A taxonomic framework for interpreting evolution within the *Amytornis textilis-modestus* complex of grasswrens

A taxonomy of *A. textilis-modestus* grasswrens

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Abstract. Recent evidence points to the *Amytornis textilis-modestus* complex of grasswrens being not one but two species; *Amytornis textilis* Western Grasswren (including *A. t. myall*) and *Amytornis modestus* Thick-billed Grasswren. We present morphological support for this change and evidence of diversity within both *A. t. textilis* and *A. modestus*. In the latter we reinstate currently unrecognised subspecies, *A. m. modestus* from the valleys of the MacDonnell Ranges, presumed extinct and *A. m. indulkanna*, ranging northwest of Lake Eyre and Lake Torrens. Other discrete populations are described at the periphery of the northern Flinders Ranges and in the south-western Lake Frome Basin. The former resembles *A. m. indulkanna* but has sexually dimorphic tails. The latter has longer sexually dimorphic tails but is more strongly marked, darker and less consistently "thick-billed". Populations northeast of Lake Eyre and in New South Wales are incompletely evaluated. Molecular genetic studies are planned to clarify relationships between all extant and extinct populations of the complex.

Introduction

Recent checklists recognise the Thick-billed Grasswren *Amytornis textilis* as one of 10 species of grasswrens (Maluridae: *Amytornis*) (Schodde and Mason 1999, Christidis and Boles 2008) with three subspecies *A. t. textilis, A. t. myall* and *A. t. modestus*. Phylogenetic analysis (Christidis *et al*. 2010) advocates increasing this by separation of *A. modestus* from *A. textilis* (see also Black 2004).

Here we present further evidence of species-level recognition of *A. textilis* and *A. modestus*. We also address geographical distribution, patterns of phenotypic diversity, and taxonomic status of populations within these two species. Our focus is on populations currently known as *A. t. myall* in north-eastern Eyre Peninsula as well as those currently considered as the monotypic species *A. modestus* across its entire range in central and inland south-eastern Australia.

Our study follows recent distributional surveys of *myall* and *modestus* (Black et al. 2009 and unpublished) and is based on a review of all specimens of the complex in Australian museums, including recently collected material (Fig. 1). It first assesses distribution, plumage and morphometry in *textilis*, *myall* and *modestus* and whether separate species status is warranted for *modestus* and then examines differentiation among populations within *modestus* and *textilis.*

(INSERT Fig. 1.)

Materials and methods

AB examined all non-juvenile *textilis, myall and modestus* specimens in the South Australian Museum, Adelaide (SAMA), Western Australian Museum, Perth (WAM), Australian National Wildlife Collection, CSIRO, Canberra (ANWC), Australian Museum, Sydney (AM) and Museum Victoria, Melbourne (MV) as follows: *textilis* (29), *myall* (17) and *modestus* (54). Plumage traits were compared directly and contemporaneously among all ten central Australian *modestus* skins in the H. L. White Collection (MV), the only specimens from New South Wales (NSW) (AM O. 10581) and from northeast of Lake Eyre (MV 8315) and the 14 *myall* and 31 *modestus* skins in SAMA. Digital colour images of the other seven *modestus* specimens from New South Wales in the Academy of Natural Sciences, Philadelphia (ANSP) and the American Museum of Natural History (AMNH) were also examined. Specimens of *textilis* were examined separately. From Shark Bay, the only extant population, there are 11 skins, from Dirk Hartog

Island (DHI) six, northern inland nine, south-west one only and south-east (Kalgoorlie) two (Fig. 1).

