Corella, 2016, 40(4): 81-90

Nestling and post-fledging growth and development in an Australian passerine: Hall's Babbler *Pomatostomus halli*

Dean J. Portelli

Centre for Ecosystem Science, School of Biological, Earth and Environmental Sciences,
University of New South Wales, Sydney NSW 2052, Australia
Email: portellidean@gmail.com

Received: 13 July 2015

Postnatal growth and development has rarely been studied in passerines of the southern hemisphere, particularly Australian species. Developmental changes in external morphology and the growth in body mass and size of nestling and juvenile Hall's Babblers (*Pomatostomus halli*) were quantified and described. Additionally, a guide to ageing nestlings to the nearest day was developed to facilitate studies of breeding biology. Nestling growth and development in Hall's Babblers were similar to that of its closest relative, the Grey-crowned Babbler *P. temporalis*. Body mass, skeletal and feather growth, but not the sequence and timing of developmental changes in external morphology, were affected by nestling body condition. Juvenile Hall's Babblers attained adult size by four months of age, and were indistinguishable from adults by one year of age. Nestling growth rate in body mass of Hall's and Grey-crowned Babblers is lower than similarly sized northern hemisphere passerines, but the relative size at fledging is similar. This suggests nestling growth rate may, like other life-history traits, differ between passerines of the southern hemisphere and those of temperate regions of the northern hemisphere. However, since nestling growth has been poorly studied in southern hemisphere passerines, the available data are inadequate to test this hypothesis.

INTRODUCTION

All passerines exhibit an altricial mode of development, whereby neonates hatch naked, blind and helpless (Starcks and Ricklefs 1998). Nestling growth pattern and rate vary widely among species, and are an integral component of avian life-history strategies (Ricklefs 1973, 1983; Remes and Martin 2002). Ecological factors are believed to play an important role in shaping passerine life-histories (Bosque and Bosque 1995; Remes and Martin 2002). For example, nestlings of species that experience higher predation pressure grow faster and fledge at an earlier developmental stage (Remes and Martin 2002). Most data from which these conclusions are drawn come from northern hemisphere passerines (Ricklefs 1973; Remes and Martin 2002), yet there are considerable differences in life-history characteristics between northern and southern hemisphere passerines, such as clutch size, within-season reproductive effort, duration of parental care and survival (Martin 1996, 2004; Russell 2000). Postnatal growth and development of southern hemisphere passerines has rarely been studied in detail (Bosque and Bosque 1995), and represents a significant gap in our understanding of the evolution and biogeography of passerine life-history strategies.

In Australia, nestling growth and development has been well-studied in only a few passerine species (e.g. Maher 1986, 1991; Boag 1987; Rowley *et al*. 1991; Frith and Frith 2004; Russell *et al*. 2004), and most comprehensively in the Grey-crowned Babbler *Pomatostomus temporalis* (Brown 1979; Dow and Gill 1984a). Compared with passerines from temperate regions of the northern hemisphere, this species has a protracted nestling period, a slow nestling growth rate, and a below average fledging body mass relative to adult mass (Ricklefs 1968; Brown 1979; Dow and Gill 1984a). Hall's Babbler *P. halli* is the closest relative of the Grey-crowned Babbler (Edwards and Wilson 1990), but little is known of its breeding biology. Gill and Dow (1983) described changes in external morphology during the early nestling period (up to day 10) for this species, but no data on nestling growth have been collected and the development of older nestlings and fledglings has not been examined.

Knowledge of nestling age is often essential in studies of breeding biology as it influences maternal care (e.g. Moreno 1987), parental (e.g. Goodbred and Holmes 1996; Lee *et al*. 2010) and alloparental (Young 2007) food provisioning, nestling energy expenditure (McCarty 1996; Anava *et al*. 2001), and parental foraging behaviour (da Silva and Melo 2009). Determining exact nestling age requires continual monitoring of nests, but repeated disturbance is often undesirable (Ibanez-Alamo *et al*. 2012). Alternatively, the age of nestlings can be estimated from body mass, size and/or external morphology (Jongsomjit *et al*. 2007). The age of nestling Grey-crowned Babblers, for instance, can be estimated to the nearest day using body mass (Dow and Gill 1984b). The aims of this study were to quantify and describe nestling growth and development, develop a guide to ageing nestlings, and document post-fledging growth and development in Hall's Babblers.

METHODS

Study site and population

The breeding biology of Hall's Babbler was studied at Bowra Sanctuary, near Cunnamulla in south-western Queensland (27°58.8'S, 145°32.8'E) in 2006–2009. Hall's Babblers live in stable kin-structured breeding units comprised of a mated pair, up to four unpaired adults and juveniles (Portelli 2012). Between 25 and 31 breeding units were monitored regularly each year. All adults, juveniles, fledglings and older nestlings in breeding units were banded with an individually numbered stainless steel band (supplied by the Australian Bird and Bat Banding Scheme) and a unique combination of three Darvic colour-bands. Adults and juveniles were caught using standard four-shelf mist nets (12 m or 18 m long, mesh size 31 mm or 38 mm) and sex was determined through genetic methods (Portelli 2014).

