Morphological sexing of Grey-crowned Babblers *Pomatostomus temporalis temporalis:* near enough is not quite good enough

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We investigated sexual dimorphism in Grey-crowned Babblers *(Pomatostomus temporalis temporalis)* focusing on whether morphological measurements can be used as a means to sex individuals in the field. Head-bill length, body mass and wing length data from two separate studies were analysed for sex differences and to determine whether Grey-crowned Babblers differed morphologically between populations. Head-bill length was found to be the most sexually dimorphic measurement. Males were larger in all age classes (excluding first-year birds), although there was some overlap in the range of measurements obtained for males and females. Body mass and wing length showed no significant differences and substantial overlap between the sexes. The best model from a Discriminant Function Analysis found that 87.1 percent of Grey-crowned Babblers could be correctly sexed using head-bill length as a measurement. Size differences between the two study populations were not significant, but as geographic variation in size has been documented in this species we recommend new models be developed for each location, where cost or time constraints preclude definitive molecular-based sexing.

INTRODUCTION

The ability to identify the sex of individual birds in a sexually monochromatic species is important for studies that examine life-history traits and ecological interactions (McDonald 2003). Molecular sexing techniques are precise and can be applied to most species (e.g. Griffiths *et al.* 1998; Vucicevic *et al.* 2012), age classes and locations with equal certainty. However, their use may be limited by cost and the delay of sample analysis, which can affect project funding (Dubiec and Zagalska-Neubauer 2006). Additionally, there are ethical considerations around sexing. For instance, banding unsexed pullus prior to dimorphic development can result in using the wrong band size in some species such as raptors, resulting in harm or the band falling off (McDonald 2003). The standard technique of plucking feathers to collect DNA may yield low amounts of poor quality DNA that are potentially unlikely to meet the molecular requirements of a study (McDonald and Griffith 2011). Furthermore, feather sampling is likely to significantly impact subject fitness and survival, such as flight performance, physiological and metabolic costs, alterations of individual status and attractiveness (McDonald and Griffith 2011). Laparotomies, a sexing technique involving a lateral incision in the posterior ribs to view the gonads, have also shown to affect the health of birds. The procedure may be harmful to the internal organs and lead to death by internal bleeding (Berthold 1969). Morphological sexing, where possible, remains an invaluable tool, and numerous sexually monochromatic species can be sexed using subtle variances in morphology (e.g. Purple-throated Carib Hummingbird (*Eulampis jugular*), Temeles *et al.* 2000; Wandering Albatross (*Diomedea exulans*), Shaffer *et al.* 2001; Blackbird (*Turdus merula*), Robertson *et al.* 2012; and Little Penguin (*Eudyptula minor*), Arnould *et al.* 2004).

Male and female Grey-crowned Babblers, subspecies (*Pomatostomus temporalis temporalis*), show no observable differences in plumage (Higgins and Peter 2002). This cooperatively breeding species lives in social groups where offspring of both sexes remain on the natal territory to raise subsequent generations of young. The species is declining in south-eastern Australia because of vegetation clearance, fragmentation and modification of woodland habitat (Garnett and Crowley 2000). It is *extinct* in South Australia, and classified as *endangered* in Victoria and *vulnerable* in New South Wales, where it is the subject of action plans and recovery programs (Davidson and Robinson 1992; Garnett and Crowley 2000). Complex social behaviour is thought to render Grey-crowned Babblers particularly susceptible to habitat fragmentation (Garnett and Crowley 2000). Important factors in population persistence, such as reproductive success, fledgling sex and recruitment, and pairing success, are linked to the sex of group members in this species (Blackmore 2006; Blackmore and Heinsohn 2007). Consequently, the ability to easily sex group members is particularly important for recovery efforts for this species (OEH 2012).

A discriminant function analysis (DFA) of body mass and size measurements was found to be reliable for sexing Grey-crowned Babblers in south-east Queensland, with single characters, especially bill length, also useful (Counsilman and King 1977). However, sexing in this study was by behaviour and calls, and could not be verified with molecular sexing. Moreover, the technique developed by Counsilman and King (1997) may not be uniformly applicable across the species range, as morphological variation in this species may be influenced by geography, phylogeny (Edwards and Kot 1995), or even social factors (Brown *et al.* 1982a). To date no reliable field sexing technique has been devised for Grey-crowned

Babblers in temperate New South Wales, where the species is suggested to be larger than in Queensland and smaller than in Victoria (Higgins and Peter 2002). The aim of this study, therefore, was to provide the first molecular evidence for sexual dimorphism in Grey-crowned Babblers in central western New South Wales using head-bill length, body mass and wing length. We use this evidence to devise a method that can be used in the field to determine the sex of an individual with a high degree of confidence, and explore the extent to which it can be applied across geographically distinct populations.

