

**Sexual size dimorphism and geographic variation in body size
in a group-living, insectivorous passerine: Hall's Babbler
*Pomatostomus halli***

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Sexual size dimorphism in birds is widely used by ornithologists to identify the sex of individuals using linear discriminant analysis of morphological measurements. The feasibility of using this approach for the sexually monochromatic Hall's Babbler *Pomatostomus halli* using 154 genetically-sexed individuals from a single population was investigated. In addition, geographic variation in size was examined using morphological measurements of museum specimens because this can reduce the accuracy of discriminant equations when applied to additional populations. Hall's Babbler exhibited clear sexual size dimorphism with males being 2–7 per cent larger than females in culmen, head-bill, wing, tail and tarsus lengths and body mass. The best performing discriminant equation, which used wing and head-bill lengths, correctly identified the sex of 88 per cent of individuals. Geographic variation in body size of Hall's Babbler was not evident for any morphological trait; therefore, the accuracy of discriminant equations may be similar across populations. Like two of its congeners, sexual size dimorphism was proportionally greatest in culmen length. Such disproportionate dimorphism may be adaptive in reducing intersexual overlap in resource use, since babblers rely heavily on their bill to probe substrates. However, data on intersexual foraging differences in babblers are currently lacking to test this hypothesis.

INTRODUCTION

Sexual dimorphism in body size is widespread among birds, but occurs to varying degrees in different species, including among closely related taxa (Amadon 1959; Selander 1966; Szekely *et al.* 2007). Three main hypotheses have been proposed to explain sexual size dimorphism in birds (Hedrick and Temeles 1989): (1) sexual selection (Selander 1972), where larger size in one sex is adaptive in intrasexual competition; (2) intersexual resource competition (Selander 1966), where it is adaptive in reducing intersexual overlap in resource use; and (3) reproductive role division (Ralls 1976), where size differences are adaptive because of the different roles of the sexes in reproduction. Sexual size dimorphism is commonly accompanied by differences in plumage colouration and/or pattern (sexual dichromatism), which permit ready identification of the sex of mature individuals. However, sexual dimorphism and sexual dichromatism are subject to different selection pressures (Owens and Hartley 1998). As a result, there are many species that are sexually dimorphic but sexually monochromatic. The lack of obvious sexual dichromatism in these species hinders the identification of the sex of individuals in field studies, yet knowledge of the sex of individuals is crucial to understanding population demography and dynamics, ecology and behaviour (Hughes 1998).

The sex of individual birds can be determined using surgical and DNA-based techniques, but such methods are invasive, time-consuming, and require considerable expertise. Sexual size dimorphism has permitted an alternative, whereby discriminant equations using morphological measurements are derived from linear discriminant analysis of individuals of known sex. These equations can then be used to identify the sex of new individuals with an estimated probability of correct identification. This technique has been used successfully with a wide range of avian taxa, including petrels (e.g. Van Franeker and Ter Braak 1993; Lo Valvo 2001), penguins (e.g. Renner *et al.* 1998; Bertellotti *et al.* 2002), gulls and terns (e.g. Hanners and Patton 1985; Ackerman *et al.* 2008), shorebirds (e.g. Skeel 1982; McCloskey and Thompson 2000), cormorants (e.g. Malacalaza and Hall 1988), birds of prey (e.g. Hayward and Hayward 1991; Balbontin *et al.* 2001), and passerines (Counsilman *et al.* 1994; Bain 2007; Hermosell *et al.* 2007). The utility and accuracy of a discriminant equation derived from one population can be considerably lower when applied to additional populations in species where body size varies geographically (Winker *et al.* 1994; Phillips and Furness 1997); yet few studies investigate geographic variation in body size when deriving discriminant equations.

The Australo-Papuan babblers (Pomatostomidae) are sexually monochromatic passerines, endemic to the Australo-

