A review of phenotypic diversity within the Copperback Quailthrush *Cinclosoma clarum* Morgan, 1926, and recognition of a third subspecies from Eyre Peninsula

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Abstract

The Copperback Quailthrush Cinclosoma clarum *is a highly variable species. The brown backed nominate subspecies* C. clarum clarum, *extensively rusty toned above in both sexes, is present in Central Australia and the Great Victoria Desert. The grey backed* C. clarum fordianum *with a narrow chestnut back band in males and a faint band or no band in females is restricted to the subhumid south-west of Western Australia and southern subcoastal regions extending into south-western South Australia. North of the latter distribution in Western Australia, the species has an extensive range, its population comprising a variety of mostly intermediate phenotypes. This constitutes a hybrid swarm. We have detected no zone of clinal intergradation, as interpreted previously. On Eyre Peninsula and in the Gawler Ranges we document a third distinct phenotype, similar to* C. clarum clarum *but with reduced rusty-toned plumage. It is distinguished from* C. clarum fordianum *in its browner tone, rusty coloured back band and limited sexual dimorphism. We reinstate this as a third subspecies* C. clarum morgani.

INTRODUCTION

Species- and subspecies-level taxonomy of quailthrush *Cinclosoma* spp. has been undergoing revision in recent years (Schodde and Mason 1999, Toon *et al.* 2012, Dolman and Joseph 2015, 2016). Much interest has centred on what was thought until recently to be a single species having a vast distribution across southern Australia, the Chestnut Quailthrush, *Cinclosoma castanotum* Gould, 1840. Under that concept, Morgan (1926) described a subspecies *Cinclosoma castanotum clarum* from the northern Gawler Ranges. Later submerged in synonymy or ambiguity, this subspecies was formally reinstated by Schodde and Mason (1999) as one of three subspecies that they recognised within *Cinclosoma castanotum*, namely *C. ca. castanotum* of the south-eastern Australian Mallee, *C. ca. clarum* of Central Australia and the Great Victoria Desert, west to Shark Bay, Western Australia (WA), and *C. ca. fordianum* Schodde and Mason, 1999 in southern WA and south-western South Australia (SA). Schodde and Mason (1999) distinguished the plumages of the three subspecies as shown in Table 1; they also found evidence of broad zones of intergradation across inland WA and Eyre Peninsula (Figure 1).

Following Toon *et al.*'s (2012) phylogenetic review of the genus and Dolman and Joseph's (2015, 2016) phylogeographic study of southern Australian birds, two sister species are now recognised, monotypic Chestnut Quailthrush, *C. castanotum* and Copperback Quailthrush, *Cinclosoma clarum*, separated across the historical biogeographical 'Eyrean Barrier' (Ford 1987), the latter with subspecies *C. clarum clarum* and *C. clarum fordianum*. The Copperback Quailthrush has a vast range in eucalypt, *Casuarina* and *Acacia* woodlands and shrublands west of Lake Torrens and Spencer Gulf, SA, through southern WA to the Indian Ocean at Shark Bay (Figure 1). It is the broad aim of this paper to further examine geographical variation within the species *C. clarum*.

The English name Copperback Quailthrush recognises the bright (*clarum*) rusty or copper-coloured plumage over much of the dorsum of what is now its nominate subspecies *C. cl. clarum*. Both the colour and its extent distinguish

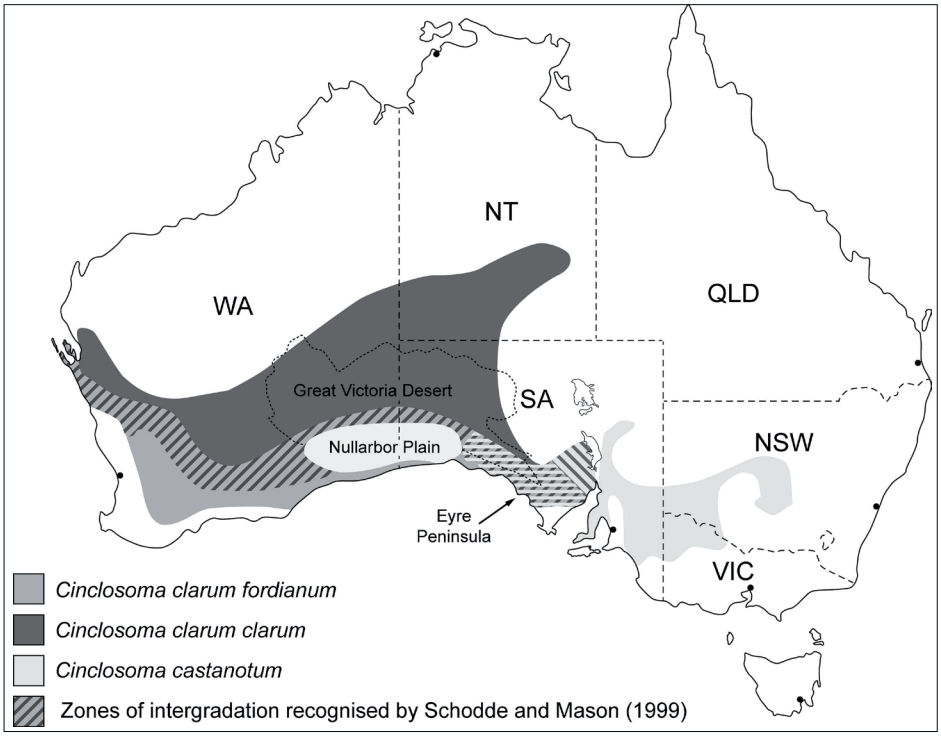

Figure 1. The distribution of sister species *Cinclosoma castanotum* **and** *Cinclosoma clarum***, as mapped by Schodde and Mason (1999), modified to recognise the two-species taxonomy. The extent of the Great Victoria Desert is outlined, including its south-eastern extension, the Yellabinna. Map B. Cale**