METHODS

Study species

Grey-crowned Babblers are cooperatively breeding, woodland birds that inhabit eastern and northern Australia and southern New Guinea (Higgins and Peter 2002). Social rank corresponds to age (King 1980), and groups usually contain subordinate helpers of either sex and a dominant pair (Blackmore and Heinsohn 2007).

Morphological measurement

Morphometric data were obtained from two independent studies conducted in the central west of New South Wales: in the eastern Pilliga Nature Reserve (149º 300E, 30º 530S) and surrounds near Coonabarabran between 2003 and 2005 (Blackmore and Heinsohn 2008); and in and around Dubbo (32°15'45"S, 148°44'25"E), including Beni State Conservation Area, during 2009 (Lambert *et al*. 2013), hereafter referred to as the Pilliga and Dubbo populations, respectively.

Birds were caught with mist nets and banded with stainless steel and coloured bands from the Australian Bird and Bat Banding Scheme. Blood samples (20 -70 µL) were taken from the brachial vein for Pilliga birds (*n* = 252; Blackmore and Heinsohn 2010), and from breast feather samples for Dubbo birds (*n* = 68; 7-8 feathers; Lambert *et al*. 2013). Adults and juveniles were aged using iris colour and plumage as described by King (1980). Individuals were placed into three distinct iris colour groups. Birds with light brown irides ranged in age from less than one to two years of age, brownish-yellow ranged from two to three years of age and individuals with yellow irides were at least three years old (Brown *et al*. 1982a and 1982b; King 1980; Counsilman and King 1977).

Head-bill length (tip of the bill to back of the head), to the nearest 0.1 mm using callipers, and wing length (the distance from the distal portion of the carpus to the tip of the longest primary feather with the wing chord flattened and straightened) were measured using a stopper rule to the nearest millimetre. These measurements were chosen because Counsilman and King (1977) found them to be the most dimorphic measurements for this species in south-east Queensland. All birds were weighed in cloth bags on a spring scale to the nearest gram. As size is highly variable in the first year depending on fledging date, we excluded individuals of 0-1 years of age, leaving 122 Pilliga and 68 Dubbo birds in this study.

Not all morphometric measurements were recorded for all banded birds; hence varying sample sizes are reported in Table 1 and with the relevant result. The DFA included only individuals with all three measurements (76 Pilliga and 49 Dubbo birds).

Molecular methods

Blood DNA extraction and sexing techniques are described in Blackmore *et al*. (2006). DNA was extracted from blood using the ammonium acetate method described in Nichols *et al*. (2008), and from feathers by Genetic Technologies Limited in Fitzroy. Sex was determined using the PCR amplification method of Griffiths *et al* (1998) to test for a sex-linked CHD (chromo-helicase-DNA-binding) gene using P8 and P2 primer pairs.

Statistical analysis

To determine the effect of age on the three body size measurements and whether there were consistent relationships between these and individual sex and site of capture, we used a three-way ANOVA. DFA was used to determine which variables were the most predictive, and to compare sexing accuracy using the more complex DFA models versus single variables. The binomial regression for response was sex with the predictors age, wing length, body mass and head-bill length. Parameters were added or removed using a 'stepwise' procedure, with a threshold of F=3.84 (p<0.05) for a variable to be entered and F=2.71 (p=0.1) for a variable to be removed. We then quantified the ability of the generated discriminate function to distinguish between male and female individuals using two methods specified by McDonald (2007). First, three quarters (*n*=94) of individuals were assigned to a 'training' dataset to generate a function for each sex. After function accuracy was assessed, the remaining one-quarter of individuals (*n*=31) were used as 'test' datasets. A comparison of DFA and single measurement sexing accuracies were compared to determine which method was more accurate for field use. Statistical analyses were performed using Minitab software (version 15) and SPSS software (version 21).

RESULTS

Mean measurements (±SE) and sample sizes for the Pilliga and Dubbo populations are reported in Table 1. Wing length did not differ between the Pilliga and Dubbo populations ($F_{1,3}$ = 0.95, p = 0.332; n = 145). Birds from Dubbo tended to be heavier than birds from Pilliga but the trend was not significant ($F_{1,3}$ = 3.88, p = 0.050, n = 164). In the absence of significant differences, measurements of wing length (Fig. 1) and body mass (Fig. 2) from the Pilliga and Dubbo populations were hereafter pooled.