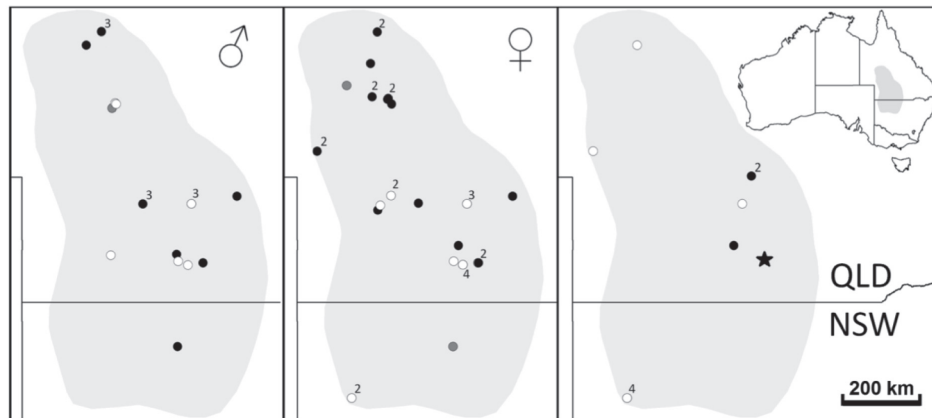


Figure 1. Collection localities of Hall's Babbler museum specimens: adult males (left; $n = 20$), adult females (middle; $n = 31$) and unknown sex (right; $n = 10$). Circles represent specimens with morphometric measurements (grey), body mass data (white), or both (black). Numbers indicate sample size for locations with multiple individuals. The location of Bowra Sanctuary, where live individuals were measured, is shown as a black star in the right panel. Shaded area represents the approximate geographic range of Hall's babbler. QLD = Queensland; NSW = New South Wales.

Papuan region, which breed cooperatively in kin-structured groups (Higgins and Peter 2002). Sex identification is critical to understanding population dynamics and the roles of males and females in such complex societies. Grey-crowned *Pomatostomus temporalis* and White-browed *P. superciliosus* Babblers exhibit sexual size dimorphism in most morphological traits, allowing for successful sex identification using linear discriminant analysis (Counsilman and King 1977; Cale 1999; Oppenheimer *et al.* 2007). In contrast, linear discriminant analysis is unreliable for sex identification of Chestnut-crowned Babblers *P. ruficeps* (Dessmann 2006) which exhibit less pronounced sexual size dimorphism than the former species. Geographic variation in body size occurs in Grey-crowned and White-browed Babblers (Ford 1971; Wooller and Richardson 1986; Higgins and Peter 2002). As a result, a discriminant equation derived from populations of White-browed Babblers in New South Wales performed poorly in identifying the sex of individuals from Victorian and Western Australian populations (Oppenheimer *et al.* 2007). Sex identification using linear discriminant analysis has yet to be examined in the remaining Australian species: Hall's Babbler *P. halli*. Few morphological data exist for this species; nevertheless, measurements of five morphological traits from a small sample of museum specimens (11 adult males, 10 adult females) suggest the species is sexually size dimorphic (Higgins and Peter 2002). The aims of this study were to: (1) investigate sexual size dimorphism in Hall's Babbler; (2) assess the feasibility of using morphological measurements to identify sex using linear discriminant analysis; and (3) examine whether Hall's Babbler exhibits geographic variation in body size.

METHODS

Morphometrics of live birds

Hall's Babblers (154 adults) were captured within a 44 square kilometres area ($27^{\circ} 58.8'S$, $145^{\circ} 32.5'E$) on Bowra Sanctuary, in south-western Queensland (Fig. 1), between July 2006 and April 2009 in the months of February, April and July–November. Babblers were caught using standard four-shelf

mist-nets (12 m or 18 m long, mesh size 31 mm or 38 mm) and banded with an individually-numbered stainless steel metal band supplied by the Australian Bird and Bat Banding Scheme (ABBBS). Body mass was measured to the nearest gram using a 100-gram Pesola spring scale. Combined head and bill length (hereafter head-bill length; tip of the upper mandible to the occipital condyle at the rear of the head), exposed culmen length (tip of the upper mandible to the edge of the skin covering the rhamphotheca at the front of the skull), and tarsometatarsus length (hereafter 'tarsus' length; proximal end of the right tarsometatarsus to the leading edge of the folded digits), were measured with dial callipers to the nearest 0.1 millimetres. Tail length was measured to the nearest millimetre with the tail flattened along a stainless steel rule inserted between the rectrices and undertail coverts and gently slid up to the base of the rectrices. Wing length was measured using a stopped rule to the nearest millimetre as the distance on the closed right wing from the foremost extremity of the carpus to the tip of the longest primary remix, with the wing held close to the body, straightened and flattened along its length. While these methods are commonly used among ornithologists (Gosler 2004), these details are described here to minimise error in sex identification of Hall's Babblers by ornithologists wishing to apply the discriminant equations developed in this study. The repeatability (as per Lessells and Boag 1987) of culmen, head-bill, wing, tail and tarsus lengths was calculated using measurements from 77 individuals (46 males, 29 females), measured on two to four occasions (median = 3) over a mean period of 419 days (range 51 – 639). Repeatability of body mass was calculated using 89 individuals (53 males, 36 females), weighed between two and eight times (median = 4) over a mean period of 606 days (range 7 – 1011). In all other analyses of morphometric data, only the most recent measurements of an individual measured on multiple occasions were used.