it from the darker and narrower chestnut back band on males of the slightly greyer Chestnut Quailthrush, *C. castanotum*. The second Copperback Quailthrush subspecies *C. cl. fordianum* more closely resembles *C. castanotum* and was long regarded as identical to that taxon (Campbell and Campbell 1926, Ford 1981). Their similarity is evident in their males both having back bands that are of similar tone and are narrower than the extensive area of brighter tone on the backs of *C. clarum clarum*. They are similar also in that the females of each have narrower and poorly defined back bands, whereas there is little difference between the sexes in the expression of that character in *C. clarum clarum*. Distinguishing *C. clarum fordianum* from *C. castanotum* are the colder grey-toned upperparts of the former, the more consistently dark feather centres of which provide streaking to the crown and patterning over the mantle (Table 1).

Ford (1974 a, b, 1981, 1983) interpreted south-to-north variation in the plumage of *C. castanotum sensu lato*, as clinal. Within its western populations [= *C. clarum*] he reported narrow back bands on Eyre Peninsula (EP) and in southern WA and broad back bands in Central Australia (CA) and the Great Victoria Desert (GVD) (Ford 1981, 1983). Johnstone and Storr (2004) recognised no subspecies in Western Australia and likewise found the extreme phenotypes [of *C. cl. clarum* and *C. cl. fordianum*] to be connected through a broad intergradient zone across the interior of WA. Earlier reviewers had recognised these intermediate forms taxonomically, with *C. castanotum dundasi* Mathews, 1912 in southern WA and *C. castanotum morgani* Condon, 1951 on Eyre Peninsula.

Our specific aims are firstly to compare the plumage of Copperback Quailthrush, *Cinclosoma clarum* with its sister species Chestnut Quailthrush, *Cinclosoma castanotum* and secondly to closely explore variation and subspeciation within the former.

METHODS

We examined skins of all adult *C. castanotum* (20 males and 13 females) in the South Australian Museum, Adelaide (SAMA) and all adult *C. clarum* (99 males and 63 females) in SAMA, Western Australian Museum, Perth (WAM) (AB only), Australian National Wildlife Collection, Canberra (ANWC) and Natural History Museum, Tring UK (PH only).

We initially examined plumages among the three identified taxa, monotypic *C. castanotum* and the subspecies *C. clarum clarum* and *C. clarum fordianum,* and compared our findings with those of Schodde and Mason (1999) (Table 1). Our review of colour made use of the web-based colour guide http://en.wikipedia.org/wiki/Shades_of_red . We then assessed each specimen of *C. clarum* from throughout its range, according to the following plumage characters: overall dorsal tone, between grey and brown, the strength of crown streaking and mantle patterning, colour of the back band, from bright/rusty to dark/chestnut, and its breadth (to the nearest 5 mm) when present, and its extension onto scapulars and tertial fringes.

We assessed an additional character (in SAMA and ANWC skins only), following the

Table 1. Distinguishing plumages of three taxa within the *Cinclosoma castanotum-clarum* complex, as provided in this review and by Schodde and Mason (1999) (SM99).

Phenotype	Crown to mantle		Back band colour and width		Extension of dorsal colour	
	This study	SM99	This study	SM99	This study	SM99
castanotum						
male	Greyish brown	Warm mid greyish brown	35-55 mm, maroon chestnut	25-45 mm, deep burgundy chestnut	As SM99	to scapulars but hardly reaching coverts
female	As males	Cold mid umber grey	30-40 mm, duller or indistinct	Little or none, deep chestnut	To scapulars in a minority	unstated
clarum						
male	Brown to greyish brown	Warm greyish brown	≥80 mm, chestnut rust to chestnut tawny	>70 mm, mid to deep chestnut rust	To scapulars, coverts and tertials	To scapulars, secondary coverts and secondaries
female	As males	As males but duller	≥75 mm and as bright	Narrower and less defined #	Similar but more variable	unstated
fordianum						
male	Cold grey	Cold mid umber grey	30-60 mm, chestnut to sienna chestnut	45-55 mm, deep burgundy chestnut	As SM99	traces to scapulars, or none
female	Grey to brownish grey	Warm mid greyish brown	20-35 mm, duller or absent	Extensive; dull deep chestnut brown #	None observed	unstated

This appears to result from a publication error, findings in female *clarum* and female *fordianum* being transposed. Our review corroborated Higgins and Peter (2002) and Johnstone and Storr (2004).

observation that the extent of the black (in males)/grey (in females) chin, throat and upper breast as a proportion of ventral plumage, while variable, appeared to differ between populations. This character, the "bib ratio", was calculated as the length of black/grey plumage from the proximal tip of feathering under the bill to its midline junction with white plumage, as a proportion of total length from the same point to the vent. In order to avoid inconsistencies arising from differences of skin preparation, including the degree of head flexion, a soft tape measure was placed along the ventral surface of the specimen, following its contours closely. All measurements are necessarily approximate. Ratios were compared between populations using the Mann-Whitney U Test https://www.socscistatistics.com/tests/mannwhitney/default2.aspx

RESULTS

Diversity in dorsal plumage

C. castanotum

Males are greyish brown above and have a narrow chestnut back band with extension to the scapulars. Females are of similar colour above but have only an ill-defined and narrower back band, and rarely with extension to scapulars.

C. clarum

We identified specimens of *C. clarum* with a wide range of phenotypes. Many corresponded closely with those given by Schodde and Mason (1999) (Table 1, Figure 2) but others showed a variety of intermediate features (Figure 3).

For simplicity we will refer to the colour of back bands as chestnut in *C. castanotum* and *C. clarum fordianum* and rusty in *C. clarum clarum*.

