Genetic Differentiation and Subspeciation in the Grey Grasswren *Amytornis barbatus* (Maluridae)

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Despite intensive studies of infra-specific variation in Australian birds over the last 50 years, there have been no concerted attempts to survey genetic diversity or to identify unique populations or gene pools throughout major taxonomic groups. This paper is one in a series investigating these aspects in the families Acanthizidae and Maluridae.

From its discovery as late as 1968, the Grey Grasswren *Amytornis barbatus* has been considered monotypic (Schodde 1982a). Principal reasons for this were its confinement to pockets of lignum *Muehlenbeckia cunninghamii* covered flood plain in the central Great Artesian Basin of Australia and the dearth of specimens available for assessing infra-specific variation after sexual dimorphism in size was taken into account.

Since then, Joseph (1982) and May (1982) have reported further localised populations on lower Cooper Creek, along the Kallakoopah anabranch of the Diamantina (= Warburton) River, and in the overflow of Lakes Machattie, Koolivoo and Mipia on Eyre Creek (Fig. 1). These discoveries led Joseph to identify three main isolated populations, one each on the Bulloo, Cooper-Diamantina and Eyre Creek systems, and to draw attention to impediments to gene flow between them. Further specimens collected for the present study now allow some resolution of these questions.

Materials and methods

Eleven specimens of *Amytornis barbatus* from the lower Bulloo drainage (eight males, three females) and twelve specimens from Goyder Lagoon (seven males, five females) were examined from the Australian Museum, Sydney (AM); the Australian National Wildlife Collection, CSIRO, Canberra (ANWC); the Museum of Victoria, Melbourne (NMV); the South Australian Museum, Adelaide (SAM); and the Western Australian Museum, Perth (WAM). No specimens are yet available from the Eyre Creek population. Measurements taken were: wing (flattened chord of the manus), tail (length of longest of two central tail feathers from base), tarsus (notch on heel to last unsplit scute on base knuckles of toes), bill (chord of exposed culmen) and weight. Because only two populations were compared, the significance of mean differences between them in morphometric traits was estimated by Student's *t*-statistic.

Liver, muscle and heart tissue from the ten freshly-collected specimens (five from the Bulloo drainage, five from Goyder Lagoon) were excised and stored in liquid nitrogen. Samples from each individual and those from other species of grasswren were

then screened electrophoretically for 37 enzyme systems representing 45 presumptive loci as outlined in Christidis & Schodde (submitted to Aust. J. Zoology). The other species examined were: Eyrean Grasswren *Amytornis goyderi* (n = 10), Black Grasswren *A. housei* (n = 3), Dusky Grasswren *A. purnelli* (n = 6), Eyre Peninsula Thick-billed Grasswren *A. textilis myall* (n = 2) and eastern Thick-billed Grasswren *A. t. modestus* (n = 8). Genetic distances in the electrophoretic data were calculated by the method of Nei (1978).

Results

Populations of *Amytornis barbatus* on Goyder Lagoon and the lower Bulloo drainage differ between one another in dorsal tone, intensity of markings and size. Those on the Diamantina are significantly larger (Table 1; *cf.* Schodde 1982a), more finely and sparsely double-streaked dusky over the breast and brighter, more reddish cinnamon dorsally with thinner and more blurred black streaks which serve to enhance the russet tone. The contrast in colouring is shown in the illustrations of Grey Grasswrens in Readers' Digest (1976 — Bulloo group) and by Weatherly in Schodde (1982a — Diamantina group). That the differences have a zoogeographical basis is indicated by the occurrence of the two populations in drainage basins that are palaeogeographically separate, as explained below.

Differentiation is not evident in tissue isozymes scored. This is surprising because *Amytornis textilis myall* and *A. t. modestus*, which are hardly more disparate morphologically (Schodde 1982a), differ at four loci with a genetic distance of 0.023. Even so, the level of genetic differentiation within *Amytornis* is lower than that in another Australian genus, *Sericornis* (Christidis *et al.*, submitted to Auk), leading us to suggest that little or no isozymic divergence would be expected if, as seems to be the case in *Amytornis*, the subspecies are recently evolved.