Sex identification of live birds

Blood (<50 μ L) was collected from each individual by venipuncture of the brachial vein using a 26-gauge syringe needle and stored in 100 per cent ethanol. DNA was extracted

from clotted blood (~1mm³) using an ammonium acetate method as described by Nicholls *et al.* (2000), except the concentration of proteinase K was doubled to speed digestion of the clot. DNA was rehydrated in 100–300 µL low EDTA TE buffer and quantified using a Nannodrop. The sex of each individual was determined by PCR amplification of the chromo-helicase DNA-binding gene on the sex chromosomes of birds, following the standard methodology of Griffiths *et al.* (1998). Specifically, the PCR was conducted using a Qiagen® multiplex PCR kit at one-fifth the recommended volume, with 0.25 µM of primers P2 and P8 (Griffiths *et al.* 1998) and 15–40 ng of template DNA. Cycling conditions followed Griffiths *et al.* (1998), but a longer initial denaturing step of 90s was used and an annealing temperature of 48°C. Fragment size analysis of PCR products was conducted on a 48-Capillary 3730 DNA Analyser (Applied Biosystems®) and scored using GeneMapper® version 3.7.

Analyses of sexual dimorphism

The relative magnitude of sexual size dimorphism was calculated for each trait as the difference between the means of male and female measurements relative to the mean value for males (Selander 1966). Differences between the sexes were tested for each morphological trait using Student's t-tests; however, tail length did not satisfy the assumption of normal distribution of residuals (Kolmogorov-Smirnov test) so a Mann-Whitney U-test was used, and body mass did not meet the assumption of homoskedasticity (Levene's test) so a Student's t-test assuming unequal variances was performed.

Linear discriminant analyses (LDA) were used to distinguish between the sexes using morphometrics. Two traits were omitted from these analyses: body mass and tail length. Body mass is generally a poor measure of body size as it typically has higher variance relative to other traits (Rising and Somers 1989; also see results), particularly in reproductively active females (e.g. White-browed Babbler; Oppenheimer 2005). Tail length was excluded as it was only moderately repeatable within an individual (see results). Although wing length was not normally distributed, it was suitable for LDA since the non-normality was due to skewness rather than outliers (see Tabachnick and Fidell 2001). Six LDA were performed to compare the utility of the different traits for sex identification and to determine the best combination of traits: one for each trait, all traits together, and a stepwise procedure using all traits (using Wilk's lambda selection method). Leave-one-out cross-validation was used to assess the accuracy of each discriminant equation in correctly classifying the sex of individuals in the sample. All LDA met the assumption of equality of covariance matrices. Where appropriate, probability contour lines were calculated for bivariate plots using equations presented in Winker *et al.* (1994), which provide a more accurate estimate of probability than those developed by Green and Theobald (1989).

Morphometrics of museum specimens

To examine geographic variation in body size, culmen, wing, tail and tarsus lengths of adult Hall's Babbler museum study skins were measured (10 male, 16 female, three unknown) – these came from collections held by the Australian Museum (AM), Queensland Museum (QM) and Australian National Wildlife Collection (ANWC, Canberra). Only two specimens

were from New South Wales, with the remainder collected across the geographic range of the species in Queensland (Fig. 1). Unlike the other traits, tarsus length had to be measured differently to live birds due to the inflexibility of study skins; measurement was from the 'notch' at the intertarsal joint to the most distal unsegmented scute on the dorsal surface of the tarsus. Head-bill length could not be measured because the rear portion of the skull is routinely removed during the preparation of skins (Proctor and Lynch 1993).

Body mass data were available for 58 specimens (19 male, 29 female, 10 unknown). These included 25 of the measured specimens (nine male, 13 female, three unknown), eight adult specimens (three male, four female, one unknown) from the ANWC, Western Australian Museum (WAM), South Australian Museum, and Zoological Museum (Berlin, Germany) that were not measured, 19 specimens (seven male, 10 female, two unknown) preserved as skeletons or stored in alcohol from the AM, ANWC, QM and WAM, and six live adult birds (two female, four unknown) captured at Mutawintji National Park in NSW (data from the Australian Bird and Bat Banding Scheme).