AB measured the following traits on all specimens to the nearest 0.1 mm, avoiding all damaged or heavily worn parts: tail length, from the emergence of the central rectrix to the tip of the central rectrix; wing length, maximum (flattened) chord, using a butted ruler (nearest 1.0 mm), from the carpal joint to the tip of the longest primary; tarsus, from the mid-point on the hind side of the tibio-tarsal joint to the joint between tarsus and middle toe in front; bill length, from the junction of the culmen and skull to the bill tip; bill depth, measured as the shortest distance from the junction with frontal feathering to the lower ramus. Following Black (2004), lower mandible profile (a concavity near its base and varying convexity in mid portion and near the tip) was scored on all SAMA material as showing either obvious overall convexity, slight or subtle convexity, or virtual straightness. For the assessment of plumage, specimens were ranked by depth of dorsal tone and intensity of ventral streaking. Three independent observers assessed the rankings of bill shape and plumage and produced consistent findings. AB made an additional plumage comparison of *myall*, inland SA *modestus* and Lake Frome Basin *modestus* skins in SAMA, using the Naturalist's Color Guide (Smithe 1975) (electronic Appendix).

Statistical Analysis

Non-parametric analyses were used initially because normal distribution was not assumed for any morphometric trait and because sample sizes were small in some subgroups. Therefore the median of each sample, 95% confidence intervals and Mann-Whitney (Wilcoxon) test were applied to allow inter-group comparisons between the *textilis* and *myall* populations and between the *myall* and *modestus* populations. Black *et al.* (unpublished) found the distribution of *modestus* to be discontinuous on the eastern flank of the Flinders Ranges. J. Norman (pers. comm.) found and J. Austin (pers. comm.) confirmed that *modestus* is genetically divided into two phylogroups on either side of Lake Eyre and Lake Torrens. Higgins *et al.* (2001) showed differences in tail length, between central Australian and southern populations of *modestus*. Thus four separate and potentially distinct *modestus* subpopulations were scored, *viz.*: central Australia (Central): north-western SA (North-western): North Flinders Ranges periphery (Flinders): and south-western Lake Frome Basin (Frome) (Fig. 1). The Kruskal-Wallis test provided an analysis

of variance and was employed initially to test the above predicted non-homogeneity of the total *modestus* sample. Comparisons were then made within *modestus* between the two subpopulations in each phylogroup, namely between Central and North-western, and between Flinders and Frome. Because of phenotypic variation among *textilis* the Kruskal-Wallis test was also applied to its three best represented samples from Shark Bay, DHI and northern inland. The raw data were subsequently log-transformed, allowing testing for normal distribution which was confirmed in the larger samples. Parametric statistics were then applied to provide support for the non-parametric findings and to perform factor analysis and discriminant function analysis.

Results

Distribution

Four populations of *modestus* are identified as Central (now extinct), North-western, Flinders and Frome (Fig. 1).

Morphometrics

Measurements of all specimens are in electronic accessory material. Sexual dimorphism in tail length was found in *textilis* ($p < 0.01$), *myall* ($p \approx 0.01$) and Flinders ($p < 0.01$); sample size precluded its testing in Frome where a strong trend suggested it nonetheless. North-western and Central showed no tail length dimorphism. Male tarsi were minimally longer than females in Flinders ($p < 0.01$) as were bill length ($p \approx 0.05$), and depth ($p \approx 0.04$) but not bill proportion. Similar but non-significant trends in bill size dimorphism were seen in other *modestus* populations but not in *textilis* or *myall*.

Statistical comparison between populations was restricted to males because of generally small female sample sizes. Tail length (Table 1) was significantly longer in *textilis* than *myall* ($p \approx 0.01$) and in *myall* than *modestus* ($p < 0.01$). Tail lengths of the four *modestus* samples were statistically different (Kruskal-Wallis test, $p < 0.001$), being longest in Central and shortest in North-western ($p < 0.01$) without overlap and longer in Frome than Flinders ($p \approx 0.025$) (Table 1). In other comparisons between *textilis* and *myall* (Table 2) wing and tarsal lengths were marginally greater in the former ($p \approx 0.05$); there were no differences in these parameters between *myall* and *modestus* or within *modestus*. Bills were longer and deeper in *myall* than in *textilis* ($p < 0.01$) with no difference in bill ratio (Table 2) while bills were longer and shallower in