Measurements and sample sizes of males and females for each age class are presented in Table 2. Male and female wing length did not differ at 1–2 years of age ($F_{1,1}$ = 0.29, p = 0.595, n = 47). However, males had longer wings than females among 2–3 year olds ($F_{1,1}$ = 6.20, p = <0.005, n = 14) and 3 year olds and over ($F_{1,1}$ = 11.83, p = <0.005, n = 84; Fig. 1). Body mass did not differ significantly between the sexes in any age

Table 1

Mean ±SE measurements and sample sizes for comparisons of Grey-crowned Babblers from Pilliga and Dubbo populations

| Population	Wing length (mm)	Body mass (g)	
		Female	Male
Pilliga	113.74 ± 0.33 (*n* = 77)	72.4 ± 1.13 (*n* = 74)	73.5 ± 0.987 (*n* = 55)
Dubbo	112.77 ± 0.5 (*n* = 68)	79.6 ± 0.998 (*n* = 25)	83.3 ± 0.64 (*n* = 22)
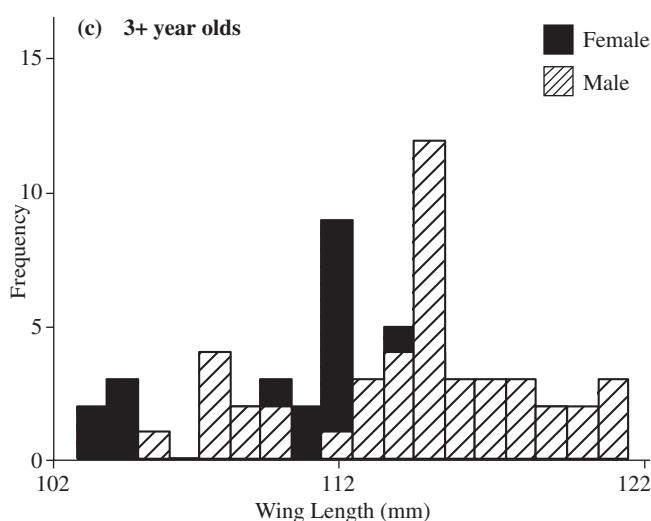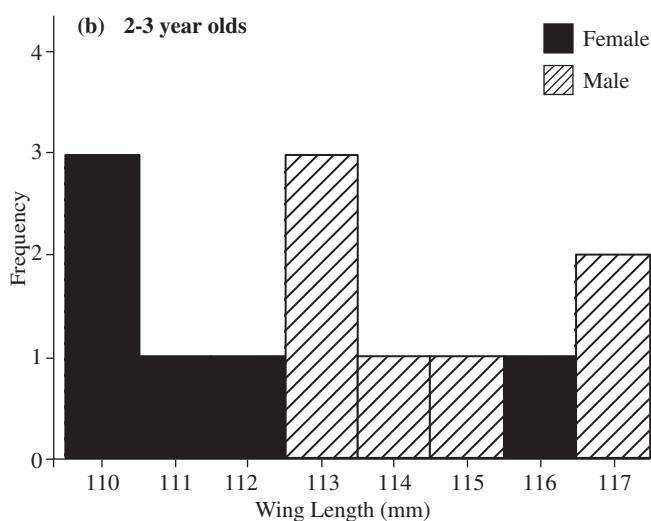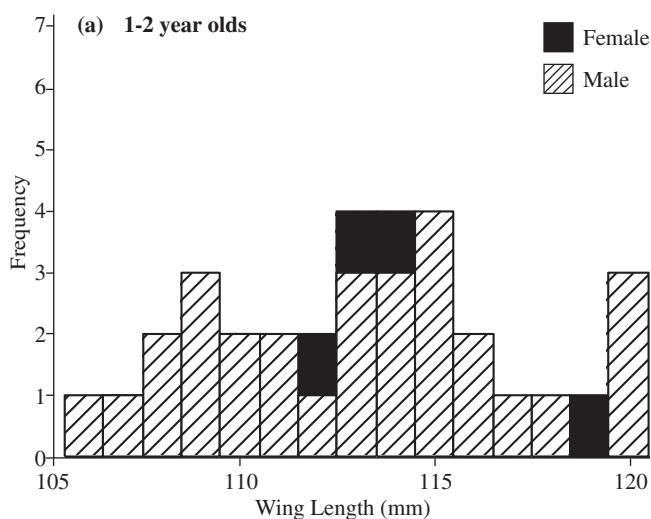
