0.5 time/h: Frith & Frith 2000). In the Black-capped Robin, incubation constancy was 11% higher than in the Grey-headed Robin (Table 4). Mean incubation on-bouts were 0.9 minute longer and off-bouts 1.6 minutes shorter in the Black-capped Robin than in the Grey-headed Robin (Table 5). However, the two species were very similar in their incubation bouts/hour and the daily number of bouts/12 hours. The mean number of feeding trips/nestling/hour and nest visits/hour were slightly less in the Black-capped Robin than in the Grey-headed Robin (Table 4). Despite the nestling period of the Grey-headed Robin being almost 10 days shorter than that of the Black-capped Robin, nest success was 14% lower in the former, though sample sizes were small in the latter species (Frith & Frith 2000; this study). The low number of visits to the nest by the male in both species may suggest that these visits to feed the female and young are constrained by nest predation (Martin & Ghalambor 1999). In the Grey-headed Robin, broods of two fed at a rate of 9.7 feeds/hour attained similar fledgling weights as broods of one, which suggests that in this species, despite moderate nest predation, food availability and quality are also important ultimate determinants of a shorter nestling period. The longer nestling period in the Black-capped Robin appears to be a response to a lower risk of nest predation but food limitation appears to be an important ultimate selection pressure.

Comparisons with White-faced Robin, White-winged Robin and Lesser Ground Robin

In lowland rainforests of Cape York Peninsula, north-eastern Queensland, the White-faced Robin has a much lower incubation constancy (55%) and higher nest predation (62.5%) than the Grey-headed Robin (Table 4). In the high-elevation White-winged Robin, during the incubation period, the high incubation constancy, high egg success, and high number of daily nest visits (150, twice that in the Black-capped Robin: Donaghey 2022; Table 4) suggests that the risk of nest predation is lower in the former species. The high rate of incubation feeding in the White-winged Robin (4.6 visits/h) may also reflect a low risk of nest predation in this species (Martin & Ghalambor 1999).

The mean number of feeding trips per nestling per hour was similar in the Black-capped Robin and Grey-headed Robin, whereas in the White-winged Robin and Lesser Ground Robin the single nestlings were fed at a mean rate of 7.2 and 7.5 feeds/hour, respectively (Table 4). Mean number of nest visits per hour by both male and female during the entire nestling period was highest for the White-winged Robin (17.6) but much lower for the Lesser Ground Robin, Black-capped Robin and Grey-headed Robin (Table 4). The high number of nest visits by White-winged Robins, long nestling period (17–21 days) and high nest success suggest that a low risk of nest predation may be a more important selection pressure influencing parental-care behaviour in that species but food limitation needs to be tested (Donaghey 2022). Studies in Arizona, USA, South Africa and Venezuela (Martin *et al*. 2011) emphasise the dominant role of nest predation as a selective force in the evolution of nestling growth rates and food-provisioning strategies per nestling in songbirds.

In the woodlands and forests of eastern Australia, the Hooded Robin, Eastern Yellow Robin and Scarlet Robin have high nest predation (50–86%) and correspondingly high nest attentiveness and a low number of nest visits during incubation (Marchant 1985; Zanette & Jenkins 2000; Fitri & Ford 2003; Debus 2006a,b). This suggests that nest predation is a major selective pressure shaping their reproductive traits (Conway & Martin 2000).

Nestling growth and development

There are few data on nestling growth rates for tropical Australasian robins. On the day before fledging, a Lesser Ground Robin nestling weighed 27.4 g (87% of mean adult weight) compared with 27.9 g (77% of mean adult weight) in the Grey-headed Robin (Frith & Frith 2000; Donaghey *et al*. 2019b; Table 4). Peak 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: this study). In the Grey-headed Robin, wing-length on the day of fledging was 49% of mean adult wing-length (Frith & Frith 2000), whereas in the Black-capped Robin at 19 days it was 56% of mean adult wing-length (this study). In contrast, the wing-length of a nestling White-winged Robin at 14 days was 53 mm (57% of mean adult wing-length) compared with 62 mm (82% of adult wing-length) at 22 days in the Lesser Ground Robin (Donaghey *et al*. 2019b). These comparisons show that in three New Guinean montane robins with low risk of nest predation, longer nestling periods of 17–22 days allow nestlings to fledge with longer wings in proportion to adults (i.e. greater flight capability) than in the Grey-headed Robin (nestling period 12–13 days).