C. clarum clarum

Males and females are similar, typically brown or greyish brown above, with a broad (see Table 1), bright rusty back band that extends to the scapulars and tertial fringes. All 10 CA and all but 2 of 27 male and 4 of 11 female GVD specimens were of this phenotype. The exceptions were mostly located towards the southern margin of the GVD. This identified the exclusive distribution of subspecies *C. cl. clarum*.

C. clarum fordianum

Males are cold grey above with dark crown streaking and mantle patterning, and a narrower (see Table 1) back band of a darker chestnut, very like that of *C. castanotum*. Most females are slightly more brownish grey above but show similar dark patterning. Some are completely unbanded, others have a faint, dull back band even narrower than in males. The exclusive distribution of *C. cl. fordianum* is established by 22 specimens of this phenotype from the sub-humid south-west of WA and across a subcoastal strip south of the Nullarbor Plain. An additional male from south-east of the Nullarbor Plain in SA was also typical (SAMA B55864).

Table 2. Bib ratios for populations in the *Cinclosoma castanotum-clarum* complex. The ratio represents the proportion of black/grey plumage from bill to vent. Results of statistical comparisons are in the right column (n.s. = not significant).

Population	Mean bib ratio (standard deviation; range; number of specimens)	Mann-Whitney U test p-values
C. castanotum	0.46 (0.04; 0.39-0.54; 36)	0.79 males *vs* females (n.s.) 0.00001 *vs C. clarum*
C. clarum	0.53 (0.05; 0.44-0.64; 48)	0.64 males *vs* females (n.s.)
C. clarum clarum	0.55 (0.05; 0.45-0.64; 27)	0.0009 *vs C. clarum* (Eyre Peninsula)
C. clarum (Eyre Peninsula)	0.50 (0.03; 0.44-0.55; 17)	0.006 *vs C. castanotum*

Figure 2. Male specimens of three taxa, showing dorsal plumage patterns discussed in the text. From left: *Cinclosoma clarum fordianum* (SAMA B55864, 67 km WNW of Yalata, western SA, L. P. Pedler 27 October 2007); *C. castanotum* (SAMA B56156, boundary of Gluepot Reserve and Parcoola Station, Murray Mallee SA, L. P. Pedler 13 April 2009)*; C. clarum clarum* (SAMA B58878, 48 km NW of Maralinga, Great Victoria Desert SA, G. H. Pfitzner 5 August 2007). Image P. Horton

Variable plumages across inland WA

In the broad intervening region occupied by *C. clarum* in inland WA, a wide range of phenotypes was recognised. Nine of 43 males and 2 of 24 females had back bands within the *C. cl. clarum* range, while 11 male and 5 female specimens had back bands of *C. cl. fordianum* width. The remaining 23 male and 17 female specimens had back bands of intermediate breadth. Many in all categories showed discordant combinations of plumage variables (see Discussion).

A third phenotype

Specimens from central and eastern Eyre Peninsula and the Gawler Ranges, excluding the holotype of *C. cl. clarum* from the northern periphery of the Gawler Ranges, showed a third consistent phenotype, unlike the variation found through much of WA. The seven males had rusty back bands of between 55 and 70 mm, the plumage colour extending to scapulars and tertials, as in *C. cl. clarum*, while ten females had similarly coloured back bands of between 40 and 65 mm, with extension of colour to the scapulars in over half and variably to tertial fringes.

Diversity in ventral plumage

We found no significant difference between males and females in bib ratio measurements for either *C. castanotum* or *C. clarum*. The sexes were therefore pooled for comparisons, initially between *C. castanotum* and *C. clarum*, and subsequently between populations within *C. clarum*. The available sample of *C. cl. fordianum* was too small for statistical analysis but samples were sufficient for comparison between *C. cl. clarum* and the Eyre Peninsula population identified above. Measurements of bib ratio are shown in Table 2.

Mapping

The distribution of phenotypic diversity is

Figure 3. Specimens of intermediate plumage. From left: *Cinclosoma clarum clarum x C. cl. fordianum* male (grey *fordianum* back colour with intermediate width band, SAMA B55919, east of Colona Homestead, western SA, L. P. Pedler 8 April 2008); Eyre Peninsula *C. clarum* male (in fresh plumage, SAMA B27520, 46 miles north of Cowell, SA Museum party 26 May 1965); Eyre Peninsula *C. clarum* female (in worn plumage, SAMA B23064, 23 miles SW of Iron Knob, F. E. Parsons 13 September 1925). Image P. Horton

illustrated in two maps. Figure 4 shows back band width in three categories, as determined for each subspecies in Table 1, and for others of intermediate width. Figure 5 gives a composite of three phenotypic variables, each given a value of between one and three. Overall dorsal tone was assessed as grey (=1), intermediate (=2) or brown (=3) and back band tone as chestnut (=1), intermediate (=2) or rusty (=3). Band widths were quantified according to those provided in Table 1: *fordianum* =1, intermediate =2, *clarum* =3. The total score for a specimen is the sum of those three values (range 3 to 9).

DISCUSSION

Plumage

Neither Ford (1981) nor Schodde and Mason (1999) found that morphometric data provided a basis for subspecific division within the *C. castanotum-clarum* complex, and so they were not considered in this study. Ford's (1981) review rested largely on the breadth of back bands. Schodde and Mason (1999) addressed additional plumage characters, allowing them to define three taxa, what is now monotypic *C. castanotum* and two subspecies, *C. cl. clarum* and *C. cl. fordianum*, of what is now recognised as *C. clarum*. Our findings support both Ford (1981) and Schodde and Mason (1999), although they differ in some details and in the taxonomic framework of recognising two species. We assessed several plumage variables independently: the overall tone of crown and dorsum and the strength of dark patterning on those parts, the breadth of the back band, and the tone of the band.