myall than *modestus* and the length/depth ratio was greater as a consequence ($p \approx 0.05$). The more slender bill-profile of *myall* corresponded with an absence of or only weak convexity of the lower mandible in ten of eleven specimens. In North-western and Flinders *modestus* the lower mandible was consistently and strongly convex in 14 of 19 specimens but in Frome these features varied. Within *textilis* the Kruskal-Wallis test revealed non-homogeneities in tarsus and bill length ($p < 0.05$) and bill length/depth ratio ($p < 0.02$) with lower values for the northern inland population.

(INSERT Tables 1 & 2)

Parametric studies of *modestus* confirmed in two-tailed t tests that Central male tails were longer than North-western ($p < 0.0001$) and Flinders ($p < 0.001$), whereas Frome were longer than Flinders ($p \approx 0.05$) and North-western ($p < 0.01$). Comparing *myall* with the three adequately sampled *textilis* sub-populations two-tailed t tests showed that tails were shorter in *myall* than in northern inland ($p < 0.04$) and DHI ($p < 0.03$). Bills of *myall* were longer than in Shark Bay ($p < 0.001$), DHI ($p \approx 0.02$) and northern inland ($p < 0.0001$) and deeper than Shark Bay ($p < 0.01$) and DHI ($p < 0.003$) but not northern inland. Bill length/depth ratio was thus smaller in northern inland than *myall* ($p < 0.001$), DHI ($p \approx 0.005$) and Shark Bay ($p < 0.005$). Factor analysis showed complete separation of *textilis-myall* from *modestus* populations. Further, there was separation of Central from North-western *modestus* and of *myall* from three northern *textilis* subpopulations (Fig. 2), principally due to measurements of tail and bill. Discriminant function analysis allowed correct assignment of all *modestus* and all *textilis-myall* to respective species. Within these two entities assignment, though imperfect, was accurate within *modestus* in five of six Central, six of eight North-western all eleven Flinders and one of three Frome; and within *textilis-myall* in all 13 *myall*, all five Shark Bay, two of three DHI and three of four northern inland.

(INSERT Fig. 2)

Plumage

All *textilis* and *myall* are darker above and more intensely streaked below than any *modestus*. North-western and Flinders *modestus* are much paler and only subtly streaked and Frome is intermediate. Central Australian specimens are darker dorsally, most falling within the Frome range, and show a rufous tan coloration to the wing and tail feathers that is barely recognised in other *modestus*; ventrally they are less streaked than most *modestus* but are darker on the flanks and bellies. The single specimen from northeast of Lake Eyre (MV R. 8315) is the palest of all. Streaking and tone in NSW skins from AM, AMNH and ANSP are variable. Seasonality, maturity (all specimens exhibiting adult basic plumage) and the age of specimens did not affect the findings. Plumages of *textilis* specimens were analysed separately from *myall* and *modestus*. DHI birds are, with one exception, darker than Shark Bay and some northern inland birds are paler. Those from the south-west and south-east (Kalgoorlie) are darker than northern representatives and resemble *myall* in this respect.

Discussion

Discriminant function analysis of morphometrics and plumage characters of tone and ventral streaking independently allow confident classification of each specimen examined either as *modestus* or *textilis-myall*. We affirm the distinction between *textilis* and *myall* and find differentiation among other populations within *textilis*. The bills of *myall* are relatively long and slender, in contrast with the "thick bills" of adjacent North-western *modestus*. The most abrupt changes in tone, ventral streaking and tail length are seen at this same boundary.

We also reveal significant, geographically structured phenotypic diversity among at least four distinct allopatric subpopulations of *modestus*. Tail length separates them. Tails in Central and North-western show no sexual dimorphism and are longer in the former. Tails in Flinders and Frome are sexually dimorphic and in males the latter are longer. Central *modestus* is more rufous and a little darker than all but Frome but is barely streaked ventrally. Some phenotypic diversity is also seen within *textilis*. Southern and Dirk Hartog Island birds are relatively darker than other *textilis* and northern inland birds are paler and have relatively "thicker" bills.