Within *Amytornis*, however, *A. barbatus* does stand apart from the other species genetically, as predicted by Schodde (1982a), from its morphological traits (*pace* Ford 1974). Based on differentiation at the 45 presumptive loci, the genetic distance between *barbatus* and other species is 0.234 (*s.d.* 0.048, *s.e.* 0.012) compared with a mean distance of only 0.120 (*s.d.* 0.030, *s.e.* 0.012) among the other species. Accordingly, the *barbatus* lineage is distinguished here as a new monospecific subgenus and its Diamantina River river population named as a new subspecies:

Amytornis *subgenus* Maluropsis, subgen. nov.

Type species: *Amytornis barbatus* Favaloro & McEvey, 1968.

Diagnosis: Face patterned black and white with broad white superciliary stripe and black stripe from lores through eyes linked to thin black malar line around sides of throat; tail greatly attenuated with tapered rectrices, the centre pair of which extend > 5 mm beyond the adjacent pair; no sexual dimorphism in colour of flanks or belly. Eggs heavily marked.

The name *Maluropsis* reflects the *Malurus*-like traits of this species in morphology and behaviour (Schodde 1982a).

Amytornis barbatus diamantina, *subsp. nov.*

Holotype: ANWC 40144 (field no. D167), female adult: vicinity of Koonchera Water-hole, Goyder Lagoon, Diamantina (= Warburton) River, SA; coll. J.C. Wombey, 10 September 1985. Wing 59 mm, tail 107 mm, tarsus 28.5 mm, exposed culmen 9.8 mm, weight 21 g.

Paratypes: ANWC 40141, 40145 male adults, ANWC 40142 female adult, Koonchera Water-hole; SAM B30318, male adult, SAM B30317, female adult, Pandiburra Bore, Goyder Lagoon.

Diagnosis: Dorsum bright reddish cinnamon without greyish bloom; dusky edges to white shaft streaks narrow and rather diffuse, giving the impression of sparser and duller dusky dorsal streaking than in nominotypical *barbatus*. Ventral surface marked with rather fine and sparse

dusky double-streaks across breast, often fading out on mid breast. Size large: wings 60-64 mm ♂♂, 57-60mm ♀♀; tails 105-115 mm ♂♂, 99-109 mm ♀♀; exposed culmen 10-12 mm ♂♂, 10-10.5 mm ♀♀.

Distribution: flood plains of lower Diamantina (= Warburton) River system south (downstream) to the Kallakoopah Creek junction, South Australia, and north (upstream) presumably to the overflows of Lakes Mipia, Koolivoo and Machattie on Eyre Creek, Queensland. It is probably also this form that has been recorded on Lake Cudappan on the Diamantina–Cooper divide in far south-west Queensland and at Embarka Water-hole on Cooper Creek west of Innamincka where it may extend through other flood pans north to the Coongee Lakes, S.A. (Fig. 1)

Origin and subspeciation

Amytornis goyderi and *A. barbatus* are the two grasswrens endemic to a huge central Australian drainage basin centring on Lake Eyre, the Birdsville structural basin (Veevers & Rundle 1979; Wasson 1982). This sunk-land extends west to the central Precambrian shield and central Australian ranges, north to the Selwyn Range-Winton ridge, south to the Olary Arch-Barrier Ranges, and east to the Gowan Range and other western outliers of the Great Dividing Range (Fig. 1). Because the two grasswrens are sedentary ground and tussock living birds, the more recent palaeogeographic history of the basin can be expected to hold clues to their origin and evolution. Since early to mid-Tertiary times, the lakes and rivers that prevailed over its landscape gradually declined as climate became more arid, culminating in the development of two large dune deserts, the Simpson and Strzelecki, within the last million years

TABLE 1 Morphometric comparison of available samples of *Amytornis barbatus* from the Bulloo River overflow and Goyder Lagoon. (Data for each variable are its mean ± one standard deviation.)