Student's t-tests were used to test for differences between the sexes of museum specimens in each morphological trait. All traits met the assumptions of normality of residuals and homoskedasticity. Ordinary least squares regression analyses were used to investigate geographic variation in each morphological trait. Three analyses were performed for each trait with either latitude or longitude as the independent variable: males and females were analysed separately, and in the third analysis all specimens were pooled to increase sample size. Residual plots did not suggest any non-linear relationships or non-constant error variance, and residuals were normally distributed. All statistical analyses were performed using SPSS® version 20.

RESULTS

Eighty-six male and 68 female Hall's Babbler were captured at Bowra Sanctuary. Males were significantly larger than females in all morphological measurements, though there was considerable overlap between the sexes in all traits (Table 1). The magnitude of sexual size dimorphism varied among morphological traits from 1.97 per cent to 6.86 per cent; culmen length exhibited the greatest degree of dimorphism being approximately 2–3 times greater than other traits (excluding head-bill length).

Repeatability was highest for culmen (0.81), head-bill (0.93), wing (0.76) and tarsus (0.98) lengths, indicating that there is little temporal variation within an individual for these traits. Tail length (0.61) and body mass (0.68) were only moderately repeatable. Body mass showed the greatest variation among individuals (Table 1).

Results of LDA on each of the four traits considered separately showed that culmen and head-bill lengths distinguished between the sexes equally well, and were considerably better than the remaining two traits (Table 2). The discriminant equation that included all traits performed better, correctly identifying the sex for a further 4.6 per cent of individuals. The stepwise analysis selected only two traits for inclusion in the discriminant equation: head-bill and wing lengths. This discriminant equation had the highest accuracy

Table 1

Mean ± s.e. (range) of morphological traits and sexual size dimorphism (SSD) of live Hall's Babblers (n = 86 males, 68 females) captured at Bowra Sanctuary. Results of statistical tests of differences between sexes are shown. SSD is expressed as the difference between means for males and females as a percentage of the mean value for males. CV = coefficient of variation.

Trait	Male	CV (%)	Female	CV (%)	Test statistic	P	SSD (%)
Culmen length (mm)	25.1 ± 0.11 (22.9 - 27.6)	4.02	23.4 ± 0.10 (21.7 - 26.1)	3.60	10.01 ^a	<0.001	6.77
Head-bill length (mm)	48.0 ± 0.11 (45.4 - 50.6)	2.18	45.7 ± 0.12 (43.7 - 48.0)	2.17	11.87 ^a	<0.001	4.79
Wing length (mm)	86.0 ± 0.16 (82 - 90)	1.76	84.3 ± 0.21 (79 - 88)	2.01	6.46 ^a	<0.001	1.98
Tail length (mm)	88.0 ± 0.26 (82 - 92)	2.79	85.6 ± 0.20 (80 - 91)	2.70	3986.50 ^b	<0.001	2.72
Tarsus length (mm)	27.7 ± 0.09 (25.6 - 29.4)	2.91	26.8 ± 0.10 (25.0 - 28.5)	3.16	6.39 ^a	<0.001	3.25
Body mass (g)	40.9 ± 0.22 ^c (35 - 47)	4.88	39.5 ± 0.33 (33 - 46)	6.95	3.45 ^d	0.001	3.42

^a student's t-test (df = 152)

^b Mann-Whitney U-test

^c sample size n = 84

^d student's t-test assuming unequal variances (df = 119).

Table 2

Results of linear discriminant analyses distinguishing live male and female Hall's Babblers. D = discriminant score. D^{0.5} = discriminant score where probability of being male is 0.5; where D > D^{0.5} individuals are classified as male, where D < D^{0.5} individuals are classified as female. r = canonical correlation coefficient. % = percent of individuals correctly classified using leave-one-out cross-validation. P < 0.001 for all models.

Model	Discriminant equation	D _{0.5}	r	Wilks λ	%
Culmen length (CL)	D = 1.065*CL - 25.914	-0.107	0.65	0.54	83.1
Head-bill length (HB)	D = 0.978*HB - 45.922	-0.123	0.73	0.47	83.1
Wing length (WL)	D = 0.626*WL - 53.372	-0.06	0.47	0.78	66.9
Tarsus length (TA)	D = 1.215*TA - 33.114	-0.065	0.49	0.77	66.2
All	D = 0.258*CL + 0.629*HB + 0.180*WL + 0.123*TA - 54.459	-0.13	0.74	0.46	87.7
Stepwise	D = 0.877*HB + 0.182*WL - 56.693	-0.128	0.74	0.47	88.3