Figure 1. *Histograms of observed frequencies of wing length (mm) at age (a) 1–2 years (female = 107–119mm; male = 106–120 mm); (b) 2–3 years (female = 110–116 mm; male = 113–117mm); and (c) 3 years and over (female = 104–119 mm; male = 106–121 mm) of 145 Grey-crowned Babblers from the Pilliga and Dubbo populations.*
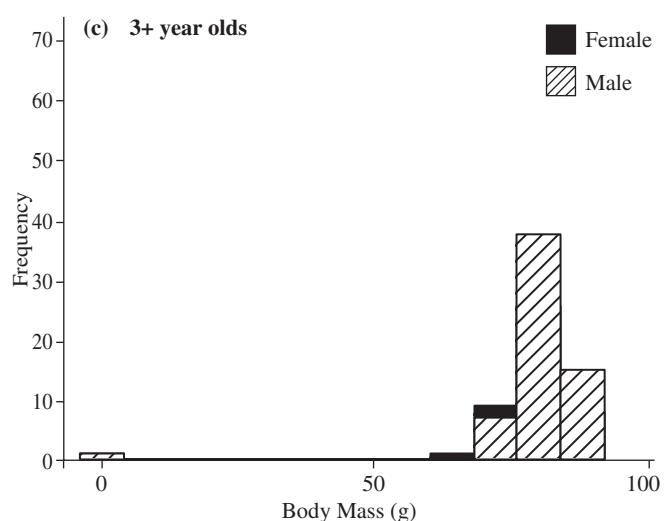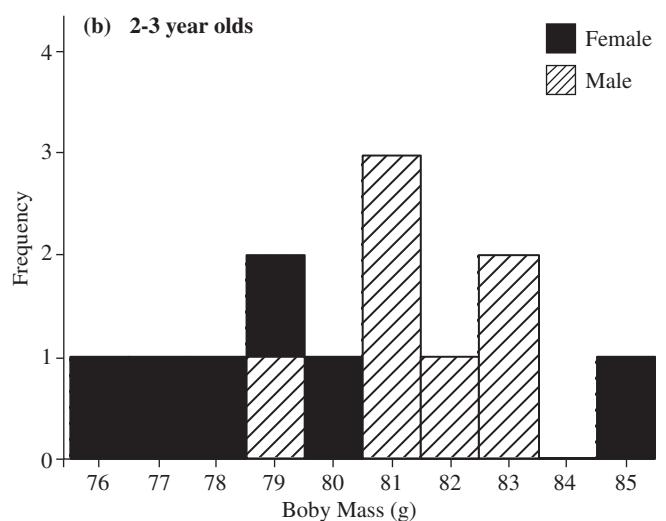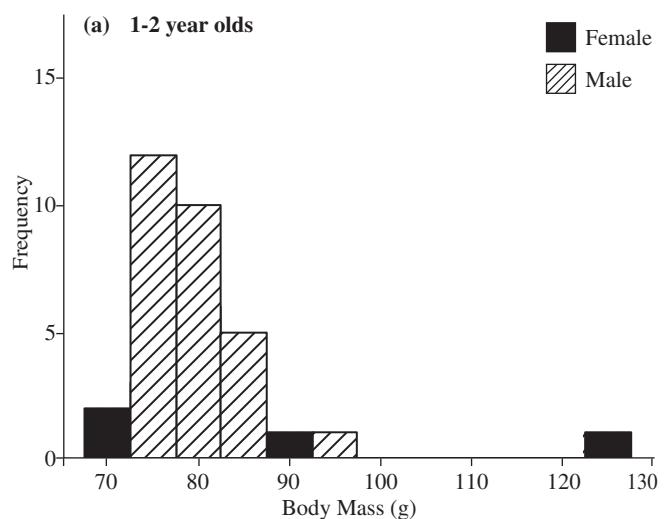
Figure 2. *Histograms of observed frequencies of body mass (g) at age (a) 1–2 years (female = 66–88 g; male = 73–97 g); (b) 2–3 years (female = 75.5–85 g; male = 79–83 g); and (c) 3 years and over (female = 66–90 g; male = 70–92 g) of 164 Grey-crowned Babblers from the Pilliga and Dubbo populations.*
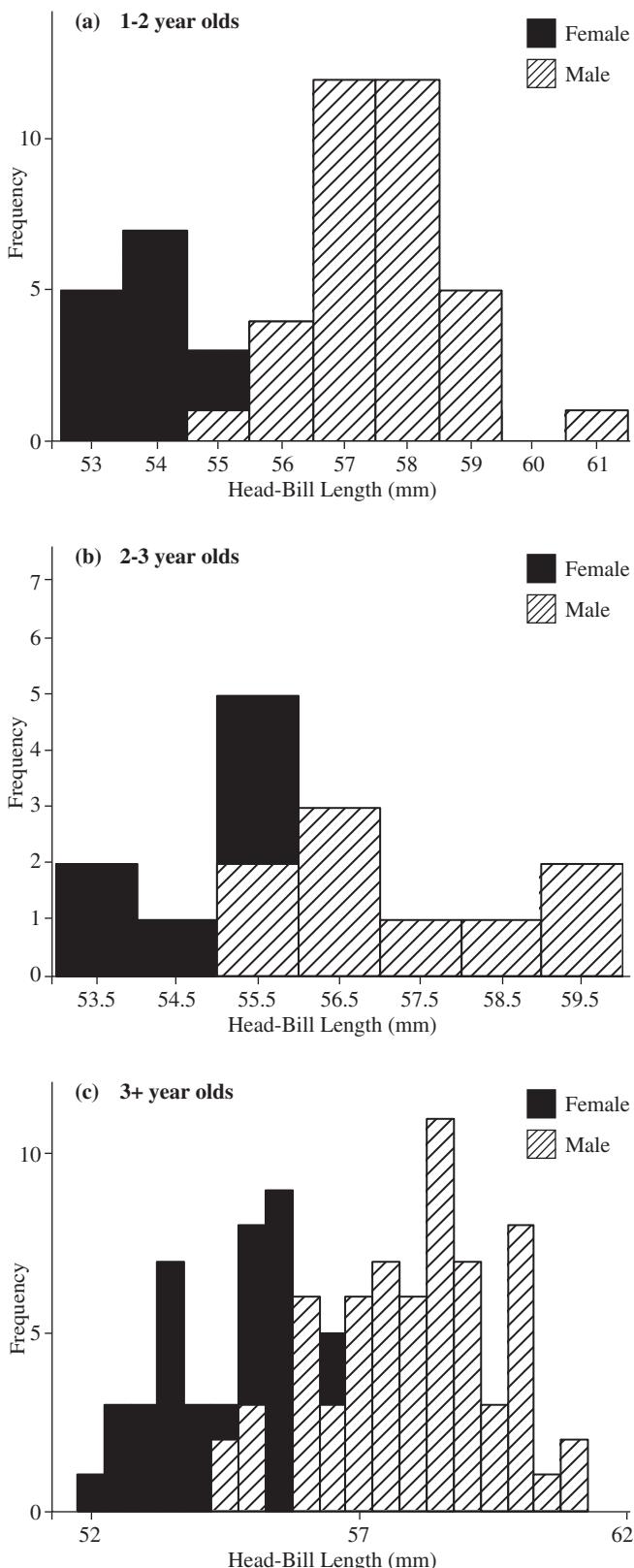
Figure 3. *Histograms of observed frequencies of head-bill length (mm) at age (a) 1–2 years (52.55–59.4 mm; male = 54.82–60.60 mm); (b) 2–3 years (female = 53.1–56.16 mm, SE = 0.40; male = 55.99–59.30 mm); and (c) 3 years l and over (female = 52.20–59.20 mm; male = 54.50–61.10 mm) of 190 Grey-crowned Babblers from the Pilliga and Dubbo populations.*