	Bulloo	Goyder Lagoon	t-value[a]
		MALES	
Sample size	8	7	
Wing	58.5 ± 1.1	62.7 ± 1.4	6.46***
Tail	101.8 ± 7.3	109.9 ± 2.9	2.74**
Tarsus	24.7 ± 0.6	25.2 ± 1.5	0.88 *n.s.*
Culmen	9.7 ± 0.7	11.1 ± 0.7	3.89***
Tail/wing ratio	1.74 ± 0.12	1.75 ± 0.04	0.25 *n.s.*
		FEMALES	
Sample size	3	5	
Wing	56.3 ± 1.5	58.6 ± 1.5	2.09 (*n.s.*)
Tail	94.3 ± 4.5	103.6 ± 5.0	2.63*
Tarsus	23.4 ± 0.4	26.3 ± 1.6	2.99*
Culmen	9.0 ± 0.8	10.1 ± 0.3	2.89*
Tail/wing ratio	1.68 ± 0.08	1.77 ± 0.09	0.14 *n.s.*

[a] Superscripts to the value of *t* indicate the following probabilities: not significant = *n.s.* > 0.05, * < 0.05 > 0.02, ** < 0.02 > 0.01, *** < 0.01. Bracketed *n.s.* indicates a probability of < 0.10 > 0.05 close to the latter value.

(Krieg & Callen 1980; Bowler 1982; Wasson 1982, 1983). Although lacustrine conditions have shrunk since the Miocene they never disappeared and still persist locally today among the dune fields (Wasson 1983).

Within the basin, *Amytornis goyderi* occupies hummock canegrass *Zygochloa paradoxa* on the sand ridges of both dune deserts, that are linked to one another throughout the Mulka corridor or Kopperamanna gap and Tirari Desert (Fig. 1; *cf.* Schodde 1982a; Wasson 1983). These dune fields, probably formed in the Bruhnes normal palaeomagnetic epoch, would be less than 700 000 years before present (BP) in age and perhaps no older than 600 000-500 000 years (Twidale 1972; Wasson 1982, pers. comm.), and they date the earliest possible origin of *Amytornis goyderi* unless it arose in regions outside. This, incidentally, is a remarkably precise date and can be used for calibrating rates of protein evolution in *Amytornis* and, indeed, birds in general, given molecular change at a constant rate through time (Avise & Aquadro 1982).