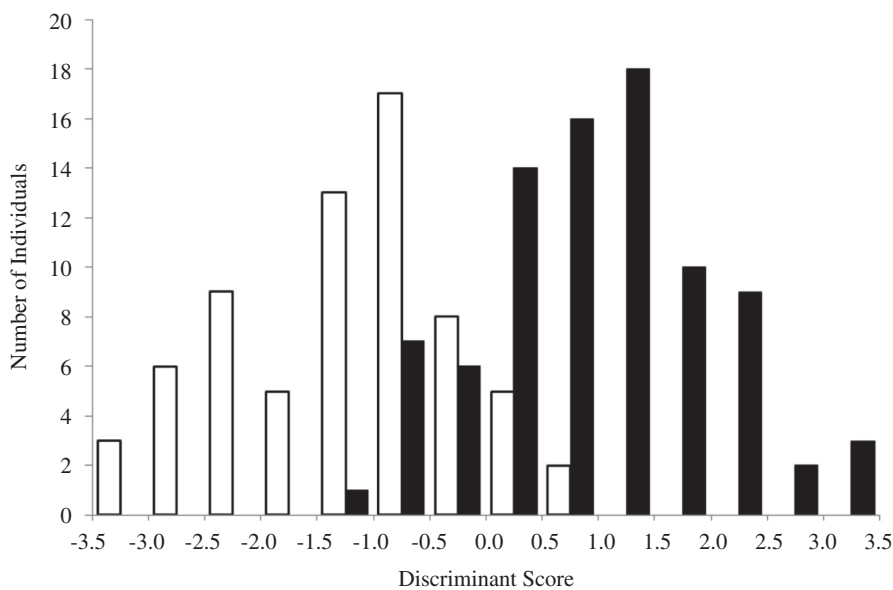


Figure 2. Frequency histogram of the discriminant scores from the stepwise model (see Table 2) for males (solid columns) and females (open columns).

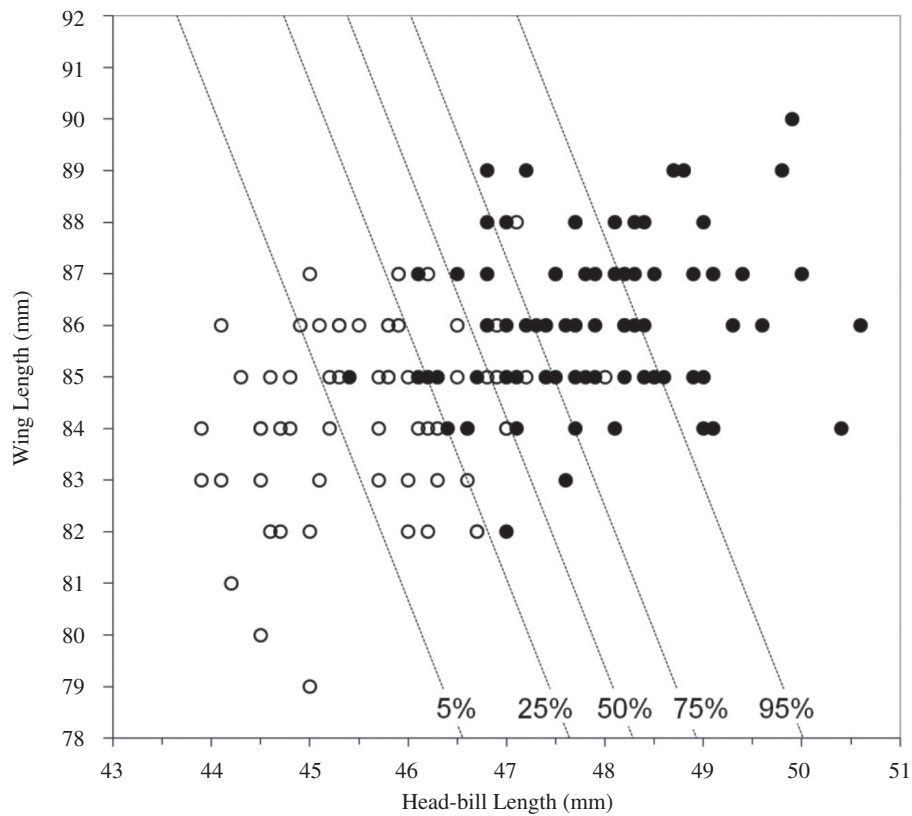


Figure 3. Sexual dimorphism in head-bill and wing lengths in Hall's Babbler. Males are shown as solid black circles, females as open circles. Probability contour lines represent the probability of an individual being male, expressed as a percentage.