class ($F_{1,2} = 0.81$, $p = 0.368$; Fig. 2). On average, males had significantly longer head-bill measurements than females in all age classes ($F_{1,2} = 163.56$, $p <0.005$; Fig.3), although there was some overlap in the range of measurements (Fig. 3). Within each sex there was overlap between age classes and also between the sexes within each age class (Fig.3).

At each step of the DFA, the variable that minimises the overall Wilk's Lambda is entered with a maximum number of six steps. The step-wise DFA using head-bill length, wing length and body mass found that head-bill length alone was the most accurate measurement for sexing Grey-crowned Babblers, as it generated a significant Wilk's Lambda score ($F_{1,91}= 152.2$, $p < 0.005$, Eigenvalue = 1.672).

The following discriminate function formula was found to determine sex based on measurements of head-bill length:

$$D = (0.776*head\text{-}bill\ length) - 43.920$$

Using this formula, if D was above the cut off score of 1.017 it was a male and if it was below 1.610, it was a female. The DFA model with head-bill length resulted in the correct sexing of 87.1 percent of Babblers (88.2% correctly classified for the training data and 87.1% correctly classified for the test data).

The DFA was found to be more accurate than using head-bill length alone in the field. As our results found no difference between age classes, measurements were pooled. Of the 190 birds measured from the two habitats, only 123 would have been sexed correctly from head-bill data. Sixty-four birds fell into the overlap range and three would have been incorrectly assigned, giving a 64.7 percent chance of sexing an individual. In comparison, the DFA accurately sexed 87.1 percent of all individuals correctly.

DISCUSSION

Similar to the findings of Counsilman and King (1977) in south-east Queensland, this study found that head-bill length in Grey-crowned Babblers was the only morphological character that was significantly different between the sexes, in all age classes in central western New South Wales. A single morphological measurement for sexing that could be applied in the field would be most efficient due to the reduced time needed, potentially fewer errors from measuring numerous variables and providing a straight forward cut off between males and females without further measurement analysis. However, this study found overlap between the sexes that precluded complete accuracy in field sexing based on head-bill length. Using a discriminant function provided a more accurate method with an accuracy of 87.1 percent, whereas, using a head-bill length measurement alone only provided an accuracy of 64.7 percent. Generally, surgical or molecular sexing remains the only completely dependable methodology for studies of Grey-Crowned Babblers that require sex information. Required precision should shape researchers' use of methods, but for some studies our error rate may be sufficient.