Nestling growth and development

Ten nests were selected to examine nestling growth and development. At least half of nest attempts on the study site failed due to predation (Portelli 2012), so the ten nests were enclosed by wire in an attempt to protect nestlings from predators; however, this failed and the eggs in six nests were depredated. The growth and development of eight nestlings from the remaining four nests, were recorded daily. Two broods were from the same breeding unit: one nestling hatched on 21 July 2007 (brood A), and two nestlings hatched on 10 and 11 November 2007 (brood B). The third brood (C) comprised two nestlings that hatched on 26 and 27 July 2007. The final brood (D) comprised three nestlings that hatched on 21 August 2007, but they were depredated when three (n = 1) and seven (n = 2) days old.

Nestlings were measured daily at about the same time of day (1300 ± 1 hr), beginning on the day of hatching (day 0). Body mass was measured to the nearest 0.5 gram with a 60 grams Pesola spring scale. Tarsus length (proximal end of the tarsometatarsus to the leading edge of the folded digits), exposed culmen length (tip of the upper mandible to the edge of the skin covering the rhamphotheca) and total head and bill length ('head-bill length'; tip of the bill to the occipital condyle) were measured with dial callipers to the nearest 0.1 mm. Flattened wing and tail lengths were measured to the nearest millimetre using stainless steel rules; a butted rule was used for wing length.

Logistic growth curves for body mass and tarsus length were fitted for each nestling from broods A–C using DataFit version 9 (Oakdale Engineering www.curvefitting.com), which took the form $Y = A/(1 + e^{-K(t-i)})$, where A = asymptote, K = growth rate, t = age in days, and i = age when maximum growth rate occurs. Logistic growth curves provided the best fit for these traits in Grey-crowned Babbler nestlings (Dow and Gill 1984a) and other similar studies (Ricklefs 1968; Remes and Martin 2002). ANOVA was performed for each fitted curve to determine whether the fit explained significantly more variance in the data than a null model; the coefficient of determination (r^2) is reported as a measure of the proportion of the variance explained by the fitted curve. Linear regressions were fitted for culmen, head-bill, wing and tail lengths for each nestling from broods A–C using SPSS® version 21. Growth was non-linear for head-bill and wing lengths, so data were truncated at the age when growth rate ceased to be linear prior to fitting regression models.

The day when nestlings were absent from the nest was treated as the day of fledging. To determine relative size at fledging, measurements of nestlings on the day before fledging were converted to proportions of body size of adults (body mass and culmen, head-bill and tarsus lengths) or full-grown juveniles (wing and tail lengths). Juvenile wing and tail lengths were used as these were significantly shorter than in adults. Additionally, the ratio of the asymptote of the logistic growth curve to adult size for body mass and tarsus length (*R, sensu* Ricklefs 1968) was calculated. Data for adult (Portelli 2014) and juvenile (this study) male and female babblers were obtained from the same population. For each nestling, mean measurements of adults or juveniles of the same sex were used for comparisons.

Each nestling was photographed daily to record developmental changes in external morphology, minimising the time spent handling nestlings. The commencement of three stages of feather development in different tracts was recorded: 1) the appearance of follicles beneath the skin, 2) emergence of feather pins from the skin, and 3) eruption of feathers from their sheaths. The day when the following developmental milestones were reached was also recorded: eyelids split, eyes opened, and maxilla and mandible tips met. Lastly, the general appearance of the plumage was described daily once feathers erupted from their sheaths.

Nestling age estimation

Three methods to estimate nestling age were derived from the nestlings of known age that were measured daily. These included developmental changes in external morphology, and growth patterns of morphological traits. The third method was derived by fitting linear regressions with age as the response variable to pooled data for the eight nestlings for initial tarsus growth – which was approximately linear – and tail growth. Because these methods were derived from only eight nestlings, the representativeness of this small sample was assessed using a larger sample of 22 additional nestlings (ten broods from eight breeding units). These were first measured and photographed within ten days of hatching (see Gill and Dow 1983) and again 6–12 days later. Each time a nestling was examined its age was predicted from the age-specific developmental changes in external morphology and growth curves derived from the nestlings measured daily. Photographs of nestlings were randomly ordered and the author was blind to the identity of the nestling when predicting age. Predicted ages from growth curves produced a range in days for each trait, so a single day that was the most consistent among traits was chosen. Additionally, age was predicted using the linear equation for the relationship between tail length and age for nine of the 22 nestlings that were photographed and measured twice once their tail had begun to grow. To investigate consistency among the three ageing methods the predicted ages from each method were compared for each capture. To assess whether the three ageing methods accurately predicted changes in morphology and growth rate, the number of days between first and last captures (Δ days) was compared with the difference in predicted ages between captures (Δ age).

Post-fledging growth

Thirteen male and 11 female Hall's Babblers that had been measured as nestlings were recaptured post-fledging. These individuals were recaptured 1–6 times post-fledging (n = 97 captures), up until the age of 49 days to 2.6 years (mean 1.2 years; age was based on estimated age when measured and photographed as a nestling). Body mass was recorded for all but two recaptures and the other morphological traits described above were re-measured for 79–83 recaptures. Logistic growth curves were fitted to pooled data for males and females separately as described above.

Seventeen males and 19 females were captured within their first year after they had completed growth of remiges and rectrices and before they commenced the post-juvenile primary moult. This sample of juveniles included some juveniles banded as nestlings and others banded post-fledging. Wing and tail lengths were compared to those of adults using Mann-Whitney U-tests (adult data were not normally distributed). Additionally, eight males and five females banded as nestlings were recaptured after they had completed post-juvenile primary moult and were in second basic plumage (*sensu* Howell *et al*. 2003; estimated ages 0.8–1.1 years). Wing and tail lengths were compared to those of juvenile and adult plumages.