(88.3%) of all models. Discriminant scores for each sex in the stepwise equation overlapped between -1.0 and 1.0 (Fig. 2). The separation between the sexes using head-bill and wing lengths is shown as a scatterplot in Fig. 3, with contour lines representing the estimated probability of an individual being male. The classification accuracy of discriminant equations did not differ appreciably between males and females (e.g. 88.2% of females and 88.4% of males correctly classified using the stepwise analysis), except for the discriminant equation using only wing length, where 76.5 per cent of females compared with 59.3 per cent of males were correctly classified.

Morphometric data from museum specimens also indicated males were larger than females, with the exception of body mass (Table 3). Differences were only significant for culmen and wing lengths, but observed statistical power of all tests were low (0.13–0.39) owing to the small sample sizes. Ranges in values were notably similar to ranges for live birds (Table 2). No significant relationships between latitude or longitude and morphological traits were evident, irrespective of whether sexes were analysed separately or all individuals pooled (Table 4). Sample sizes and consequently statistical power were low, so these analyses may have been unable to detect statistically significant relationships between body size and latitude or longitude if they existed; however, any trends in the data were weak and inconsistent in direction (i.e. positive or negative) among traits and/or between the sexes.

DISCUSSION

Sexual size dimorphism and sex identification

Hall's Babbler exhibits the predominant pattern of sexual size dimorphism seen in birds (Amadon 1959; Szekely *et al.* 2007): males are significantly larger than females in all morphological traits examined. Although the degree of sexual size dimorphism was small, it was sufficient to permit identification of the sex of individual Hall's Babblers with moderately high accuracy (88%) using the discriminant equation derived from head-bill and wing lengths. Sex can be identified in one of two ways: the discriminant score (D) for an individual can be calculated using the equations in Table 2, or sex can be identified using head-bill and wing lengths in consultation with Fig. 3. The advantage of the latter method is that it can facilitate field studies of social behaviour and behavioural ecology, since it is quick, can be done while the bird is being held, and provides an indication of the probability of correct sex identification. For example, marking methods can be tailored for each sex. A more precise estimate of the probability of correct sex identification can be obtained by using the equations derived by Winker *et al.* (1994; equations 9 and 10): p_m (probability of being male) = $(1 + e^q) - 1$, where $q = -D * [1 + |\ln(1.265^4)|] - [r * \ln(1.265)]$.

Discriminant equations that include wing or tail lengths are inappropriate for birds in juvenile plumage (identifiable by yellow pigmentation on the rictus), since both are significantly

Table 3

Mean \pm s.e. (range) of morphological traits and relative sexual size dimorphism (SSD) of Hall's Babbler museum specimens. SSD is expressed as the difference between means for males and females as a percentage of the mean value for males. CV = coefficient of variation.

Trait	Male	CV (%)	Female	CV (%)	t	P	SSD (%)
Culmen length (mm) ^a	24.5 \pm 0.44 (21.4 – 26.1)	5.66	23.2 \pm 0.19 (21.7 – 24.7)	3.36	3.23	0.004	5.57
Wing length (mm) ^a	85.1 \pm 0.72 (80 – 87)	2.68	82.9 \pm 0.68 (77 – 87)	3.26	2.16	0.041	2.61
Tail length (mm) ^a	85.0 \pm 0.87 (81 – 89)	3.23	83.8 \pm 0.96 (77 – 91)	4.57	0.85	0.404	1.4
Tarsus length (mm) ^a	27.4 \pm 0.32 (26.4 – 29.9)	3.68	26.7 \pm 0.25 (24.9 – 28.5)	3.71	1.74	0.095	2.55
Body mass (g) ^b	39.7 \pm 0.80 (31 – 47)	8.82	40.8 \pm 0.64 (33 – 47)	8.25	1.07	0.29	-2.74

Sample sizes: a 10 male, 16 female; b 19 male, 28 female

Table 4

Results of linear regression analyses investigating geographic variation in morphological traits of Hall's Babbler museum specimens..