Assigning individual sex using our DFA results could be less reliable in other geographic regions, as there is geographic morphological variation in this species (Higgins and Peter 2002). The function used for this study was more successful than the one developed by Counsilman and King (1977) in Queensland, where birds are generally larger and where only 76 percent of individuals could be classified accurately. Similarly, White-

Table 2

Mean ±SE measurements and sample sizes for comparisons of male and female Grey-crowned Babblers in each age class. Data from the Pilliga and Dubbo populations are pooled.

Age	Wing length (mm)		Body mass (g)		Head-bill length (mm)	
	Female	Male	Female	Male	Female	Male
1	112.67 ± 0.63	113.03 ± 0.73	81.64 ± 3.55	79.34 ± 1.01	54.61 ± 0.36	57.49 ± 0.19
	(n = 18)	*(n = 29)*	*(n = 14)*	*(n = 28)*	*(n = 21)*	*(n = 35)*
2	111.71 ± 0.84	114.57 ± 0.69	79.78 ± 0.95	81.43 ± 0.53	54.89 ± 0.26	57.18 ± 0.49
	(n = 7)	*(n = 7)*	*(n = 9)*	*(n = 7)*	*(n = 9)*	*(n = 9)*
3	112.05 ± 0.62	114.60 ± 0.57	79.24 ± 0.88	79.49 ± 1.43	55.00 ± 0.22	58.01 ± 0.20
	(n = 39)	*(n = 45)*	*(n = 44)*	*(n = 61)*	*(n = 51)*	*(n = 65)*

browed Babblers (*Pomatostomus superciliosus*) in New South Wales could only be sexed by a discriminant equation derived from that population, performing poorly for those in Victoria and Western Australia (Oppenheimer *et al*. 2007). Consequently we would recommend calculating a new discriminant function for each study population.

The evolutionary basis for the small but consistent sex difference in head-bill length in an otherwise monomorphic species is unclear. Sexual dimorphism may evolve through ecological pressures acting differently on the sexes or inter-sexual competition for resources (Slatkin 1984). Babblers spend the majority of their time foraging as a group in leaf litter and probing and gleaning substrates for invertebrates (Lambert unpub. data; Portelli *et al*. 2009; Taylor 2003). Previous studies have suggested that culmen dimorphism in Hall's Babbler (*Pomatostomus halli*) may be used to lessen intersexual resource competition, as the sexes forage in a group within the same microhabitat (Portelli 2014). Intersexual foraging niche partitioning has been linked to sexual dimorphism in bill length in cooperatively breeding Green Wood Hoopoes (*Phoeniculus purpureus*; Radford and Du Pleissis 2003) but not in the Middle Spotted Woodpecker (*Dendrocopos medius*; Pasinelli 2008) and a study on 3000 species did not find any evidence of a role for resource-partitioning in sexual dimorphism (Szekely *et al*. 2007).

Another explanation for morphological sex differences may arise from complex patterns of sex allocation in this species. Theoretically, sex allocation can occur either pre-ovulation (via segregation distortion at the first meiotic division or through differential provisioning of ova of different sexes to influence hatch order) or post-ovulation (via re-absorbing eggs of the wrong sex or egg dumping). Additionally, clutches are heavily biased towards producing male offspring first, the more helpful sex in cooperative breeding. A progressive female bias is less common in larger clutches where environmental conditions such as reduced food abundance are less influential (Blackmore 2006; for mechanisms of sex allocation see Komdeur (2004); Alonso-Alvarez 2006 and references therein). Clutches are incubated after the first or second egg is laid (Counsilman 1979), but the whole brood fledges on the same day (pers. obs.), and female fledglings probably receive lower investment by group members and are less likely to survive to independence (Blackmore 2006). Therefore surviving female babblers could be expected to be generally smaller and lighter than males. However, our study found the only significant sex differences were in head-bill length and not in other measures of size or mass, so sex allocation does not appear to affect dimorphism but may explain the trend.

Sexual dimorphism in morphological characters has been attributed mainly to sexual selection (Andersson 1994), with morphological differences greater in polygamous than in monogamous species (Payne 1984).While most cooperative breeders are sexually monomorphic in plumage and similar in size (Dunn *et al.* 2001), the low levels of extrapair fertilisation found in Grey-crowned Babblers (Blackmore and Heinsohn 2008) may provide sufficient pressure for mild selection on a single trait.