RESULTS

Nestling growth

The single nestling in brood A fledged 19 days post-hatching. The two nestlings in brood C fledged on the same day at 18 and 19 days post-hatching. Nest lining material (mainly sheep wool) had been pulled out through the nest entrance and strewn on the sides of the nest. This is usually an indication of nest predation (Portelli 2012) so it is possible disturbance by a predator hastened fledging. The two nestlings in brood B had poor body condition and died on the same day, 17 and 18 days post-hatching. This was probably due to exposure to unusually heavy rainfall as both nestlings were saturated when found dead. Malnourishment is an unlikely cause of death for the older nestling because its body mass and size on the previous day was similar to healthy nestlings of the same age (Fig. 1). Growth patterns were consistent among nestlings from broods A, C and D and, with the exception of body mass, the older nestling from brood B (Fig. 1). The growth of the younger nestling from brood B was clearly stunted (Fig. 1). Logistic growth curves explained a significant proportion of the variance in body mass and tarsus length growth for each nestling (Table 1). Body mass gain was sigmoidal, exhibiting little increase during the final week; growth rates (K) were 0.377–0.392 (Table 1). Maximum rate of gain in body mass for the three nestlings from broods A and C was approximately 2.5 g day-1. Tarsus growth was similarly sigmoidal, reaching an asymptote at approximately 13–14 days post-hatching. Tarsus growth rate was slower ($K = 0.268$–0.286) than body mass, but reached an asymptote earlier (Table 1); growth rate of the older nestling in poor body condition fell within the range of values for the three healthy nestlings. Culmen growth was linear throughout the nestling period in the three healthy nestlings (Table 2), but slowed after day 9 and 11 in the youngest and oldest nestlings that had poor body condition respectively (Fig. 1). Head-bill and wing growth was initially linear but slowed after day 11–14 and 13–14 respectively (younger nestling in poor body condition excluded; Table 2, Fig. 1). Tail growth was strongly linear throughout the nestling period in all nestlings (Table 2, Fig. 1).

The three healthy nestlings from broods A and C fledged when they were between two-thirds and three-quarters full-grown in most morphological measurements (Table 3). Exceptions included tarsus length, which completed growth before fledging, and culmen and tail lengths, which were the least developed upon fledging. Values were similar among nestlings, with a maximum difference of five percent (wing length 0.70–0.75). Relative size for the older of the two nestlings in poor body condition, which had attained a similar age to the other nestlings before its death, was similar (the younger nestling from brood B was excluded because its growth was clearly stunted); though values for culmen and tail lengths were slightly lower (Table 3).

Nestling development

Developmental changes in external morphology followed a distinct sequence (Table 4, Fig. 2). Almost all developmental stages of feather tracts commenced within a two-day age range. Some of this variation was attributable to measuring age in days rather than time since hatching; for example, the two siblings of brood C hatched later in the day than the single nestling of brood A (down was dry and fluffy in the latter) and consequently appeared to lag behind in development. Where the timing of developmental changes overlapped, not all nestlings followed the same sequence. Rectrices, for example, emerged from the skin either the same day, one or two days later, or one day earlier than the greater secondary coverts. Eruption of feathers from their sheaths generally followed the sequence of feather emergence. Eyelids split open and eyes opened at 4–5 and 6–9 days post-hatching respectively. The bill gradually changed from yellow to black; the transition from mostly yellow to mostly black occurred at 8–9 days. The age at which the tip of the maxilla reached the tip of the mandible was more variable at 5–11 days. The tips of the outer greater secondary coverts reached the distal ends of the sheaths of the secondaries on day 13; those of the primaries did so on day 14–15. On day 15, nestlings appeared 'fully feathered' with only sheaths of the rectrices, anterior capital tract, and interramal and submalar tracts visible. The egg tooth and some down on the sides of the crown (coronal patch) were retained throughout the nestling period. The developmental sequence and timing for the two nestlings in poor body condition did not diverge from that of the three healthy nestlings.

Nestling age estimation

A linear regression fitted to pooled data for tail growth from four nestlings (younger nestling in poor body condition excluded) yielded the following equation: age = 0.273*tail length + 6.558 ($F_{1,36} = 3072.52$; $r^2 = 0.99$; $P < 0.001$). Although tarsus growth was non-linear, growth up until about day 10 was sufficiently linear to develop a linear equation to facilitate ageing: age = 0.576*tarsus length – 3.381 ($F_{1,61} = 2943.49$; $r^2 = 0.98$; $P < 0.001$).