Sex	Trait	Latitude			Longitude		
		r	F	P	r	F	P
Male	Culmen length ^a	0.07	0.15	0.709	0.22	0.31	0.594
	Wing length ^a	-0.18	0.35	0.568	0.31	0.22	0.651
	Tail length ^a	-0.41	1.41	0.268	0.45	0.32	0.588
	Tarsus length ^a	0.18	2.22	0.174	-0.45	3.14	0.115
	Body mass ^b	-0.12	0.10	0.756	0.29	0.13	0.725
Female	Culmen length ^c	0.08	0.73	0.409	-0.06	0.17	0.690
	Wing length ^c	0.42	1.71	0.212	-0.17	1.78	0.203
	Tail length ^c	-0.18	0.13	0.720	-0.13	0.03	0.863
	Tarsus length ^c	-0.05	0.16	0.700	-0.07	0.18	0.737
	Body mass ^d	-0.52	3.56	0.070	0.47	0.90	0.353
All	Culmen length ^d	0.08	0.58	0.453	<0.00	<0.00	0.995
	Wing length ^d	0.12	0.20	0.600	-0.21	0.29	0.593
	Tail length ^d	-0.30	1.11	0.302	0.11	0.05	0.817
	Tarsus length ^d	0.07	0.36	0.551	-0.25	1.83	0.187
	Body mass ^e	-0.21	1.42	0.238	0.08	0.06	0.812

Sample sizes: ^a10; ^b19; ^c16; ^d29; ^e58

shorter than those of subsequent plumages (unpubl. data); alternative equations (Table 2) may be appropriate provided skeletal growth is complete. Sex identification using linear discriminant analysis is biased toward individuals at the extremes of the range in body size, with intermediate birds having lower probabilities of correct sex assignment. I recommend genetic methods or behavioural observations be used to identify the sex of such individuals. Since inter-observer differences in measuring birds can increase error in sex identification (Hedd *et al.* 1998), it is imperative field workers closely replicate the measurement techniques used here when applying discriminant equations to Hall's Babblers.

Geographic variation in body size

Geographic variation in size can reduce the accuracy of sex identification using a discriminant equation in populations other than that used to derive the equation (Evans *et al.* 1993; Winker *et al.* 1994; Weidinger and van Franeker 1998; Oppenheimer *et al.* 2007). No indication of geographic size variation was

found in Hall's Babbler museum specimens collected across the geographic range of the species. Although the sample size of specimens was small, and thus may have been insufficient to detect statistically significant relationships between size and latitude or longitude, there was no consistency in trends between the sexes or among traits. Furthermore, the size of male and female museum specimens (Table 3) collected throughout the geographic range of Hall's Babbler largely fell within the range of respective values obtained from live birds from a single population (Table 1). Only wing and tail lengths were appreciably different, but this was probably due to inconsistency in measurements obtained from live birds compared with dried museum skins (Winker 1993). Insufficient specimens have been collected, particularly from the southern third of the geographic range (Fig. 1), to confidently conclude there is no appreciable variation in body size. Nevertheless, the data collected in this study suggest any variation is likely to be relatively minor and the accuracy of discriminant equations may be similar across populations.

Table 5

Sexual size dimorphism in Australo-Papuan babblers. The relative magnitude of sexual size dimorphism is expressed as the difference between male and female means as a percentage of male mean. *denotes differences between sexes statistically significant at $\alpha = 0.05$.

Species	Culmen length	Head-bill length	Wing length	Tail length	Tarsus length	Body Mass
Hall's Babbler	6.9*	4.5*	2.0*	2.3*	3.3*	3.6*
Grey-crowned Babbler (QLD) ^a	13.2*		2.7*	1.9	1.7*	3.0*
Grey-crowned Babbler (NSW) ^b	9.4*	5.3*	1.9*	1.9	2.3*	1.8
White-browed Babbler (NSW) ^c	6.2*		3.0*		2.6*	1.8*
White-browed Babbler (VIC) ^d	6.9*	4.9*	2.6*	1.5	4.0	4.2*
White-browed Babbler (WA) ^e		4.7*	2.4*			5.4*
Chestnut-crowned Babbler ^f		1.5*	0.4		0.8	-0.3

Data sources: ^a Councilman and King (1977; oldest age category); ^b Caroline Blackmore (unpubl. data; individuals three years or older, n = 57–91), ^c Oppenheimer et al. (2007); ^d Taylor (2003); ^e Cale (1999); ^f Dessmann (2006).