Intrasexual competition may also drive head-bill dimorphism in this species. Grey-crowned Babbler often form same-sex coalitions to disperse (Blackmore *et al.* 2010). Males are much more likely to form coalitions than females, and high turnover of male compared with female breeders suggests that male coalitions attack incumbent breeders to gain a territory and then fight for dominance (Blackmore 2006). Larger head-bills could therefore play a valuable role in agonistic male intrasexual dominance disputes.

CONCLUSION

The results of this study found that Grey-crowned Babblers in central western New South Wales had sexually dimorphic head-bill lengths. However, there was overlap between the sexes and between age classes for wing length and body mass. Although males had larger head-bill measurements on average, our data showed some overlap between the sexes within age classes, and using this character to sex individuals was not accurate enough for perfect sex assignment in the field. Nonetheless, using head-bill length as a predictor in a discriminant function model yielded an accuracy of 87.1 percent, which may be sufficient for studies where accurate sexing is not crucial and where there are cost and time constraints. Given geographic size variation across the species range, we recommend new models be developed at other locations and, if complete sexing information is required, molecular techniques be deployed for this morphologically variable species.

ACKNOWLEDGEMENTS

REFERENCES

Anderson, M. (1994). *Sexual Selection.* (Princeton: Princeton University Press.)

Alonso-Alvarez, C. (2006). Manipulation of primary sex-ratio: an updated review. *Avian and Poultry Biology Reviews* **17**(1), 1-20.

Arnott, G. and Elwood, R. W. (2009). Assessment of fighting ability in animal contests. *Animal Behaivour* **77**: 991–1004.

Arnould, J. P. Y., Dann, P. and Cullen, J. M. (2004). Determining the sex of Little Penguins (*Eudyptula minor*) in northern Bass Straight using morphometric measurements. *Emu* **104**: 261–265.

Berthold, P. (1969). Die Laparotomie bei Vögeln. *Zool Gart* **37**: 271–279.

Blackmore, C. J. (2006). 'Breeding biology and behaviour of the Grey-crowned Babbler', PhD thesis, Australian National University, Canberra. (unpub.)

Blackmore, C. J., Adcock, G. J., Ebert, D. and Heinsohn, R. (2006). Microsatellite loci for population and behavioural studies of Grey-crowned Babblers (*Pomatostomus temporalis*: Aves). *Molecular Ecology Notes* **6**: 412–414.

Blackmore, C. J. and Heinsohn, R. (2007). Reproductive success and helper effects in the cooperatively breeding Grey-crowned Babbler. *Journal of Zoology* **273**: 326–332.

Blackmore, C. J. and Heinsohn, R. (2008). Variable mating strategies and incest avoidance in cooperatively breeding Grey-crowned Babblers. *Animal Behaviour* **75**: 63–70.

Blackmore, C. J., Peakall, R. and Heinsohn, R. (2010). The absence of sex-biased dispersal in the cooperatively breeding Grey-crowned Babbler. *Journal of Animal Ecology* **80**: 69–78. doi:

Brown, J. L., Brown, E. R. and Brown, S. D. (1982a). Morphological variation in a population of Grey-crowned Babblers: Correlations with variables affecting social behavior. *Behavioral Ecology and Sociobiology* **10**: 281–287.

Brown, J. L., Brown, E. R., Brown, S. D. and Dow, D. D. (1982b). Helpers: effects of experimental removal on reproductive success. *Science* **215**: 421–422.

Counsilman, J. J. (1979). Notes on the breeding biology of the Grey-crowned Babbler. *Bird Behaviour* **1**: 114–124.

Counsilman, J. J. and King, B. (1977). Ageing and sexing the Grey-crowned Babbler (*Pomatostomus temporalis*). *Babbler* **1**: 23–41.

Davidson, I. and Robinson, D. (1992). 'Grey-crowned Babbler action statement No. 34'. (Department of Sustainability and Environment: Victoria.)

Dubiec, A. and Zagalska-Neubauer, M. (2006). Molecular techniques for sex identification in birds. *Biological Letters* **43**: 3–12.

Dunn, P. O., Whittingham, L. A. and Pitcher, T. E. (2001). Mating systems, sperm competition, and the evolution of sexual dimorphism in birds. *Evolution* **55**: 161–175.

Edwards, S. V. and Kot, M. (1995). Comparative methods at the species level: geographic variation in morphology and group size in Grey-crowned Babblers (*Pomatostomus temporalis*). *Evolution* **49**: 1134–1146.

Garnett, S. and Crowley, G. M. (2000). The Action Plan for Australian Birds. (Environment Australia, Canberra.)