In an assessment of ventral plumage, we found that a previously unrecognised character, the mean bib ratio, was significantly smaller for

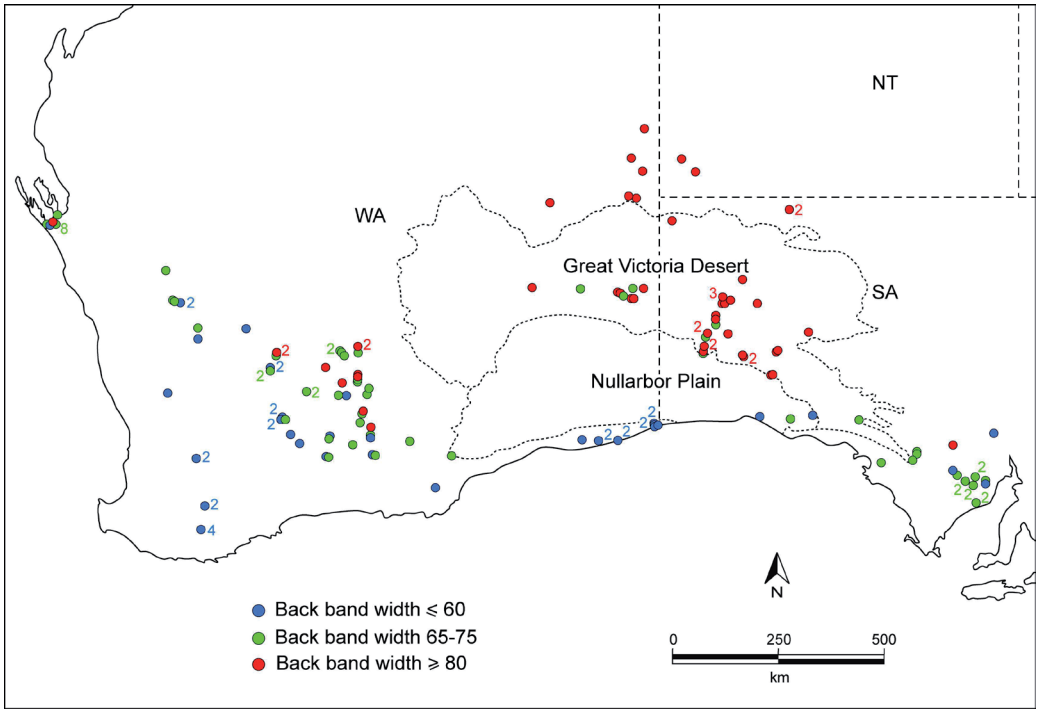

Figure 4. Distribution of phenotype, according to back band width, for all specimens. Note that red circles indicate bands ≥75 mm in females, blue circles ≤35 mm and green circles bands of intermediate width (measurements for males only are given on the map). Map B. Cale

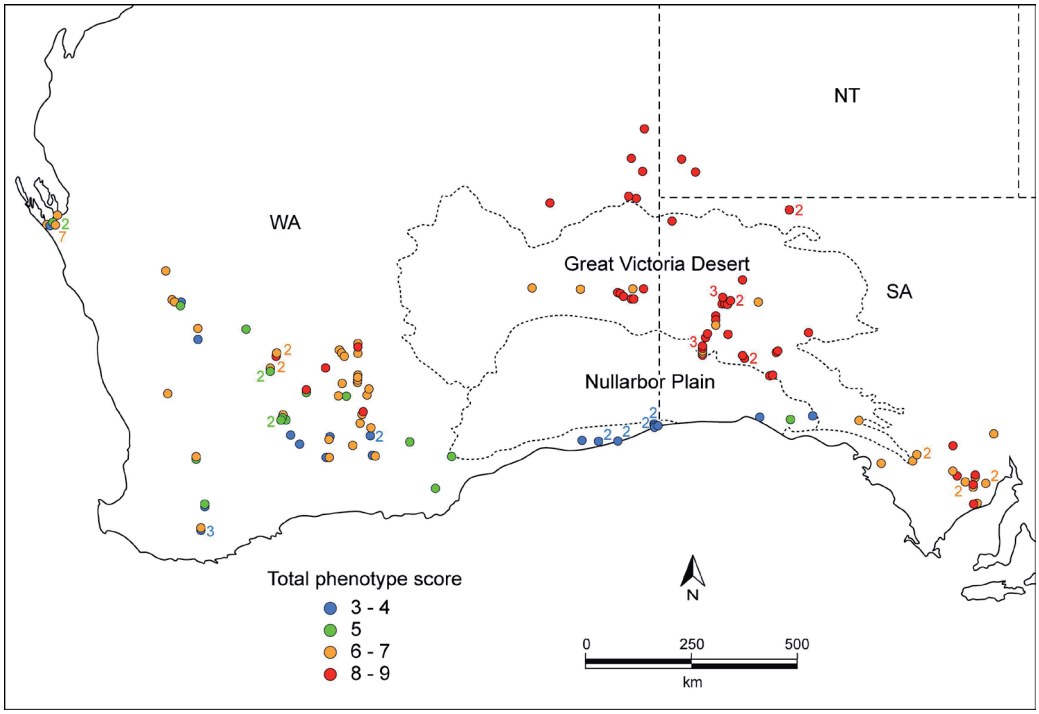

Figure 5. Distribution of phenotype, according to a composite of three variables, dorsal tone, back band tone and band breadth, as described in the text. Total scores of 3 or 4 are shown as blue, a score of 5 as green, 6 or 7 as orange, and 8 or 9 as red. Map B. Cale