Predicted ages derived using the three ageing methods were in agreement for 90.9 percent of the 22 additional nestlings when they were first examined, and 54.5 percent when examined a second time. Where predicted ages disagreed ($n = 11$ cases), the maximum difference between predicted ages was one (91.7%) or two (8.3%) days. The number of days between first and last capture (Δ days) did not differ from the difference in

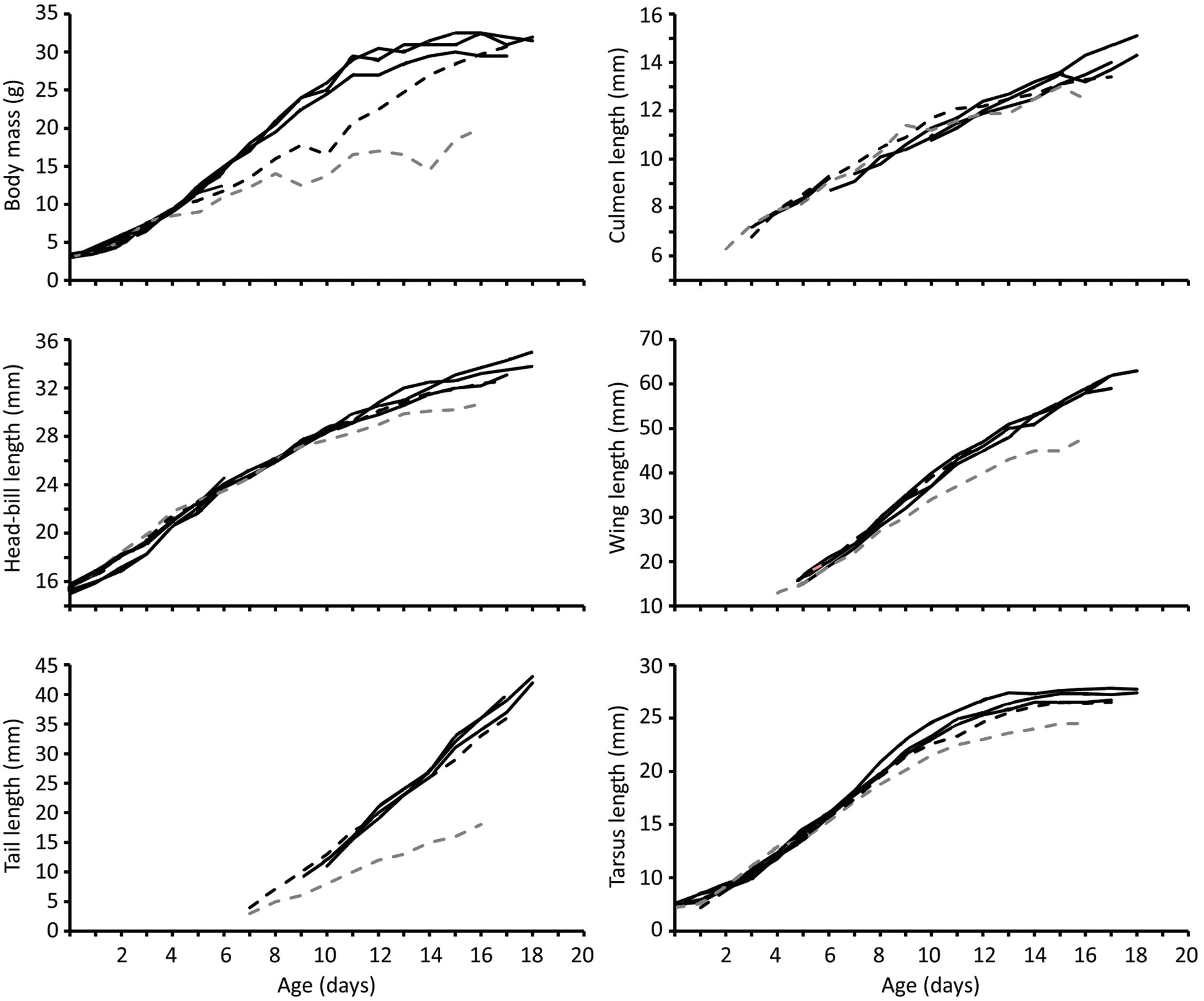

Figure 1. *Growth of Hall's Babbler nestlings. Individuals measured daily are shown by solid (six healthy nestlings, broods A, C and D) or dashed (two nestlings in poor body condition from brood B) lines.*

Table 1

Parameters of logistic growth curves fitted to body mass and tarsus growth of four Hall's Babbler nestlings. Growth curves take the form $Y = A/(1 + e^{-K(t-i)})$ where Y = body mass or tarsus length, A = asymptotic size, K = growth rate, t = age in days, i = age when maximum growth rate is reached. n indicates the number of consecutive days each nestling was measured. Results of ANOVA for each fitted logistic curve are reported; $r^2 \geq 0.99$ for all fitted curves.

Brood	Nestling (sex)	*n*	Body mass					Tarsus				
			A	***K***	***i***	***F***	***P***	***A***	***K***	***i***	***F***	***P***
A	1 (♀)	19	32.8	0.377	6.5	2175.18	<0.001	29.2	0.286	4.8	1018.20	<0.001
B*	1 (♀)	17	-	-	-	-	-	28.0	0.274	3.9	4212.08	<0.001
C	1 (♂)	19	32.9	0.392	6.5	2582.00	<0.001	29.0	0.268	5.1	1134.98	<0.001
C	2 (♀)	18	30.6	0.379	6.3	4877.98	<0.001	28.4	0.268	4.9	1439.41	<0.001
Mean			32.1	0.385	6.4			28.7	0.274	4.7		

* logistic growth curve inappropriate for data on body mass gain for this nestling, which was in poor body condition

