Plumage diversity in the Adelaide Rosella: a case for taxonomic revision

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ABSTRACT – In a quantitative and statistical analysis of plumages in the Adelaide Rosella we show variation throughout its distribution and latitudinal change from chiefly red in the south through orange in the centre to yellow in the north, consistent with Gloger's ecophenotypic rule. We find that the change is clinal through southern and central populations, whereas a northern population in the South Flinders Ranges is essentially allopatric and shows no recognisable latitudinal change. Sexual dichromatism is present in northern populations. Our results highlight the potential influence, on plumages at endpoints in the cline, of the Kangaroo Island Rosella in the south and Flinders Rosella in the north, suggesting past and/or continuing gene flow. We propose a taxonomic revision for the Adelaide Rosella that reflects our findings.

INTRODUCTION

The Crimson Rosella *Platycercus elegans* (Gmelin, 1788) group of parrots occurs widely in eastern and south-eastern Australia, west to the South Australian gulfs (Forshaw 1981), in a complex pattern of distribution and variation that has defied taxonomic consensus for over a century (Mathews 1912, 1913, 1916–17, 1918, 1920, 1930, 1931, 1946; Ashby 1917, 1925; Cayley 1938; Condon 1941; Cain 1955; Keast 1961; Schodde 1997; Collar 1997; Joseph *et al.* 2008; Forshaw and Knight 2011).

Two isolated populations, *P. e. nigrescens* Ramsay, 1888 and *P. e. filewoodi* McAllan and Bruce, 1989, are present in northern and mid-eastern Queensland respectively. Populations at present recognised as the nominate subspecies *P. e. elegans* are part of a widespread south-eastern Australian clade that is sister to the forementioned pair in the phylogenetic analysis of Joseph *et al.* (2008). They extend from south-eastern Queensland into south-eastern South Australia, north and west to Bordertown, Keith and Salt Creek (see Gazetteer for SA localities). In the same clade, the Yellow Rosella *P. e. flaveolus* Gould, 1837 occurs in River Red Gum *Eucalyptus camaldulensis* forests and adjacent woodlands of the Murray, Murrumbidgee, Lachlan and lower Darling Rivers. In South Australia it has been recorded south to the mouth of the Marne River at Wongulla and to Mannum (Figure 1; Mathews 1912; Condon 1968; Schodde 1997).

Finally, there is a phenotypically and taxonomically complex but genetically coherent group (Joseph *et al.* 2008) of South Australian populations occupying the South Flinders Ranges, Mid North, Mount Lofty Ranges, Fleurieu Peninsula and Kangaroo Island (Figure 1; see https://birdssa.asn.au/wp-content/uploads/Crimson-Rosella-28-05-2020.png for details of distribution across the state). The Crimson Rosella on Kangaroo Island is the distinctive deep crimson subspecies *P. e. melanopterus* North, 1906. All remaining populations across the Flinders and Mount Lofty Ranges regions are variable and are conventionally known as the Adelaide Rosella, whose unsettled early taxonomy is summarised in the Appendix. It is now well known that some Adelaide Rosellas of the Fleurieu Peninsula are scarlet in body plumage and are assigned to *P. e. fleurieuensis* Ashby, 1917. Ashby (1918) gave their northern