Griffiths, R., Double, M. C., Orr, K. and Dawson, R. J. G. (1998). A simple DNA test to sex most birds. *Molecular Ecology* **7**: 1071–1075.

Higgins, P. J. and Peter, J. M. (eds) 2002. 'Handbook of Australian, New Zealand and Antarctic Birds'. Volume 6: Pardalotes to Shrike-thrushes. (Oxford University Press: Melbourne).

King, B. R. (1980). Social organization and behaviour of the Grey-crowned Babbler *Pomatostomus temporalis*. Emu **80**: 59–76.

Komdeur, J. 2004. Sex-ratio manipulation. In: Ecology and Evolution of Cooperative Breeding in Birds (Ed. By W. D. Koenig & J. Dickinson), pp. 102-116. Cambridge: Cambridge University Press.

Lambert, K. T. A., Geering, D. and Ford, H. (2013). Group size and composition in the Grey-crowned Babbler *Pomatostomus temporalis* in an urban environment. *Corella* **37**: 57–61.

McDonald, P. G. (2003). Nestling growth and development in the Brown Falcon, *Falco berigora*: an improved aging formula and field-based method of sex determination. *Wildlife Research* **30**: 411–418.

McDonald, P. G. (2007). Provisioning calls of cooperatively breeding Bell Miner *Manorina melanophrys* encode sufficient information for individual discrimination. *Journal of Avian Biology* **38**: 113–121.

McDonald, P. G. and Griffith, S. C. (2011). To pluck or not to pluck: the hidden ethical and scientific costs of relying on feathers as a primary source of DNA. *Journal of Avian Biology* **42**: 197–203.

Office of Environment and Heritage. (2012). Grey-crowned Babbler (eastern subspecies) – priority actions, Environmental Issues – Threatened species, Office of Environment and Heritage. http://www.environment.nsw.gov.au/threatenedspeciesapp/profile.aspx?id=10660

Oppenheimer, S., Astheimer, L., Anderson, M. J. and Buttemer, B. (2007). Morphometric measures as a moderate predictor of gender in the White-browed Babbler *Pomatostomus superciliosus gilgandra*. *Corella* **31**: 15–18.

Pasinelli, G. (2008). Sexual dimorphism and foraging niche partitioning in the Middle Spotted Woodpecker *Dendrocopos medius*. *Ibis* **142**: 635–644.

Payne, R. B. (1984). Sexual selection, lek and arena behavior, and sexual size dimorphism in birds. *Ornithological Monographs* **33**: 1–53.

Portelli, D. J. (2014). Sexual size dimorphism and geographic variation in body size in a group-living, insectivorous passerine: Hall's Babbler (*Pomatostomus halli*). *Corella* **38**: 1–9.

Portelli, D. J., Barclay, H., Russell, D. J. F., Griffith, S. C. and Russell, A. F. (2009). Social organisation and foraging ecology of the cooperatively breeding Chestnut-crowned Babbler (*Pomatostomus ruficeps*). *Emu* **109**: 153–162.

Radford, A. N. and Du Plessis, M. A. (2003). Bill dimorphism and foraging niche partitioning in the Green Woodhoopoe. *Journal of Animal Ecology* **72**: 258–269.

Robertson, H. A., Whitaker, A. H. and Fitzgerald, B. M. (2012). Morphometrics of forest birds in the Orongorongo Valley, Wellington, New Zealand. *New Zealand Journal of Zoology* **10**: 87–97.

Shaffer, S. A., Weimerskirch, H. and Costa, D. P. (2001). Functional significance of sexual dimorphism in Wandering Albatrosses, *Diomedea exulans*. *Functional Ecology* **15**: 203–210.

Slatkin, M. (1984). Ecological causes of sexual dimorphism. *Evolution* **38**: 622–630.

Szekely, T., Lislevand, T. and Figuerola, J. (2007). Sexual size dimorphism in birds. In 'Sex size and gender roles'. (Eds. D.J. Fairbairn, W.U. Blanckenhorn and T. Szekely). Pp. 27–37. (Oxford University Press: Oxford).

Taylor, S. G. (2003). Habitat use by White-browed Babblers *Pomatostomus superciliosus* in box-ironbark forest in south-east Australia. PhD thesis, La Trobe University, Victoria. (unpub.)

Temeles, E. J., Pan, I. L., Brennan, J. L. and Horwitt, J. N. (2000) Evidence for ecological causation of sexual dimorphism in a hummingbird. *Science* **289**: 441–443.

Vucicevic, M., Stevanov-Pavlovic, M., Stevanovic, J., Bosnjak, J., Gajic, B., Aleksic, N. and Stanimirovic, Z. (2012). Sex determination in 58 bird species and evaluation of CHD Gene as a universal molecular marker in bird sexing. *Zoo Biology* **31**: 1–13.