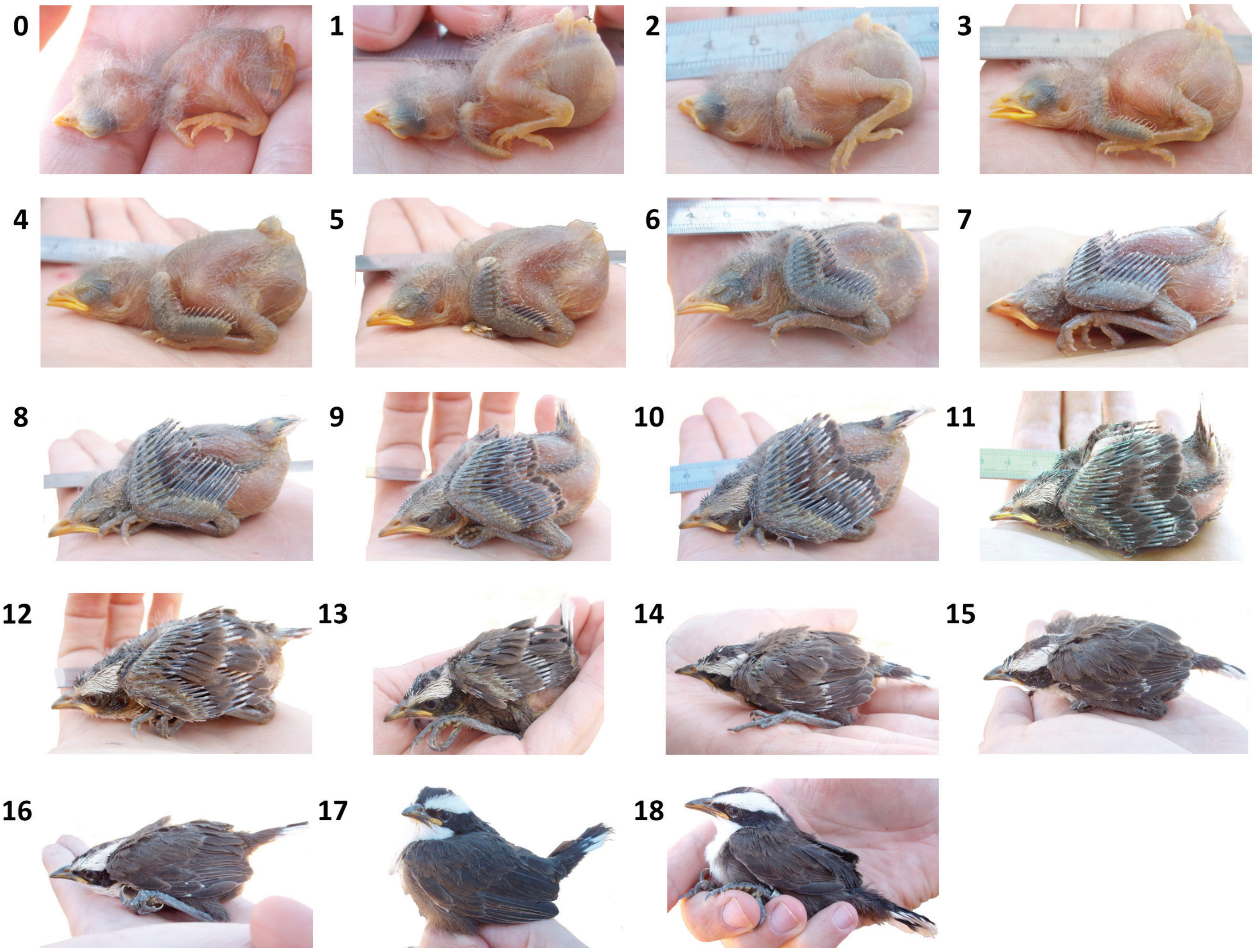

Figure 2. *Daily development of the single Hall's Babbler nestling from brood A. The number of days since hatching is shown next to the top left of each image.*

Table 2

Linear growth of culmen, head-bill, wing and tail length of four Hall's Babbler nestlings from broods A–C (the younger nestling in very poor body condition from brood B was excluded). Mean slope and intercept were derived from regressions fitted to each nestling individually (r^2 ≥0.95 and P<0.001 in all cases).

Trait	Slope			Intercept		
	Mean	Min.	Max.	Mean	Min.	Max.
Culmen[a]	0.47	0.41	0.52	6.32	5.89	6.96
Head-bill[b]	1.30	1.20	1.41	15.42	14.73	16.09
Wing[b]	4.35	4.26	4.40	-5.74	-6.22	-5.27
Tail	3.71	3.21	3.93	-24.77	-27.04	-18.79

[a] nestling from brood B excluded as culmen growth was non-linear

[b] data truncated before growth rate slowed at day 11–14 for head-bill length and day 13–14 for wing length

Table 3

Fledging size as a proportion of full-grown size of four Hall's Babbler nestlings. The age of nestlings on the day before fledging (broods A and C) or death (brood B) is shown in days. Values of *R* (asymptote value as a proportion of adult size; Ricklefs 1968) for body mass and tarsus are shown in parentheses.