Figure 6. Male specimens of three taxa, showing ventral plumage patterns. From left: *Cinclosoma clarum clarum* (SAMA B58875 [= ANWC B51856], 130 km N of Cook, Great Victoria Desert SA, L. P. Pedler 28 July 2007; SAMA B58878 [= ANWC B52089], 48 km NW of Maralinga, Great Victoria Desert SA, L. P. Pedler 5 August 2007); *C. clarum* (Eyre Peninsula) (SAMA B27520, 46 miles N of Cowell, Eyre Peninsula SA, SA Museum party 26 May 1965; SAMA B58003, 13 miles NE of Kimba, Eyre Peninsula SA, H. J. Eckert 3 January 1974); *C. castanotum* (SAMA B30920, ½ mile W of Red Tank Dam, Danggali Conservation Park, Murray Mallee SA, H. J. Eckert and R. Robinson 12 June 1977; SAMA B23067, Karoonda, Murray Mallee SA, F. E. Parsons 25 July 1928). Image P. Horton

C. castanotum than for *C. clarum* (Table 2), i.e. the former has proportionately less black/grey on the underside and more white (Figure 6). This provides an additional character that distinguishes the sister species. We also found significant variation in the bib ratio within *C. clarum*. The Eyre Peninsula population on average has proportionately less black/grey on the underside than the nominate subspecies (Table 2, Figure 6). The limited data available for *C. cl. fordianum* suggest that it too has less black/grey on the underside, the bib ratios being similar to those for Eyre Peninsula birds, but further measurements will be required to confirm this.

Effects of moult and specimen age

Variation in tone was evident among specimens of all three identified taxa, including the effective browning or "foxing" of many older specimens, especially those of *C. cl. fordianum* from south-western WA. Another contributing variable was the effect of moult. Ford (1981) observed that freshly plumaged specimens of *C. cl. clarum*, as now recognised, had darker back bands that faded to the typically brighter tone with exposure and wear. We confirmed this finding among examples of the species from WA, CA, the GVD and EP, and were able to identify fresh feathers of a chestnut hue among worn rusty-toned plumage on several individual specimens. We stress that this maturation of tone from chestnut to rusty was not seen in *C. castanotum* specimens. Schodde and Mason (1999) drew attention to another plumage character, dusky feather centres of upperparts, prominent on the

purer grey plumage of subspecies *fordianum*, obscure in *clarum* and usually faint in *castanotum*. While we confirmed this generalisation, we found it inconsistent among the three taxa. That feature may also depend in part on the age and wear of plumage. For simplicity, subspecific epithets for the three taxa, as above, will be used generally henceforth.

Range of plumage variation in Western Australia

The Copperback Quailthrush has an extensive distribution in WA from the central Australian ranges and GVD, west to Shark Bay, south into the semi-humid south-west and east through the Great Western Woodlands and subcoastal mallee south of the Nullarbor Plain.

Specimens of typical *clarum* are present from the central ranges and GVD. Elsewhere in WA, there were nine male and two female specimens with equally broad back bands, but in only two, a male (WAM A16797) from the Die Hardy Range and a female (WAM A13251) from 70 km N of Kalgoorlie, were they of a typical rusty colour. One male (ANWC B58847) from north-west of Kalgoorlie also had a typical brown dorsum but others showed intermediate hues of both dorsum and back band and, in one exceptional case, (WAM A13299 from Tamala, Shark Bay region), the pure grey dorsum of the *fordianum* phenotype.

The *fordianum* phenotype was determined from 22 specimens from its likely exclusive range in the south and south-west. Elsewhere, 11 of 43 male and 5 of 24 female specimens, had back bands of *fordianum* width, although only 1 male (WAM A16806 from Norseman) was typical in having the tone of both dorsum and back band of the *fordianum* phenotype. Further, back bands of *fordianum* width were mostly in the upper range for that subspecies and those of females were well defined and mostly of intermediate tone. Well-defined back bands, found infrequently in females within the exclusive distribution of the subspecies, suggest intergradation (see below).

Regional plumage diversity in Western Australia

In the Tamala/Shark Bay area, toward the species' north-westerly distributional limit, five of twelve specimens had the cold grey dorsal coloration of the *fordianum* phenotype but only one of them (WAM A13285) had a narrow back band within the range of that subspecies, while one male's band (WAM A13299, as above) was of *clarum* breadth (Table 3a). The other ten from the area had back bands of intermediate width. Band colour was intermediate in nine, while the remaining three had rusty bands (all of intermediate width).

Of 19 specimens from the vicinity of Kalgoorlie and Menzies, 6 had broad back bands within the *clarum* range, 1 a narrow band in the *fordianum* range (of intermediate colour) and 12 had intermediate width bands (Table 3b). Dorsal tone was brown as in *clarum* in two and intermediate in all others. Five had rusty coloured back bands, only one of which was of clarum breadth, while one had a chestnut back band (of 65 mm, almost as narrow as *fordianum*) and the remainder were intermediate in colour.

To the south, in the Norseman/Lake Dundas region, of 14 specimens, four had back bands of *fordianum* width, eight were of intermediate width and two (WAM A13297, from Higginsville and ANWC B58773 from 91 km north of Norseman) were of *clarum* width (Table 3c). Dorsal tone was brown in two specimens and grey in all four specimens with *fordianum* band width plus one of intermediate band width. The remaining seven specimens were intermediate in dorsal tone. Colour of back bands varied from rusty in three intermediate-breadth specimens to chestnut in one *fordianum*-like specimen and two intergrades. We therefore confirm Ford (1981) and Schodde and Mason (1999) in finding that Mathews's (1912) holotype of *C. castanotum dundasi* from near Lake Dundas is from a region of intergradation.

In other regions of inland WA, from Yalgoo

south-east to Die Hardy Range and Boondine Hill and further south to the Nevoria and Burbidge goldmine area, 22 specimens showed a similar cluster of intermediate phenotypes with a wide scatter of other combinations of character states (Table 3d). Noteworthy among the latter is a male (WAM A18168) from Lake Barlee Homestead with grey dorsal tone and narrow back band as in *fordianum* but with the rusty band colour of *clarum*.