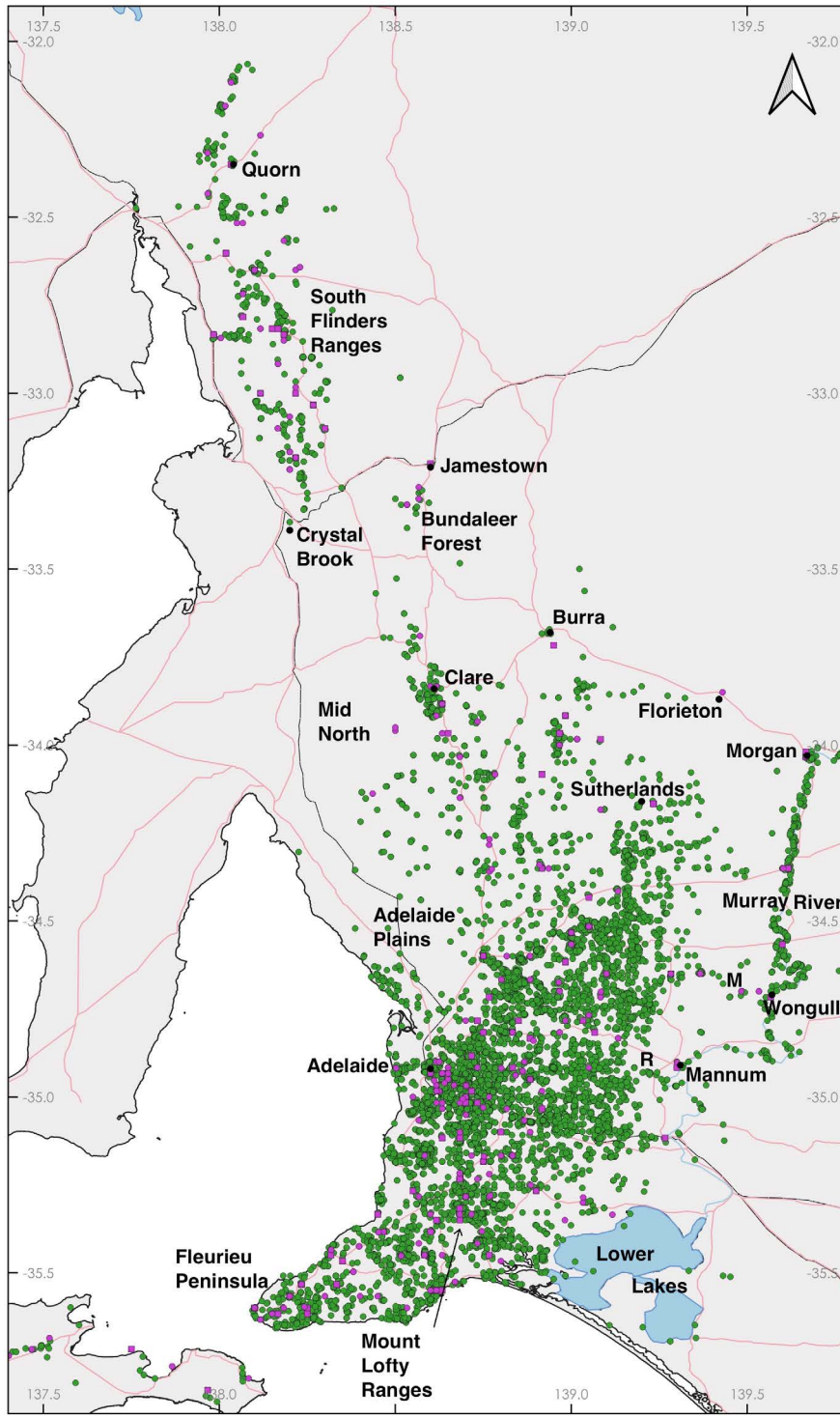

Figure 1. Map of specimen (purple) and sight (green) record localities for the Adelaide Rosella, and for the Yellow Rosella along the Murray River, showing contact between the two at the junction of the Marne (M) and Murray Rivers at Wongulla and more tenuously further south along Reedy Creek (R) near Mannum. The largely isolated population of Adelaide Rosellas in the South Flinders Ranges and some Kangaroo Island Crimson Rosella records are also shown.

limit as Meadows, but Schodde (1997) defined it as the Inman and Bungala Rivers (Normanville and Yankalilla), Hindmarsh Valley and Crows Nest Range [*sic* = Road] northwest of Port Elliot. Adelaide Rosellas in the South Flinders Ranges by contrast are predominantly yellow and were earlier considered Yellow Rosellas *P. (e.) flaveolus* (Campbell 1900; North 1912; Ashby 1917, 1925; RAOU 1926; Mathews 1930, 1931). Now assigned to *P. e. subadelaidae* Mathews, 1912, they are distributed in eucalypt forests and woodlands from the Beetaloo Valley north of Crystal Brook, north to beyond Quorn as far as Buckaringa (Schodde 1997) (Figure 1).

The geographically intervening central populations of Adelaide Rosella are intermediate in colour, generally orange but highly variable. They range through the Mount Lofty Ranges, extending west onto the Adelaide Plains and east to the Murray River and Lower Lakes and sporadically beyond the Murray. Northwards they are recorded in the hills beyond Bungaree (north of Clare) and near Burra, and north-east to Sutherlands (Boehm 1959), Florieton (Forshaw 1981; Schodde 1997) and Brookfield Conservation Park (Birds SA records). A small outlier occurs around Jamestown and Bundaleer (Figure 1).

Condon (1941: 136) described the progression in colour changes from south to north as a 'well defined geocline series which comprises *fleurieuensis*, *adelaidae* and *subadelaidae*' and retained all three subspecies in subsequent lists (Condon 1968, 1975), but Schodde (1997) treated the geographically and phenotypically intermediate group (*adelaidae*) as an intergradient or hybrid population and taxonomically as *P. e. subadelaidae* – *P. e. fleurieuensis*. This entity, now lacking a subspecific name, is consequently missing from BirdLife Australia's Working List of Australian Birds (https://www.birdlife.org.au/conservation/science/taxonomy). The name *P. e. adelaidae* Gould, 1840 continues nonetheless to be applied in published accounts, either to these extensive central populations or to all Adelaide Rosellas (Collar 1997; Higgins 1999; Eckert 2000; Gower 2012; Carpenter and Black 2015; Ribot *et al.* 2019). As if to emphasise the taxonomic uncertainty of the central group, Forshaw and Knight (2011) labelled them *P. e. fleurieuensis* x *P. e. subadelaidae* x *P. e. flaveolus*.