Brood	Nestling (sex)	Age	Body mass	Tarsus	Culmen	Head-bill	Wing[a]	Tail[a]
A	1 (♀)	18	0.80 (0.83)	1.03 (1.09)	0.61	0.74	0.78	0.51
B	1 (♀)[b]	17	0.79 -	0.99 (1.04)	0.57	0.71	0.73	0.43
C	1 (♂)	18	0.78 (0.81)	0.99 (1.05)	0.59	0.73	0.76	0.51
C	2 (♀)	17	0.75 (0.77)	1.00 (1.06)	0.59	0.72	0.73	0.48
Mean			0.80 (0.80)	1.00 (1.06)	0.59	0.73	0.75	0.48

[a] calculated using mean lengths of juveniles because those of adults were significantly longer (Table 6). Adult measurements were used for the other traits.

[b] logistic growth curve inappropriate for body mass data for this nestling, which was in poor body condition

predicted ages between captures (Δ age) for 45.5, 50.0 and 44.4 percent of nestlings when age was predicted from external morphology, growth curves and the equation predicting age from tail length, respectively. Δ days was one day greater than Δ age for 50.0, 50.0 and 44.4 percent of nestlings for the three respective ageing methods, and Δ days was one day lower than Δ age for 4.5, 0.0 and 11.1 percent of nestlings for the three respective ageing methods.

Post-fledging growth and ageing

Body mass reached an asymptote when fledglings were c. 8–12 weeks old. There was considerable variation in body mass among individuals, resulting in a poor fit of the logistic growth curve compared with other traits (Table 5). Culmen and head-bill lengths approached an asymptote at about nine weeks old, and reached a peak at about 16–17 weeks old. Wing and tail lengths of the juvenile plumage were significantly shorter than those of adults (Table 6). Logistic growth curves were therefore fitted only to data collected from juveniles recaptured prior to beginning the post-juvenile primary moult. Wing and tail lengths reached maximum length at about five weeks old for both males and females. Juveniles in second basic plumage did not differ appreciably from adults in wing or tail length (Table 6), but this was not tested statistically because of an insufficient sample size.

Iris colour of nestlings and fledglings was darker than in adults, but lightened post-fledging to become reddish-brown. The rictus (gape) was bright yellow in nestlings with a conspicuous fleshy rictal flange, which remained visible for at least the first two months post-fledging. The commisure (including rictal flange) then darkened and the yellow pigmentation gradually receded to the sides, until the entire rictus was pinkish. The age when this occurred varied among individuals; most had only slight traces of yellow by 30–35 weeks old, but one individual still retained some yellow pigmentation at 40 weeks old. The bill was completely black at fledging, but gradually the lower part of the proximal two-thirds of the mandible turned light grey as in adults. The age when this occurred was highly variable: of six individuals 76–79 days old, the bill was completely black in one, becoming pale at the base only in another, partially complete in two siblings, and complete in another two siblings.

DISCUSSION

The sequence and timing of developmental changes in the external morphology of Hall's Babbler nestlings was stereotypical, even in nestlings in poor body condition. Gill and Dow (1983) found similar results for eight Hall's Babbler nestlings, except they observed remiges and rectrices erupting from their sheaths somewhat earlier: days 6–7 c.f. days 7–8 for remiges, and days 6–7 c.f. days 8–10 for rectrices. Hall's and Grey-crowned Babblers attain a 'fully-feathered' appearance, with feather sheaths visible only on the head and tail, at a similar age: c.15 days for Hall's Babbler c.f. 15–17 days for Grey-crowned Babbler (Gill and Dow 1983). Growth rate (*K*) of nestling body mass in Hall's Babblers (0.377–0.392) appeared to be slightly faster than in Grey-crowned Babblers (mean 0.349; Dow and Gill 1984a), but intraspecific variation in growth rate of some passerine species is of a similar or greater magnitude than this difference (Ricklefs 1968, 1976). The age at which growth rate of body mass peaked occurred earlier in Hall's Babblers (6.3–6.5 days) than in Grey-crowned Babblers (7.5 days; Brown 1979). Nestling body mass of both species stabilised during the last week of the nestling period, at about three-quarters the body mass of adults (Dow and Gill 1984a). Such a pattern of growth is not atypical of passerines (Ricklefs 1968). Unlike body mass, tarsus growth rate of Hall's Babblers (0.268–0.286) was similar to that of the Grey-crowned Babbler (mean 0.283; Dow and Gill 1984a).

Three methods were derived to estimate nestling age of Hall's Babblers using the sample of eight nestlings measured daily: age-specific changes in external morphology, growth

Table 4

Timing and sequence of development of feather tracts of eight Hall's Babbler nestlings from broods A–D. The number of nestlings that commenced the developmental stage of the respective feather tract on each day is shown. Total number of nestlings examined each day is shown in the last row.