No subspecies are currently recognised within *modestus* (Schodde and Mason 1999) but several names have been applied previously, namely:

1. *modestus* (North, 1902), based on specimens taken west of Alice Springs.
2. *indulkanna* (Mathews, 1916), based on specimens taken near Indulkana Springs in north-western South Australia.
3. *inexpectatus* (Mathews, 1912), based on darker specimens from northern and central New South Wales (Parker 1972, MacAllan 1987, 2000).
4. *obscurior* (Mathews, 1923), based on pale and relatively unstreaked specimens from north-western New South Wales (McAllan 2000).

We reject treating *modestus* and *indulkanna* as synonyms because we have shown that the populations of *modestus* here termed North-western are paler and have much shorter tails. We recognise these as *A. m. indulkanna*. We apply *A. m. modestus* to the extinct central Australian population (Fig. 1) that occupied riverine sandhill canegrass shrubland, a habitat unique within the species (Black unpublished). We do this under the application of trinomials to diagnosable allopatric populations within species (Patten and Unitt 2002, Rising 2007, De Queiroz 2007, Winker and Haig 2010). The relationship between the Flinders, Frome and other less studied populations and the previously described subspecies (3 and 4 above) is not resolved here.

Taxonomic Summary

Species:

Amytornis textilis Western Grasswren: body generally dark brown, slightly paler below, with white shaft-streaks providing a strongly streaked appearance above and below; tail long to very long and longer in males; bill rather slender, generally lacking a strong convexity to the lower ramus.

Amytornis modestus Thick-billed Grasswren: body generally mid to pale brown (dark to light drab) above, much paler (light drab to drab grey) below, with white shaft-streaks providing a moderately streaked appearance above, moderately to barely streaked below; tail varying from moderately long to short, longer or of the same length in males; bill deep, the lower ramus generally showing a moderate or strong convexity.

Subspecies:

Amytornis textilis textilis (Dumont, 1824). Shark Bay region, formerly more widespread in Western Australia, description as for species above. Other presumed extinct populations currently considered under this taxon show variation in plumage and morphology as shown above and might represent one or more additional subspecies.

Amytornis textilis myall (Mathews, 1916). North-eastern Eyre Peninsula, SA. Distinguished from *A. t. textilis* by its shorter tail (Schodde 1982, Schodde and Mason 1999, Higgins *et al.* 2001, this study) and genetic divergence (Christidis *et al.* 2008) and from *A. modestus* by its longer tail in males (median 86.5, range 81.0-94.0 mm), darker plumage, heavier ventral streaking, more slender bill and allozyme differentiation (Christidis 1999).

Amytornis modestus modestus (North, 1902). Valleys of the MacDonnell Ranges, presumed extinct, distinguished from all other *modestus* populations in habitat choice, rufous tan toning in wing and tail feathers and darker but barely streaked underparts, from all but *A. m. indulkanna* by sexually monomorphic tail, and from *indulkanna* by its much longer tail (males, median 80.8, range 76.1-83.6 mm, females, median 80.9, range 74.1-83.0 mm).

Amytornis modestus indulkanna (Mathews, 1916). West of Lake Eyre and Lake Torrens, distinguished from the nominate by its shorter tail (males, median 68.8, range 65.1-73.8 mm, females, median 66.8, range 64.6-73.5 mm) and from other populations by sexually monomorphic tail.

Amytornis modestus subspecies. Flinders, Frome and populations north-east of Lake Eyre and in New South Wales, phenotypically diverse as shown above but incompletely evaluated.