Nest predation and nest-predation risk

Risk of nest predation appears to be lowest in the high-elevation montane White-winged Robin (Donaghey 2022) based on this species' high nest success, short mean incubation bouts (3.35 minutes), high number of incubation bouts (150/day), long nestling period and high nest-visitation rates during the incubation and nestling periods (17.1 and 18/h, respectively). In the mid mountains of the YUS CA (elevation 2200–2500 m asl), risk of nest predation in the Black-capped Robin appears to be low, based on its relatively high nest success (67%), longer incubation bouts and fewer nest visits during the nestling period, than those in the White-winged Robin (Table 4). This difference suggests that risk of nest predation may be higher in the mid-montane Black-capped Robin than in the White-winged Robin but this needs to be verified. There are very few data on nest predation for lowland-rainforest birds of New Guinea. Nest success was very low (12%) and nest predation very high (88%) at 24 open nests of pigeons, a jewel-babbler, flycatchers and a butcherbird, in rainforest at Brown River, south-eastern PNG (Bell 1982). Nest predation was high (62.5%) in the White-faced Robin in lowland tropical rainforest on Cape York Peninsula (Donaghey unpubl. data) compared with that in the Grey-headed Robin in upland tropical rainforest in north-eastern Australia (Frith & Frith 2000). In lowland dipterocarp equatorial rainforest at Semengo Forest Reserve, Sarawak, Borneo, reproductive success was low for all species, and nest predation (excluding hole-nesters) was high (86%) (Fogden 1972). Boyle (2008) plotted the data of Skutch (1985) and Robinson *et al*. (2000) for sites in Central America from lowland Panama to highland Guatemala and showed that nest predation declined with elevation. By using artificial nests along an elevational gradient from La Selva Biological Station to ~3000 m in Braulio Carrillo National Park, Costa Rica, Boyle (2008) discovered that overall nest predation declined with increasing elevation but risk of nest predation was highest at 500–650 m asl. Robinson *et al*. (2000) found that nest success was lower (29%) for understorey passerines in lowland central Panama, but varied with species, nest type and between years, compared with a mean nest success of 53% in open-cup-nesting birds in temperate North America.

Breeding strategy

The female Black-capped Robin alone incubates the single-egg clutch. The male contributes to parental care indirectly by feeding the female off the nest. Incubation behaviour is characterised by high incubation constancy (75.5%), short incubation on-bouts (7.66 minutes) and off-bouts (2.32 minutes), a high daily number of incubation bouts (72), and a high number of female visits to the nest (6.0/h).

Parental nestling care in the Black-capped Robin is characterised by a long nestling period (22 days) compared with most Australian robins, and a higher incidence of female brooding (57.7% for the entire nestling period) than other montane Australasian robins. Food-delivery rates per hour per nestling (4.4) were similar for the congeneric Grey-headed Robin (4.8) but total food-delivery rates were 7.2/hour in the latter species for a brood size of two. Martin (2015) found that small clutch sizes of tropical birds allow adults to increase food-delivery rates per young and reduce mortality risk to adults and juveniles. Adult longevity is apparently high (up to 18 years) in the Black-capped Robin (Anon. 2006). By comparing nestling growth rates in phylogenetically paired tropical and temperate songbirds with the same nestling period, Martin (2015) discovered that tropical nestlings have slower peak growth but faster subsequent growth of wings than temperate songbirds, enabling tropical fledglings to better evade predators. Compared with the Grey-headed Robin, the apparent lower risk of nest predation in the Black-capped Robin enables nestlings to stay in the nest longer and fledge with longer wings to escape predators, but almost nothing is known about predators and avian juvenile mortality in montane New Guinea. The higher food-delivery rates for a brood of two in the Grey-headed Robin compared with those for a brood of one in the Black-headed Robin suggest that food limitation may be a more important selection pressure in the latter species. Thus, it appears that the selection pressures of a low risk of nest predation and food limitation interact to shape the reproductive strategy of the Black-capped Robin.

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Appendix 1. Time (minutes) that a female Black-capped Robin spent on and off Nest 2 during the nestling period, YUS CA, Huon Peninsula, PNG, 2014. Day = day of nestling period; dates are given as day.month; Obs. = observation time (minutes); C% = brooding constancy.