The naming of subspecies as geographically restricted, differentiated populations within the species acknowledges their potential for evolutionary independence and their significance as units of conservation management (Schodde and Mason 1999; Rising 2007; Remsen 2010; Patten 2015; Patten and Remsen 2017). Present taxonomy of the Crimson Rosella complex (Schodde 1997) supposes that, within their defined distributions, the two named Adelaide Rosella subspecies are of a consistent and diagnosable phenotype, while the intervening population, being of hybrid origin, is variable and less readily defined. Yet varied plumage has been reported within the distribution of *P. e. fleurieuensis* (Ashby 1917; Lendon 1968, 1973; Higgins 1999) and, although not explicitly by most authors, also in *P. e. subadelaidae* (Morgan in North 1912; L. Pedler, pers. comm.).

In this study, we provide qualitative information on plumage colouration in the Crimson Rosella complex and a quantitative analysis of plumage variation in the Adelaide Rosella across its range. We test which of the following patterns is best supported statistically in seeking the most appropriate taxonomic treatment:

1. A single clinally variable population and therefore one subspecies.

2. Two populations (as subspecies) *sensu* Schodde (1997): one northern in the South Flinders Ranges and predominantly yellow, a second from the Fleurieu Peninsula and predominantly red, and a hybrid/intergradient zone between them.

3. Two populations: one northern, predominantly yellow, in the South Flinders

Ranges and the second comprising all other populations from the Fleurieu Peninsula to Bundaleer. This also warrants two subspecies.

4. Three populations *sensu* Condon (1941, 1968, 1975): red in the Fleurieu Peninsula, orange in the extensive central distribution and yellow in the South Flinders Ranges. This warrants three subspecies.

METHODS

Plumage

One of us (AB) first assessed plumage colouration of adult specimens of the Crimson Rosella complex in the South Australian Museum, Adelaide (SAMA) by reference to the colours of Smithe (1975). They comprised 173 Adelaide Rosellas, 17 Crimson Rosellas from the South East of South Australia and Victoria, 13 from Kangaroo Island, and 13 Yellow Rosellas. Adults were recognised by black lesser wing coverts and the absence of green in body plumage.

A plumage scoring method was developed, each specimen given a value (0–6), according to the colouration of dorsal and ventral plumage, following a method described below and applied by Bocalini and Silveira (2015), Black *et al.* (2019) and Lima *et al.* (2020). Using this scoring method, all adult specimens of the Adelaide Rosella in SAMA and the Australian National Wildlife Collection, Canberra (ANWC) (total N = 424) were assessed by AB in the final survey. Upperparts assessed for colour were nape and rump and the fringes of black-centred mantle and scapular feathers and tertials; underparts examined included breast, belly, flanks, vent and undertail.

Plumages of Adelaide Rosellas were scored within the range of colours between those of Yellow Rosellas and Crimson Rosellas, as follows:

0: bright yellow above and below with a red-orange frontal band and sparse orange on the underparts in some (Yellow and palest Adelaide Rosellas);

1: yellow or creamy yellow above and yellow below but with mottled orange in the breast, vent and undertail;

2: as for 1 but more extensively orange below;

3: creamy yellow above but largely or fully orange below, or orange above but with orange and yellow below;

4: fully orange above and below;

5: red (scarlet) below but orange or paler above;

6: truly red both above and below (as in typical Crimson Rosellas).

In view of the close similarity between Yellow Rosellas and the palest Adelaide Rosellas, we scored both and compared their plumages closely to investigate possible distinguishing traits.

The names and numbers of Smithe's colours used in this study and their relationship to the scoring of Adelaide Rosellas are shown in Table 1.

Statistical analysis

The extent to which variation in colour score could be partitioned into geographic areas was explored using k-means analysis (MacQueen 1967), which allocates samples into k groups, where k is nominated by the investigator. For this purpose, we used the collection locality to allocate each specimen to one of eight 0.5° latitudinal bands between -36° and -32°. The optimal k value is the one with the lowest within-cluster sums of squares, i.e. with the least variation within each identified cluster. This approach was used to explore whether rosellas from any latitudinal bands were consistently grouped together based on the frequency of colour scores with k values between two and six.