Amytornis barbatus is restricted to structurally similar hummocks of dense lignum (*Muehlenbeckia*) but, by contrast, on major drainage lines between the dune systems.
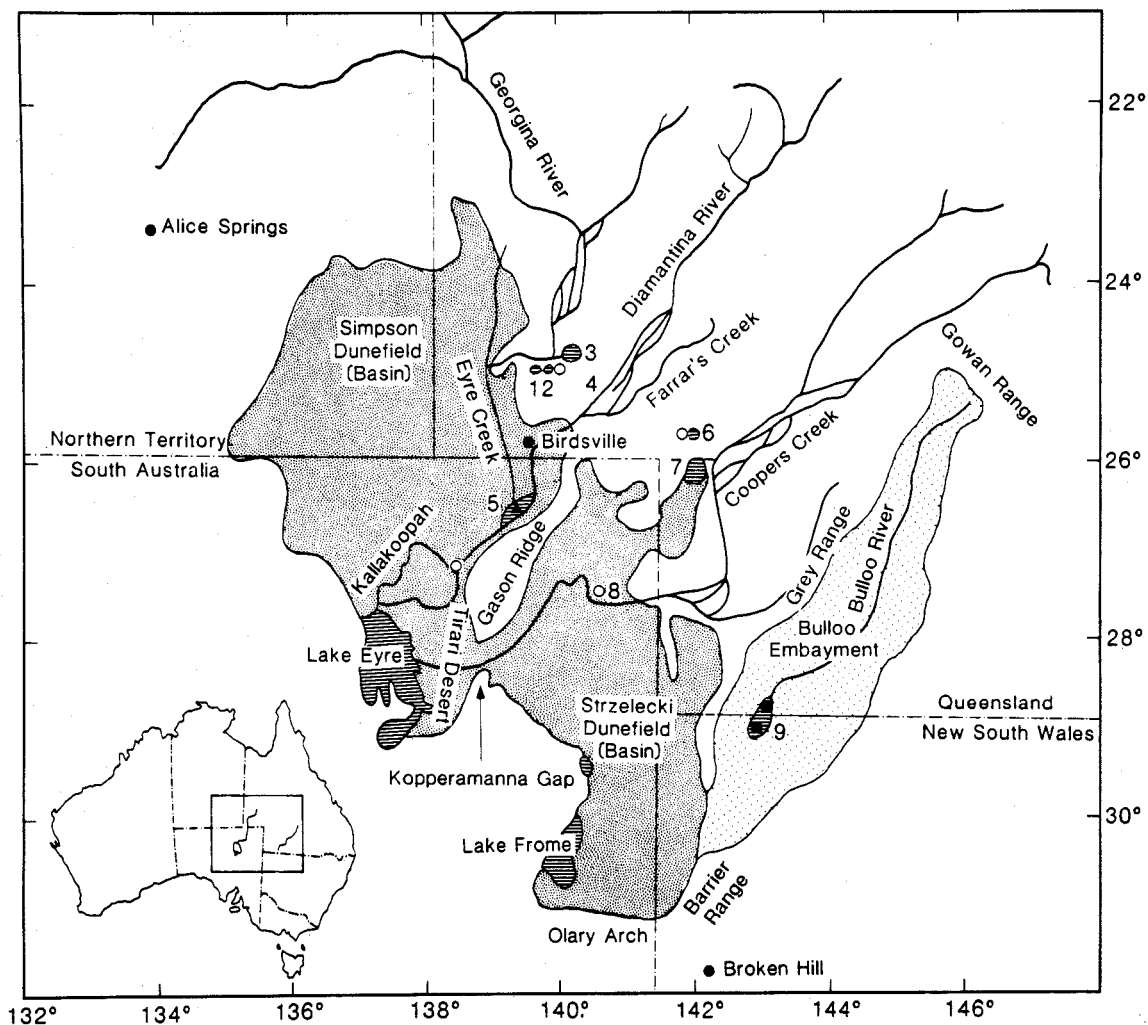

FIGURE 1 Structural features and localities in Birdsville structural basin. Numbers indicate additional localities mentioned in text, as follows: 1 Lake Mipia; 2 Lake Koolivoo; 3 Lake Machattie; 4 Bilpa Morea Claypan; 5 Goyder Lagoon; 6 Lake Cudappan; 7 Lake Yamma Yamma; 8 Embarka Water-hole; 9 Bulloo overflow. Legend to symbols: ▲ — specimen records of *Amytornis barbatus diamantina* o — presumed sight records of *A.b. diamantina* ■ — specimen records of *A. b. barbatus.*

Ford (1974) contended that it and *goyderi* were derivatives of the Striated Grasswren *Amytornis striatus*, that had adapted to non-spinifex (*Triodia*) habitats, so implying that both had speciated parapatrically and recently. Mayr's (1986) arrangement of the species of *Amytornis* reflects this relationship. Schodde (1982a, b), however, interpreted *barbatus* as a separate and older form on the grounds of its morphological traits and occurrence in a relict or at least older lacustrine habitat in the Birdsville basin. The genetic distances quoted above between *barbatus* and other species of *Amytornis* support this latter view. Even so, it is not yet possible even to guess how proto-*barbatus* diverged from ancestral stocks of *Amytornis* and established itself in the region.

The dune systems that connect populations of *A. goyderi* in the Birdsville basin today divide and fragment those of *A. barbatus*. In such a communally territorial species with weak powers of flight (Schodde 1982a), dispersal is limited and even local isolation may promote divergence and subspeciation. Enclaves of *barbatus* are potentially in contact only along continuous drainage lines, such as those of the Georgina, Diamantina, Cooper or Bulloo river systems. For this reason it seems likely, pending confirmation from specimens, that the various groups on the Kallakoopah anabranch of the Diamantina, at Lakes Machattie-Mipia, and probably on Lake Cudappan and Embarka Waterhole on the Cooper, belong to the same form as those on Goyder Lagoon, despite distances of up to 200 km between them (*cf.* Joseph 1982). All of them occur on interconnected drainage lines, through which Lakes Machattie-Mipia are linked directly to Goyder Lagoon via Eyre Creek or the Bilpa Morea claypan and Diamantina River; and where Lake Cudappan and Embarka waterhole are linked to the lower Diamantina by a system of lignum-covered pans along the lower Cooper and through the Tirari Desert (Fig. 1). Each local population may be isolated from one another today, but they were probably in contact during pluvial lacustrine phases in arid Australia between 50 000-20 000 years BP and perhaps again between 8000-6000 years ago when the climate was wetter than now (Bowler *et al.* 1976; Bowler & Wasson 1983). During those times, surface waters and fringing lignum-covered pans were probably more widespread through the Simpson-Strzelecki Deserts, effecting a spreading of local enclaves of *A. barbatus* there and more extensive gene flow among them.