Day	*Date*	*Time (h)*	*Obs. (min.)*	*Time (min.) female spent on nest*						*Time (min.) female spent off nest*		
				Brooding			*Perched at nest*		*Total*	*No. absences*	*Min. off*	*Min./h*
				Min. on	*Min./h*	*C%*	*Min. on*	*Min./h*	*min. on*			
1	5.11	1500–1700	120	102.21	51.11	85.18	2.81	1.41	105.02	23	14.98	7.49
2	6.11	0700–0900	120	96.34	48.17	80.28	3.19	1.60	99.53	21	20.47	10.24
2	6.11	0900–1100	120	109.97	54.99	91.64	1.00	0.50	110.97	10	9.03	4.52
3	7.11	0700–0900	120	101.04	50.52	84.20	4.78	2.39	105.82	32	14.18	7.09
4	8.11	0700–0900	120	95.76	47.88	79.80	0.98	0.49	96.74	19	23.26	11.63
4	8.11	0900–1100	120	91.25	45.63	76.04	1.24	0.62	92.49	19	27.51	13.76
5	9.11	0700–0900	120	103.90	51.95	86.58	0.85	0.43	104.75	18	15.25	7.63
6	10.11	0700–0900	120	88.28	44.14	73.57	2.76	1.38	91.04	28	28.96	14.48
6	10.11	0900–1100	120	107.58	53.79	89.65	1.21	0.61	108.79	17	11.21	5.61
7	11.11	0700–0900	120	106.33	53.17	88.61	3.17	1.59	109.50	21	10.50	5.25
8	12.11	0700–0900	120	80.76	40.38	67.30	1.96	0.98	82.72	29	37.28	18.64
8	12.11	0900–1100	120	84.67	42.34	70.56	2.31	1.16	86.98	25	33.02	16.51
9	13.11	0700–0900	120	88.47	44.24	73.73	1.55	0.78	90.02	25	29.98	14.99
10	14.11	0700–0900	120	79.80	39.90	66.50	1.98	0.99	81.78	16	38.22	19.11
10	14.11	0900–1100	120	94.48	47.24	78.73	2.73	1.37	97.21	25	22.79	11.4
11	15.11	0600–0800	120	76.58	38.29	63.82	2.28	1.14	78.86	24	41.14	20.57
11	15.11	0800–1000	120	60.59	30.55	50.91	2.63	1.07	63.22	28	56.78	28.39
11	15.11	1000–1200	120	33.95	16.98	28.29	1.05	0.53	35.00	11	85.00	42.50
11	15.11	1200–1400	120	63.79	31.90	53.16	0.78	0.39	64.57	19	55.43	27.73
12	16.11	0900–1100	120	33.64	16.82	28.03	2.32	1.16	35.96	11	84.04	42.02
14	18.11	0700–0900	120	101.89	50.95	84.91	2.63	1.32	104.52	24	15.48	7.74
15	19.11	0700–0900	120	40.88	20.44	34.07	2.20	1.10	43.08	16	76.92	38.46
15	19.11	0900–1100	120	27.27	13.64	22.73	1.05	0.53	28.32	10	91.68	45.84
16	20.11	0700–0900	120	59.53	29.77	49.61	3.24	1.62	62.77	17	57.23	28.62
17	21.11	0700–0900	120	28.29	14.15	23.58	2.95	1.48	31.24	14	88.76	44.38
17	21.11	0900–1100	120	44.87	22.44	37.39	6.23	3.12	51.10	16	68.90	34.45
18	22.11	0700–0900	120	73.83	36.92	61.53	3.76	1.88	77.59	17	42.41	21.21
19	23.11	0700–0900	120	18.20	9.10	15.17	4.94	2.47	23.14	15	96.86	48.43
19	23.11	0900–1100	120	25.81	12.91	21.51	2.14	1.07	27.95	8	92.05	46.03

Appendix 1 continued

Day	Date	Time (h)	Obs. (min.)	Time (min.) female spent on nest						Time (min.) female spent off nest		
				Brooding			Perched at nest		Total	No. absences	Min. off	Min./h
				Min. on	Min./h	C%	Min. on	Min./h	min. on			
20	24.11	0700–0900	120	39.96	20.00	33.30	4.17	2.09	44.13	18	75.87	37.94
21	25.11	0700–0900	120	45.52	22.76	37.93	4.03	2.02	49.55	16	70.45	35.23
22	26.11	0700–0900	120	10.53	5.27	8.78	4.81	2.41	15.34	13	104.66	52.33
Totals and means												
Days 1–11			2280	1665.75		73.1	39.26		1705.01		574.99	
Days 12–22			1560	550.22		35.3	44.47		594.69		965.31	
Days 1–22			**3840**	**2215.97**		**57.7**	**83.73**		**2299.70**		**1540.30**	

Appendix 2. Black-capped Robin nestling care (brooding and feeding young) at Nest 2, YUS CA, Huon Peninsula, PNG, 2014. Day = day of nestling period; dates are given as day.month; Obs. = observation time (minutes); F = female, M = male, Y = young.