A distributional gap in the western Great Victoria Desert

Johnstone and Storr (2004) illustrated inferred discontinuities in the species' range, in particular, west of Neale Junction in the GVD (see Figures 4 and 5). While Ford (1983) described the species as present throughout the GVD, he included only two sight records from that area, 83 km west of Neale Junction, and near the Plumridge Lakes to the south, towards Rawlinna on the Nullarbor Plain. There have been very few subsequent records (Blakers *et al*. 1984, Barrett *et al.* 2003, Atlas of Living Australia http://www.ala.org.au) and there are no specimens (Ford 1981, this study). Within the western GVD and to the north, the species is replaced by the Western Quailthrush, *Cinclosoma marginatum*. Ford (1974a, 1983) identified hybrid specimens between what we now know as *C. cl. clarum* and *C. marginatum*, including one from near Menzies and another from the western GVD. Toon *et al.* (2012) confirmed the occurrence of such hybridisation in a separate specimen (ANWC B54296) from the western GVD, 24 km east of Neale Junction.

Table 3. Combinations of plumage scores for intergradient specimens of *Cinclosoma clarum* from various regions in Western Australia. Scores for dorsal tone: 1 = grey, 2 = intermediate, 3 = brown; for back band tone: 1 = chestnut, 2 = intermediate, 3 = rusty; for back band width: 1 = narrow, 2 = intermediate, 3 = wide (measurement limits are given in the text). F = female, M = male.

a) Tamala (12 specimens)

Dorsal tone	Band tone	Band width 1	Band width 2	Band width 3
1	1			
1	2	1M	2F	1M
1	3		1F	
2	1			
2	2		4M, 1F	
2	3		1F	
3	1			
3	2			
3	3		1M	

b) Kalgoorlie/Menzies (19 specimens)

Dorsal tone	Band tone	Band width 1	Band width 2	Band width 3
1	1			
1	2			
1	3			
2	1		1M	
2	2	1F	5M, 2F	3M, 1F
2	3		1M, 2F	1F
3	1			
3	2			1M
3	3		1M	

c) Norseman/Dundas (14 specimens)

Dorsal tone	Band tone	Band width 1	Band width 2	Band width 3
1	1	1M	1F	
1	2	3M		
1	3			
2	1		1M	
2	2		1M, 1F	2M
2	3		2M	
3	1			
3	2		1M	
3	3		1F	

d) other WA inland localities (22 specimens)

Dorsal tone	Band tone	Band width 1	Band width 2	Band width 3
1	1			
1	2	2M	1M	
1	3	1M		
2	1			
2	2	3M, 4F	1M, 4F	1M
2	3		2M, 1F	1M
3	1			
3	2		1M	
3	3			

The type locality of *C. cl. clarum* and the question of nomadism

The type locality of *C. clarum* and therefore of its nominate subspecies, Wipipippee at the northern margin of the Gawler Ranges (see Appendix), warrants some comment as it is well removed from the core distribution of *C. cl. clarum*. Ford (1981) speculated that it is evidence of the occurrence of nomadism in *C. cl. clarum*, which he regarded as "extremely mobile (pers. obs.)" (Ford 1981: 191). For example, he referred to dispersal rather than high rate of reproduction when he reported "large increases in quail-thrushes after periods of heavy rain" (Ford 1981: 190) in the area near Menzies. This question of nomadism and its relationship to local rainfall requires further scrutiny.

We offer an alternative but non-opposing perspective by observing that August 1902, when the holotype was collected, was during the final and driest year of the Federation Drought (Godfree *et al.* 2019; https://en.wikipedia.org/wiki/Federation_Drought) and therefore at a time when arid zone birds could be expected in southerly localities. It is plausible that the few observations in the western GVD, as well as those observations accepted by Ford (1983) from outside the species' range, including some within that of the Western Quailthrush (as above) provide supportive evidence for nomadism in the subspecies.

Ford (1981) and Schodde and Mason (1999) found nonetheless that the holotype specimen's (SAMA B7705) plumage is characteristic and affirmed its status. We observed that it shows distinct crown streaking, as present most prominently in *fordianum* specimens. This might reflect the variation in this character that we found among individuals of all subspecies and, in other respects, we confirm its phenotype as typical of *C. clarum clarum*.

Populations in South Australia: the Eyre Peninsula phenotype

In comparison with the diversity of phenotypes present through much of its WA distribution, the plumage pattern of Copperback Quailthrush specimens from Eyre Peninsula and the Gawler Ranges SA is more consistent. There, both male and female specimens bear a resemblance to the *clarum* phenotype. The seven males other than the holotype have brown or grey-brown upper parts and back bands of rusty *clarum* or intermediate hue but of reduced width. In addition, we find distinction in its smaller mean bib ratio, compared with that of the nominate subspecies. The ten females have similarly toned upper parts and back bands, the latter generally narrower than those of males and all of intermediate width. The faintly banded or unbanded female phenotype of *fordianum* (and *castanotum*) is not seen among Eyre Peninsula specimens, nor is the cold grey dorsum of *fordianum*.

West of the type locality of *C. clarum* are specimens of two males and one female taken on Yardea Station on 9 November 2001 and now in the collection of the Academy of Natural Sciences of Drexel University, Philadelphia (ANSP). Digital images reveal that each has a rusty or intermediate coloured back band of the Eyre Peninsula (EP) phenotype. Upperparts vary however and the tone of one male (ANSP 189706) appears to be the cold grey of *fordianum*.