Isolated in the lower Bulloo basin by the Grey Range, the local population of *A. barbatus* has been separated from those in the Cooper-Diamantina drainage for a longer period, sufficient for significant morphological divergence. This could date theoretically from the epeirogenic raising of the Grey Range in Oligocene-early Miocene times to the final closing of the Bulloo embayment, perhaps as recently as 40 000-50 000 years BP (Wopfner 1974; Wasson 1982, pers. comm.). Because there is yet little or no isozymic

differentiation between Bulloo and Diamantina populations, the latter date is probably much the closer.

There remains the issue of the conservation of unique populations of Grey Grasswrens. If, as seems likely, the scattered enclaves through the lower Diamantina-Cooper drainages belong to a single form, that subspecies is in little immediate danger. The distinct population restricted to the lower Bulloo, however, is much more vulnerable because of its limited range. Protection of it and its habitat should come first in any ranking of priorities.

Acknowledgements

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The Unusual Syrinx Morphology of Australian Treecreepers *Climacteris*

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The six species of Australian treecreepers constitute a fairly homogeneous group usually now considered to constitute a distinct family Climacteridae. The group has given considerable difficulty to taxonomists, who disagree on whether the treecreepers evolved within a general bark-foraging assemblage that includes the holarctic creepers (*Certhia*), nuthatches (*Sitta*) and sittellas (*Daphoenositta*), among others, or within an Australo-Papuan oscine radiation. The latter view, which appears to be gaining prevalence, has been expounded by Sibley *et al.* (1984), who provide an excellent taxonomic history of the genus *Climacteris*. They provide evidence from DNA-DNA hybridisation that the treecreepers represent an ancient diversion from the evolutionary line that produced the rest of the Australo-Papuan oscines. Parker (1982), in a paper arguing for a relationship between the treecreepers and the honeyeaters (Meliphagidae), also summarises the taxonomic history of the treecreepers. In this paper, I provide evidence from the syringeal morphology supporting the view that the treecreepers diverged from the oscine line long ago.

In a broad survey of the passerine syrinx (Ames 1971, 1975), I studied the syrinx in four specimens, representing three of the six species of treecreepers: *Climacteris rufa* (two specimens), *C. affinis*, and *C. melanura*. I found in all three species a striking departure from the basic muscle

pattern that prevails throughout the rest of the oscines. Unfortunately, the uniqueness of the syrinx in the treecreepers has so far prevented its use in determining their nearest relatives.

I removed the syrinx from the preserved whole bird or skinned 'carcass' essentially as described by Ames (1971). Following the recording of muscle patterns on a layer-by-layer basis, the muscles of one side were removed so as to note the structure of the underlying bony and cartilaginous elements.

The nomenclature of syringeal muscles employed here is that of Owen (1866), modified slightly (for synonymy, see Ames 1971; George & Berger 1966; or Baumel *et al.* 1979). There are two pairs of extrinsic muscles, *M. tracheolateralis* and *M. sternotrachealis*, and four pairs of intrinsic ones *M. bronchotrachealis posticus, M. bronchotrachealis anticus, M. bronchialis posticus* and *M. bronchialis anticus*. The last of these usually comprises two parts, *pars medialis* and *pars lateralis*, which may be quite distinct or may be one continuous muscle sheet.

The oscine syrinx

In all oscines described before this paper, about 800 species from warblers to ravens, including all of the purported