Day	*Date*	*Time (h)*	*Obs. (min.)*	*Nest visits*										
				By female				*By male*			*No. feeding trips*		*No. nest visits*	
				No. brooding bouts	*F fed Y and brooded*	*F fed Y and left nest*	*Total F visits*	*M fed F at nest*	*M fed F which fed Y*	*M fed Y directly*	*Total*	*No./h*	*Total*	*No./h*
1	5.11	1500–1700	120	22	8		22	1			8	4	23	11.5
2	6.11	0700–0900	120	20	6	1	21				7	3.5	21	10.5
2	6.11	0900–1100	120	11	1		11				1	0.5	11	5.5
3	7.11	0700–0900	120	34	11	1	35				12	6	35	17.5
4	8.11	0700–0900	120	16	3	2	18				5	2.5	18	9
4	8.11	0900–1100	120	15	5	3	18				8	4	18	9
5	9.11	0700–0900	120	17	2	1	18				3	1.5	18	9
6	10.11	0700–0900	120	23	8	2	25				10	5	25	12.5
6	10.11	0900–1100	120	15	4	3	18				7	3.5	18	9
7	11.11	0700–0900	120	18	7	2	20				9	4.5	20	10
8	12.11	0700–0900	120	26	8	2	28				10	5	28	14
8	12.11	0900–1100	120	24	5	2	26				7	3.5	26	13
9	13.11	0700–0900	120	17	8	6	23				14	7	23	11.5
10	14.11	0700–0900	120	12	3	4	16				7	3.5	16	8
10	14.11	0900–1100	120	19	5	5	24				10	5	24	12
11	15.11	0600–0800	120	20	9	4	24				13	6.5	24	12
11	15.11	0800–1000	120	23	9	6	29				15	7.5	29	14.5
11	15.11	1000–1200	120	9	2	1	10			1	4	2	11	5.5
11	15.11	1200–1400	120	12	2	2	14				4	2	14	7
12	16.11	0900–1100	120	8	2	3	11				5	2.5	11	5.5
14	18.11	0700–0900	120	22	9	4	26	2			13	6.5	28	14
15	19.11	0700–0900	120	14	9	1	15		1		11	5.5	16	8
15	19.11	0900–1100	120	5		4	9				4	2	9	4.5
16	20.11	0700–0900	120	15	7	4	19				11	5.5	19	9.5
17	21.11	0700–0900	120	9	9	4	13				13	6.5	13	6.5
17	21.11	0900–1100	120	10	3	4	14				7	3.5	14	7
18	22.11	0700–0900	120	12	7	4	16				11	5.5	16	8

Appendix 2 continued

Day	*Date*	*Time (h)*	*Obs. (min.)*	*Nest visits*										
				By female				*By male*			*No. feeding trips*		*No. nest visits*	
				No. brooding bouts	*F fed Y and brooded*	*F fed Y and left nest*	*Total F visits*	*M fed F at nest*	*M fed F which fed Y*	*M fed Y directly*	*Total*	*No./h*	*Total*	*No./h*
19	23.11	0700–0900	120	5	3	9	14				12	6	14	7
19	23.11	0900–1100	120	5	4	2	7				6	3	7	3.5
20	24.11	0700–0900	120	10	7	6	16				13	6.5	16	8
21	25.11	0700–0900	120	9	5	8	17				13	6.5	17	8.5
22	26.11	0700–0900	120	5	4	6	11				10	5	11	5.5
Totals			**3840**	**482**	**175**	**106**	**588**	**3**	**1**	**1**	**283**		**593**	
Mean feeding trips/h and nest visits/h														
Days 1–11												**4.1**		**10.6**
Days 12–22												**5.0**		**7.4**
Days 1–22												**4.4**		**9.3**