Further west, in the Yellabinna Region, a south-eastern extension of the GVD, a single specimen from north of Ceduna (ANWC B52266) has a back band typical of *clarum*, except for its slightly reduced width but it too is greyer dorsally. Six specimens from Ooldea and Maralinga to the north-west, are typical *clarum* with broad back bands although three have intermediate dorsal toning, and further west in the GVD, there are others with slightly narrower bands. These observations support Schodde and Mason's (1999) identification of the area as a narrow zone of intergradation.

In the far south-west of SA, there are three male specimens from mallee on the south-eastern fringe of the Nullarbor Plain. One (SAMA

B55864) is typical of *fordianum* (Figure 2). The other two are *fordianum*/*clarum* intergrades, SAMA B46039 having slightly more intermediate dorsal tone and back band colour, while SAMA B55919 has a pure grey dorsum but a broader band of 75 mm (Figure 3). To the north, the Yellabinna specimen (ANWC B52266) and Yardea specimen (ANSP 189706) referred to above are also greyer. These few specimens provide evidence of intergradation in the region between the Nullarbor Plain and Gawler Ranges.

A summary of phenotypic diversity and its distribution within the species

The Copperback Quailthrush is a species of highly variable phenotype. The nominotypical subspecies *C. clarum clarum* occurs exclusively in the dune fields of the central Australian ranges and northern GVD. The subspecies *C. clarum fordianum* is limited to southern, largely subcoastal regions of Western Australia and south-western South Australia.

The area between them in inland WA is occupied by a highly diverse mix of intergradient phenotypes showing varied combinations of character states, most obviously in having back bands of intermediate width, 40 of 67 specimens judged intergradient on that count alone. Other evidence of intermediate or mixed plumage includes broad and intermediate width back bands on a grey *fordianum*-toned back, a narrow but rusty, *clarum*-toned band on a grey back (WAM A18168 from Lake Barlee), and other combinations of back colour and back band tone and width.

This population is best characterised as a hybrid swarm https://en.wikipedia.org/wiki/Hybrid_swarm (Hale *et al.* 2005; see also Anderson 1953, Short 1969, Lowe and Abbott 2015), which is likely to have limited reproductive contact with *C. cl. clarum* across the largely unoccupied western GVD. Further east, in the southern GVD there is evidence of more restricted hybridisation, with individuals only subtly distinguished from the *clarum* phenotype, some with back bands of reduced width and others with intermediate tones of dorsum and band.

The occurrence of five female specimens from the hybrid swarm in WA having distinct back bands of intermediate tone but within the width range of *fordianum*, prompted review of the *fordianum* phenotype. In its restricted exclusive distribution, 4 of 12 females had only faint and even narrower bands of 20 mm and 4 were entirely unbanded. Specimens of *fordianum* from its most westerly localities, where it is now extinct (Ford 1981, 1983, R. Johnstone pers. comm.), were all taken between 1903 and 1906. Most are browner than expected due to foxing from exposure.

Ford (1981) analysed back band width by grouping specimens for statistical purposes among 20 localities for males and 18 for females and provided mean measurements for each locality. That method prevented him from demonstrating local diversity. By assessing each specimen individually, we show that variation across the range of *C. clarum* in WA is not clinal, as Ford interpreted it.

A key new finding of our study is that a third phenotype in this species is found on Eyre Peninsula and in the Gawler Ranges. Ford (1981) considered the whole EP and Gawler Ranges population to be intergradient, with an abrupt change from the *C. cl. clarum* phenotype through the Barton Sandhills [=Yellabinna] in the southern GVD. Schodde and Mason (1999) suggested that the EP population was intergradient not only between what are now *C. cl. clarum* and *C. cl. fordianum* but also with *C. castanotum*.

That interpretation alluded to the population's distinctive phenotype and its close similarity to *C. castanotum*. Now, with the insight provided by Dolman and Joseph's (2015, 2016) recognition of two species, its distinctiveness can be interpreted as that of a regional differentiate, a subspecies (compare Figures 2 and 7).

Figure 7. Comparing, from left, holotype male of *Cinclosoma clarum clarum* Morgan, 1926 (SAMA B7705, Wipipippee, Gawler Ranges 17 August 1902), with female *Cinclosoma clarum morgani* (SAMA B7704, Donald's Plains, Yardea, Gawler Ranges, A. M. Morgan 12 August 1902), and male holotype of *C. clarum morgani* Condon, 1951 (SAMA B5673, 18 miles NW of Kimba (see Appendix for precise locality), Eyre Peninsula, A. M. Morgan 19 September 1925). Image P. Horton