Stage	Feather Tract	Day										
		0	1	2	3	4	5	6	7	8	9	10
Follicles visible below skin	Alar	1	7									
	Capital	1	6	1								
	Spinal	1	5	2								
	Caudal		2	6								
	Ventral		2	6								
	Femoral		1	7								
Emergence of feathers from skin	Primaries			2	6							
	Secondaries				6	2						
	Greater secondary coverts				3	4						
	Rectrices				1	2	2					
	Greater primary coverts				3	5						
	Median secondary coverts					1	3	3				
	Humeral						2	4				
	Uppertail coverts						4	1				
	Spinal						2	5				
	Capital							6				
	Ventral							6				
	Femoral							4	2			
	Throat							2	3			
	Crural								4	1		
	Median primary coverts.								3	1	1	
Eruption of feather from sheath	Primaries								3	2		
	Secondaries								3	2		
	Greater secondary coverts								2	3		
	Greater primary coverts								2	3		
	Median secondary coverts									3	2	
	Humeral									3	2	
	Uppertail coverts									3	2	
	Spinal									3	2	
	Ventral									2	3	
	Rectrices									2	2	1
	Femoral										5	
	Capital										2	3
	Crural										2	3
	Median primary coverts										1	4
	Throat											5
No. nestlings		8	8	8	8	7	7	7	5	5	5	5

Table 5

Parameters of logistic growth curves fitted to pooled data for juvenile male (*n* = 13) and female (*n* = 11) Hall's Babblers. Growth curves take the form $Y = A/(1 + e^{-K(t-i)})$ where Y = trait, A = asymptotic size, K = growth rate, t = age in days, and i = age when maximum growth rate is reached. Results of ANOVA are presented.

Trait	Sex	*A*	*n*	*K*	*i*	*F*	*df*	*P*	r^2
Body mass	♂	40.5	52	0.091	3.1	104.44	2, 48	<0.001	0.813
	♀	37.7	44	0.053	-6.9	115.05	2, 41	<0.001	0.841
Culmen	♂	25.4	42	0.048	10.1	768.96	2, 39	<0.001	0.975
	♀	23.7	36	0.043	8.4	679.79	2, 33	<0.001	0.976
Head-bill	♂	47.9	46	0.059	1.9	1863.67	2, 43	<0.001	0.989
	♀	46.0	37	0.051	-1.9	870.17	2, 34	<0.001	0.981
Wing	♂	84.1	17	0.156	11.0	387.44	2, 14	<0.001	0.982
	♀	79.5	24	0.182	10.6	1678.81	2, 21	<0.001	0.994
Tail	♂	83.0	17	0.206	17.9	773.87	2, 14	<0.001	0.991
	♀	79.9	24	0.228	16.9	924.28	2, 21	<0.001	0.989

Table 6

Wing and tail lengths (mean ± s.e.) of juvenile, second basic and adult plumages of Hall's Babbler. Results of Mann-Whitney U-tests comparing juvenile and adult plumages are presented in the last two columns; sample sizes for second basic plumage were insufficient for statistical analyses.

Trait	Sex	Juvenile[a]	Second basic[b]	Adult[c]	*U*	*P*
Wing length	♂	82.8 ± 0.51	85.8 ± 0.49	86.0 ± 0.16	152.00	<0.001
	♀	80.4 ± 0.38	84.4 ± 0.68	84.3 ± 0.21	79.50	<0.001
Tail length	♂	84.8 ± 0.70	87.1 ± 0.90	88.0 ± 0.26	299.50	<0.001
	♀	83.1 ± 0.64	84.8 ± 1.24	85.6 ± 0.20	264.00	<0.001

[a] ***n*** = 17 males; ***n*** = 19 females; [b] ***n*** = 8 males; ***n*** = 9 females; [c] ***n*** = 86 males; ***n*** = 68 females

patterns of morphological traits, and an equation predicting age from tail length. Each method predicted changes in morphology and growth to within one day for 22 additional nestlings; thus the ageing methods can be used to accurately estimate nestling age. Skeletal and feather growth and developmental sequence and timing were consistent among most Hall's Babbler nestlings. The exception was skeletal and feather growth of the younger nestling in poor body condition, but importantly, other developmental changes in external morphology of this nestling were unaffected (see images in Portelli 2012). Body mass is the most common measurement taken on nestling passerines (Jongsomjit *et al*. 2007), and has been used to estimate the age of nestling Grey-crowned Babblers to the nearest day (Dow and Gill 1984b). However, the reliability of body mass as an age estimator may vary with environmental conditions, which influences patterns of body mass gain in nestling passerines (Boag 1987; Lepczyk and Karasov 2000). This was evident in Hall's Babbler where body mass gain in the two nestlings in poor body condition deviated considerably from other nestlings. Growth rates of linear measurements of body size are generally less sensitive to environmental conditions (Lepczyk and Karasov 2000; Jongsomjit *et al*. 2007); hence they are more reliable estimators of nestling age (Murphy 1981). Skeletal and feather measurements (Fig. 1) and/or external morphology (Table 4; Fig. 2) are therefore recommended for estimating nestling age of Hall's Babbler. Tarsus and head-bill lengths are the most reliable age estimators up to 7–10 days post-hatching, while wing and tail lengths are the best estimators from 5–7 days post-hatching onward. The age of fledglings can be estimated using the equation predicting age from tail length, since tail feathers grows linearly up until growth ceases at approximately five weeks of age. However, this method is only suitable for healthy fledglings as demonstrated by the stunted growth of the younger nestling in poor body condition.