A larger and more representative museum skin collection has allowed us to resolve several uncertainties surrounding the phenotypic diversity, taxonomy and nomenclature of the *A. textilis-modestus* group of grasswrens (Parker 1972; Schodde 1982, Schodde and Mason 1999).

We affirm that there are two species and show statistically that each is polytypic, despite small sub-sample size in some cases.

The four local populations of *A. modestus* defined here occupy a number of reasonably discrete drainage systems. *A. m. modestus* occurred in river valleys of the central Australian mountain ranges while *A. m. indulkanna* covers rivers draining into Lake Eyre from the west, reaching the Stuart Shelf in the west and crossing into the western Lake Torrens Basin in the south. The Flinders population is defined by the many watercourses draining the North Flinders Ranges towards southern Lake Eyre, Lake Blanche and Lake Callabonna and the Frome population by those of the south-western Lake Frome Basin. Further, *A. t. myall* generally occupies the two largest drainages of north-eastern Eyre Peninsula, Myall Creek and Pine Creek.

Understanding the causes of the diversity we have shown in both species and more that is incompletely evaluated is a challenge for future work. Christidis *et al.* (2010) showed that plumage differentiation in *Amytornis* is taxonomically significant and not as much influenced by ecophenotypic variation as previously thought; the near total loss of these grasswrens from Western Australia, New South Wales and the Northern Territory is not only contraction of range but extinction of local populations, some at least with taxonomic status. Conservation action is ineffective unless diversity is recognised, preferably taxonomically; some taxa within the *A. textilis-modestus* complex may be extinct before their true status is known.

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Table 1. Comparison of male tail lengths between populations

Population	N	Range	Median	95% CI	Significance
textilis	17	82.4-101.4	91.9	87.2-93.8	*1
myall	12	81.0-94.1	86.5	84.1-88.1	*1, 2
modestus					*2
Central	6	76.1-83.6	80.75	76.1-83.6	*3
North-west	8	65.1-73.8	68.8	65.1-73.8	*3
Flinders	11	69.3-77.8	74.6	70.9-77.4	*4
Frome	3	77.6-78.8	78.0		*4

*1 *textilis* > *myall* $p \approx 0.01$

*2 *myall* > Central $p < 0.01$; *myall* > all *modestus* $p < 0.01$

*3 Central > North-west $p < 0.01$

*4. Frome > Flinders $p \approx 0.025$

Table 2. Comparison of other parameters between *textilis* and *myall*

	Population	N	Median	95% CI	Significance
Wing	*textilis*	16	66	64-68	
	myall	13	63	62-66	$p \approx 0.05$
Tarsus	*textilis*	13	26.8	24.8-28.1	
	myall	13	25.5	24.1-26.4	$p \approx 0.05$
Bill length	*textilis*	16	12.4	12.2-13.4	
	myall	13	13.9	13.5-14.6	$p < 0.01$
Bill depth	*textilis*	16	5.45	5.3-5.7	
	myall	13	5.8	5.7-6.1	$p < 0.01$
Bill ratio	*textilis*	16	2.3	2.2-2.48	
	myall	13	2.36	2.3-2.46	NS

Fig. 1. Localities of *myall* (arrowed) and *modestus* (other populations) specimens examined (closed circles), defining distributional records of populations (open squares), place names (closed triangles). Insert shows accepted *textilis, myall* and *modestus* records across Australia; Dirk Hartog Island and Shark Bay arrowed.

Fig. 2. Factor analysis of male specimens; within *modestus*, Central (open squares), North-western (open triangles), Flinders (+), Frome (open diamonds); within *textiles, myall* (closed squares), northern inland (asterisks), Shark Bay (closed triangles), DHI (closed diamonds) and the south-east specimen (grey diamond). Loadings for Factor 1 are tail length (0.89), wing length (0.77) and bill depth (-0.71); for Factor 2 bill length (-0.87) and bill ratio (-0.87). Note that plumage variables separating many populations and tail length sexual dimorphism are not represented in this analysis.