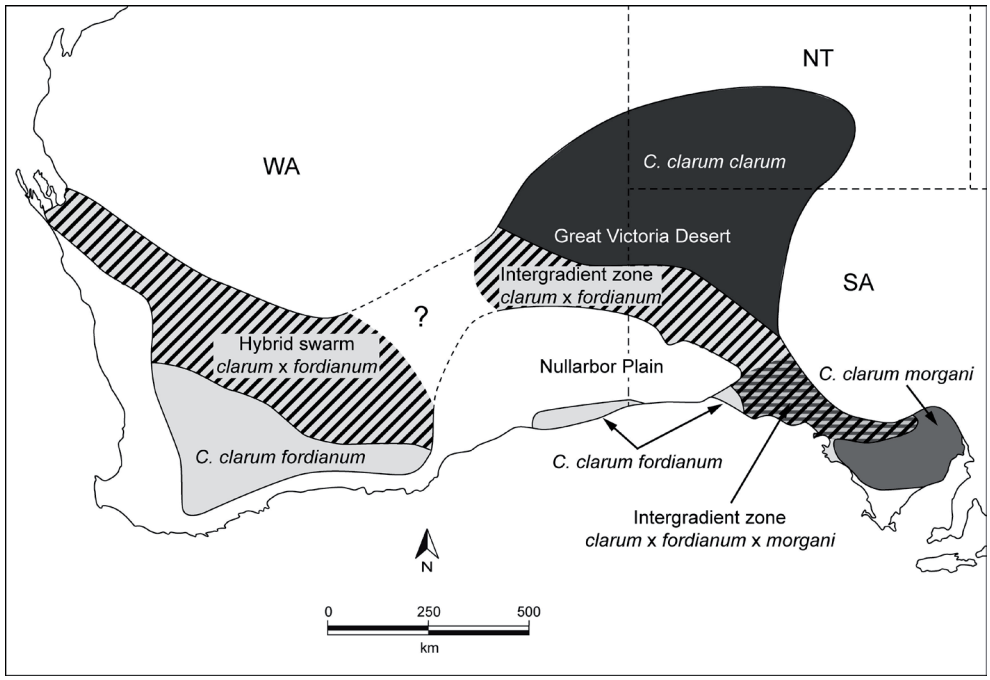

Figure 8. Distribution of the Copperback Quailthrush, including that of its three subspecies and zones of hybridisation or intergradation. Map B. Cale

We find that the EP/Gawler Ranges population closely resembles *C. cl. clarum* in having a similarly toned back pattern and limited sexual dimorphism, differing essentially in its back band being narrower and mean bib ratio smaller. It lacks the cold grey dorsum and pronounced sexual dimorphism of *C. cl. fordianum*. This population differs quite fundamentally from the more northerly WA representatives where many and varied phenotypes form a *fordianum* x *clarum* hybrid swarm. Consistently differentiated from subspecies *clarum* and *fordianum*, we recognise this geographically restricted population as *Cinclosoma clarum morgani* Condon, 1951 (Figure 7; see also middle and right specimens in Figure 3).

Limited material from the Yellabinna and from the south-eastern periphery of the Nullarbor Plain provides evidence of intergradation between *C. cl. clarum* and *C. cl. fordianum* in that region, and of interaction between that intergradient population and *C. cl. morgani*. It is essentially a zone of three-way intergradation (Figure 8).

We conclude that the Copperback Quailthrush includes the subspecies *Cinclosoma clarum clarum*, *C. cl. fordianum* and *C. cl. morgani*. The distribution of all three subspecies and their intergradient or hybrid zones is illustrated in Figure 8. Further exploration of speciation and hybridisation within this species complex is in progress, involving the integration of morphological and genomic data.

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APPENDIX

Type localities

The male holotype of *Cinclosoma clarum* Morgan, 1926 (SAMA B7705) was collected at "Wipipippee, about five miles east of the southern end of Lake Gairdner" on northern Nonning Station, Gawler Ranges on 17 August 1902. The holotype locality, if taken as about five miles (eight km) east of the lake shore and near Wipipippee Hill, would be close to the only mapped track in the area at ≈ 32° 11.5′ S, 136° 20′ E.

The male holotype of *Cinclosoma castanotum morgani* Condon, 1951 (SAMA B5673) was collected by Dr A. M. Morgan "18 miles (≈ 30 km) north-west of Kimba", Eyre Peninsula on 19 September 1925 (Morgan 1926, Condon 1951). Sutton (1926) wrote that Morgan's party had camped 13 miles northwest of Kimba, about 1½ miles south of Cunyarie Dam near Cunyarie Rocks, and travelled "5 miles further north-west", attempting to reach Wirrigenda Dam. That dam is shown on some maps about 8 km west of Wirrigenda Hill and is almost due north of Cunyarie Dam, and the direction taken, according to Sutton's (1926) map, was not northwest but northeast in the direction of Wirrigenda Hill. The type locality might be given as about 6 km north or northeast of Cunyarie Rocks at ≈ 32° 51′ S, 136° 20′ E.

The male paratype of *C. c. morgani* (SAMA B23063) from the collection of F. E. Parsons was taken near Polygonum Tanks (present day Polygonum Dam), 23 miles southwest of Iron Knob (according to label) on 13 September 1925. This corresponds to "34 miles (≈ 55 km) north-east of Kimba" (Morgan 1926) at ≈ 32° 59′ S, 136° 55′ E.

GAZETTEER

Boondine Hill	30° 16′ S, 119° 14′ E
Burbidge	31° 33′ S, 119° 34′ E
Ceduna	32° 08′ S, 133° 41 ′E
Colona	31° 38′ S, 132° 04′ E
Cook	30° 37′ S, 130° 25′ E
Cowell	33° 41′ S, 136° 55′ E
Die Hardy Range	29° 57′ S, 119° 23′ E
Gluepot	33° 46′ S, 140° 08′ E
Higginsville	31° 45′ S, 121° 42′ E
Iron Knob	32° 44′ S, 137° 09′ E
Kalgoorlie	30° 45′ S, 121° 28′ E
Karoonda	35° 06′ S, 139° 54′ E
Kimba	33° 08′ S, 136° 25′ E
Lake Barlee	29° 10′ S, 119° 00′ E
Lake Dundas	32° 34′ S, 121° 50′ E
Maralinga	30° 10′ S, 131° 35′ E
Menzies	29° 42′ S, 121° 02′ E
Neale Junction	28° 18′ S, 125° 49′ E
Nevoria	31° 30′ S, 119° 35′ E
Norseman	32° 12′ S, 121° 47′ E
Ooldea	30° 27′ S, 131° 50′ E
Parcoola	33° 37′ S, 140° 03′ E
Plumridge Lakes	29° 41′ S, 125° 12′ E
Rawlinna	31° 01′ S, 125° 20′ E
Red Tank Dam	33° 08′ S, 140° 51′ E
Tamala	26° 42′ S, 113° 43′ E
Wipipippee Hill	32° 12′ S, 136° 16′ E
Yalata	31° 29′ S, 131° 50′ E
Yalgoo	28° 21′ S, 116° 41′ E
Yardea	32° 23′ S, 135° 31′ E