In marked contrast to Hall's Babbler, there is a strong positive relationship between body size and latitude in the White-browed Babbler over a similar latitudinal gradient in southwestern Western Australia: southern-most birds are 43 per cent heavier than the northern-most (Wooller and Richardson 1986). This cline was attributed to a gradient in potential evapotranspiration (~660 mm to ~1150 mm), which was a better predictor of size than latitude (Wooller and Richardson 1986). Similar relationships involving temperature and/or humidity have been noted in other passerines (James 1970; Niles 1973; Wooller et al. 1985; Jones et al. 2005) and are thought to reflect the relationship between heat balance and volume to surface-area ratio (James 1970; Jones et al. 2005). The small range in potential evapotranspiration across the geographic range of Hall's Babbler (1053mm at White Cliffs to 1353mm at Winton; Mather 1963) and the apparent lack of, or relatively minor, geographic size variation in the species is consistent with this hypothesis.

Sexual size dimorphism in Australo-Papuan babblers

The relative magnitude of sexual size dimorphism varies among the four Australo-Papuan babblers (Table 5). Hall's, White-browed and Grey-crowned Babblers are dimorphic in almost all traits, and generally to similar extents (except culmen length, see below). In contrast, the Chestnut-crowned Babbler is only weakly dimorphic. Males are larger than females in all dimorphic traits, but the degree of sexual size dimorphism is relatively small for all species. This is unsurprising since the magnitude of dimorphism is typically greater in polygamous bird species than in monogamous or cooperatively-breeding species such as babblers (Owens and Hartley 1998; Dunn et al. 2001). Sexual selection acting on male-male competition has been proposed as an explanation for this general pattern of larger males in birds (Selander 1972), but it does not adequately explain sexual size dimorphism in non-polygamous species. An alternative, but not mutually exclusive, explanation is the reproductive advantage of smaller size for females (Price 1984; Monaghan and Metcalfe 1986). In species that accumulate resources for egg production immediately before breeding, smaller females can accumulate resources faster, and replenish them sooner between breeding attempts (Downhower 1976). Such an explanation appears likely for babblers since they are multi-brooded (Brown et al. 1982; Cale 1999) and presumably accumulate resources for egg production immediately before each breeding attempt.

Sexual size dimorphism in babblers also varies in extent among traits, which is common among birds (Szekely et al. 2007). Culmen length exhibits the greatest degree of dimorphism in Hall's, Grey-crowned and White-browed Babblers (culmen length was not measured in the Chestnut-crowned Babbler), being three to eight times greater than other traits (Table 5). Babblers are insectivorous and forage predominantly by probing and gleaning substrates (Balda and Brown 1977; Councilman 1980; Taylor 2003; Portelli et al. 2009). Their bills are used to dig in soil and leaf litter, break up debris and termitaria, probe within and peel off bark, and break up large prey items. The importance of the bill in gaining access to food and the disproportionately large degree of dimorphism in bill length suggest the difference between the sexes may reduce intersexual resource competition (Selander 1972; Shine 1989). Such competition is expected where the sexes forage simultaneously in groups within the same microhabitat, creating potential for selection to reduce intersexual competition (Wallace 1974; Radford and Du Plessis 2003). Other primarily insectivorous birds exhibit disproportionately large sexual size dimorphism in bill length coincident with intersexual differences in foraging behaviour (Selander 1966; Wallace 1974; Bell 1982; Suhonen and Kuitunen 1991; Moorhouse 1996), including species that forage in groups similarly to babblers (Noske 1986; Radford and Du Plessis 2003). However, the relationship between sexual size dimorphism in bill length and intersexual differences in foraging behaviour among closely-related taxa has been examined only in woodpeckers of the genus *Melanerpes*, where there was a strong positive relationship (Selander 1966; Wallace 1974). A comparative analysis of sexual size dimorphism in almost 3000 bird species from several global zoogeographic regions failed to find support for the resource-partitioning hypothesis (Szekely et al. 2007). However, group foraging was not considered, and overlap in resource use between the sexes was defined only on the basis of territory overlap.

Australo-Papuan babblers are an ideal group in which to investigate the relationship between sexual size dimorphism in bill length and intersexual resource partitioning for several reasons. All species forage in groups comprised of both sexes that utilise the same microhabitats simultaneously (Balda and Brown 1977; Councilman 1980; Taylor 2003; Portelli et al. 2009). They exhibit a pronounced gradient in sexual size dimorphism in bill length from slight in the Chestnut-crowned Babbler, moderate in Hall's and White-browed Babblers, to

large in the Grey-crowned Babbler. They also differ appreciably in habitat preferences and social organisation, but foraging behaviour is similar among species (King 1980; Higgins and Peter 2002; Cale 2003; Portelli *et al.* 2009). Despite this suitability, such an investigation is not currently possible since data on intersexual differences in foraging behaviour are lacking for all species.

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