Juvenile growth and development of passerines has rarely been studied in great detail. The age when juvenile Hall's Babblers reached asymptotic body mass varied, but was generally at 2–3 months old. Immediately before fledging, wing length was about three-quarters complete and tail length was about half-grown, but both completed growth at about five weeks post-fledging. Wing and tail lengths of juveniles were significantly shorter, by 3–5 percent, than those of adults. Juveniles attained their second basic plumage at 10–11 months old, at which time wing and tail lengths were similar to those of adults. Similarly, wing and tail lengths of juvenile Grey-crowned Babblers (7–19 weeks old; $n = 6$ males, $n = 5$ females) are 4–6 percent shorter than adults (C. Blackmore unpubl. data). Culmen and head-bill lengths were the last traits to reach adult size, at c.16–17 weeks old. The most conspicuous characteristic of juvenile Hall's Babblers was the bright yellow rictus and rictal flange, which remained visible in the field for at least two months post-fledging. This pigmentation disappeared by eight months old, later than the 4–6 months reported for White-browed Babbler (Cale 1999), but earlier than the c.12 months for Grey-crowned Babbler (Brown 1979). Iris colour in Grey-crowned Babblers gradually changes over three to four years from dark brown in juveniles to pale yellow in adults (Counsilman and King 1977). In contrast, iris colour in juvenile Hall's Babblers only differed from adults during the nestling period, and began to lighten soon after fledging. This is also the case in Chestnut-crowned Babblers (pers. obs.). The juvenile plumage of Hall's Babbler lacks any conspicuous differences to subsequent plumages (pers. obs.), unlike Grey-crowned and Chestnut-crowned Babblers (Counsilman and King 1977; Higgins and Peter 2002). Some juveniles had pale brown edges at the tip of the larger alula feathers that contrasted with a darker shaft streak, which was not seen in adults, but these feathers are typically moulted in the post-juvenile moult. Consequently, juveniles are indistinguishable from adults before they reach one year old; though some juveniles retain their innermost 1–2 primaries through their post-juvenile moult, which has not been observed in adults.

Life-history strategies of passerines from temperate regions of the northern hemisphere differ from passerines of temperate regions of the southern hemisphere and tropical regions (Martin 2004). These differences include a smaller clutch size, more clutches per year, longer incubation, nestling and post-fledging periods, and higher survival rates in southern hemisphere and tropical species (Yom-Tov 1987; Rowley and Russell 1991; Martin 1996, 2004). Nestling growth rate, development, and fledging size are additional fundamental components of life-history strategies in passerines, but relatively little is known about biogeographical variation in these traits. Ricklefs (1968) found mean nestling growth rates of tropical passerines were generally slower than northern temperate species, but he did not include data for southern hemisphere passerines. Some authors have attempted to examine biogeographical variation in growth rates by using nestling period duration as a proxy for growth rate (Woinarski 1985; Bosque and Bosque 1995; Martin 2004), but the former can change independently of growth rate (O'Connor 1984). Brown (1979) and Dow and Gill (1984a) concluded Grey-crowned Babblers had a slower nestling growth rate and an unusually low ratio of fledging to adult body mass than northern hemisphere passerines. However, their analyses included northern hemisphere species that varied widely in body mass (8–100g adult body mass, Brown 1979; 40–100g asymptotic nestling body mass, Dow and Gill 1984a). Ricklefs (1968) and Remes and Martin (2002) collectively published growth rates for 15 northern hemisphere passerines from eight families that are of a similar body mass to Hall's Babbler (36–48g; see Portelli 2014), and seven species from five families with a similar body mass to the Grey-crowned Babbler (68–84g; see Counsilman and King 1977). The mean nestling growth rates of these similarly sized northern hemisphere passerines were faster than both babbler species: 0.476 (range 0.358–0.598) c.f. 0.385 in Hall's Babbler, and 0.435 (range 0.302–0.546) c.f. 0.349 in the Grey-crowned Babbler (Dow and Gill 1984a). Moreover, for each babbler species, only one similarly sized northern hemisphere passerine had a slower growth rate: Black-headed Grosbeak *Pheucticus melanocephalus* (45g; 0.358), and Florida Scrub-jay *Aphelocoma coreulescens* (83g; 0.302) respectively. In contrast, the mean ratio of fledging body mass to adult body mass (R) was similar: 0.77 (range 0.61–1.01) c.f. 0.80 in Hall's Babbler, and 0.73 (range 0.53–1.00) c.f. 0.71 in Grey-crowned Babbler (Dow and Gill 1984a). Thus, growth rate is lower for the two babbler species, as concluded by Brown (1979) and Dow and Gill (1984a), but the mean ratio of fledging both mass to adult body mass is similar (*contra* Brown 1979; Dow and Gill 1984a). This study suggests that nestling growth rates of passerines of the southern hemisphere may, like other life-history traits, differ from those of passerines from temperate regions of the northern hemisphere. However, since nestling growth has been studied in few southern hemisphere passerines, particularly Australian species, the available data are currently inadequate to test this hypothesis.

ACKNOWLEDGEMENTS

I am grateful to Ian and Julie McLaren for allowing access to their property and providing logistical support. Patrick Banville, Bob Inglis, Oliver Robertson, and Bob and Jean Wallace assisted with the capture of babblers. Caroline Blackmore generously provided unpublished data for Grey-crowned Babblers. Richard Kingsford, Eleanor Russell and Caragh Threlfall provided constructive feedback on this manuscript. This research was funded by the Australian Bird Study Association, Hermon Slade Foundation and Birds Queensland. The capture, banding, blood sampling and measurement of babblers was undertaken with approval from the Queensland Environment Protection Agency (licence number WISP03698306), the Australian Bird and Bat Banding Scheme (authority number 2435), and the Animal Care and Ethics Committee of the University of New South Wales (approvals 0632B and 0719B).

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