Table 1. Smithe's (1975) named and numbered colours employed in this study, populations where commonly found within the Crimson Rosella complex, and their application in Adelaide Rosella plumage scoring.

Smithe's colour name and number	Common name	Where exemplified in Crimson Rosella complex	Adelaide Rosella plumage score
Carmine (8)	crimson	sspp. *elegans*, *melanopterus*	
Spectrum red (11)	crimson	sspp. *elegans*, *melanopterus*	
Ruby (10)	scarlet (red)	ssp. *fleurieuensis*	5-6
Scarlet (14)	scarlet (red)	ssp. *fleurieuensis*	5-6
Flame scarlet (15)	orange	Typical Adelaide Rosella	3-4
Chrome orange (16)	orange	Typical Adelaide Rosella	3-4
Spectrum orange (17)	orange	ssp. *subadelaidae*	2
Straw yellow (56)	yellow	sspp. *subadelaidae*, *flaveolus*	0-2
Cream color (54)	yellow	sspp. *subadelaidae*, *flaveolus*	0-2
Olive yellow (52)	'lime'	sspp. *subadelaidae*, *flaveolus*	0-2

The Chi-squared statistic and adjusted residuals (Haberman 1973) were used to test for significant differences in the frequency of colour scores at the determined k value.

Regression analyses were used to describe the relationship between colour score and latitude. Linear, quadratic and cubic regressions were calculated. The magnitude of the coefficient of determination (R^2) was used to assess which equation best fitted the data.

Sexual dimorphism in colour score was tested using Oneway Analysis of Variance where the variances were homogeneous, as indicated by Levene's statistic. Where the variances were not homogeneous, a non-parametric equivalent (Mann–Whitney U statistic) was used.

All statistical analyses were performed using IBM SPSS v28 (IBM Corp. 2021). Descriptive statistics are given as mean ± standard deviation.

RESULTS

Plumage

The dorsal plumage of adult Crimson Rosellas *P. e. elegans* is between Smithe's (1975) 'spectrum red' (numbered 11), a bright mid red, and 'carmine' (8) a darker tone justifying the crimson descriptor but of similar hue. Slightly paler yet subjectively red are 'ruby' (10) and 'scarlet' (14). 'Flame scarlet' (15), 'chrome orange' (16) and 'spectrum orange' (17) are progressively paler and more orange hues (see Table 1).

Crimson Rosellas *P. e. elegans* of the South East of South Australia are between spectrum red and carmine above and a little paler below, between spectrum red and ruby. The plumage of the Kangaroo Island subspecies P. *e. melanopterus* is a stronger and darker crimson, closer to carmine above, while approximating spectrum red below.

The bright yellow underparts of adult Yellow Rosellas *P. e. flaveolus* are between 'straw yellow' (56) and slightly duller 'cream color' (54); the posterior neck and mantle and scapular fringes are between 'olive yellow' (52) and straw yellow and the rump is close to olive yellow but paler, described herein as a 'lime' colour.

The plumage of most Adelaide Rosellas, unlike the even toning of truly scarlet individuals, is generally mottled, due to variable basal and terminal yellow in orange body feathers. Variation in the palest specimens depends

largely on the extent of orange on the underparts, rather than on differences in hue.

The darkest Adelaide Rosellas from the Fleurieu Peninsula are barely distinguishable from *P. e. elegans*, between spectrum red, ruby and scarlet above, and scarlet below. Such specimens are readily identified as red or scarlet but may be distinguished from the darker crimson P. *e. melanopterus* of Kangaroo Island. Others from the Fleurieu Peninsula resemble Adelaide Rosellas of the Mount Lofty Ranges or suburban Adelaide, the plumage of their underparts varying between flame scarlet and chrome orange. There is much variation in dorsal plumage among these southern Adelaide Rosellas, colouration being strongest on the rump, less consistent on posterior neck and scapular fringes, and with mantle fringes pale and dull in all but the most highly coloured birds (Figures 2 and 5). Further north, rosellas are a paler orange (chrome orange to spectrum orange), with increasing yellow in the plumage (Figures 3 and 6).

The yellow tones of the palest Adelaide Rosellas resemble those of Yellow Rosellas and six specimens with negligible orange in body plumage are barely distinguishable, four from the Flinders Ranges, one from the Marne River and one exceptional specimen from south of Langhorne Creek (Eckert 2000, SAMA B57121, but see below). However, we found subtle plumage differences between the yellowest Adelaide Rosellas and Yellow Rosellas. Orange in the underparts of *flaveolus* appears as a wash of colour over the breast and occasionally the belly, whereas in Adelaide Rosellas with minimal orange, it is present patchily in the breast, vent and undertail and may be absent from the belly. Another distinction is in the red-orange frontal bar which is limited and well defined in *flaveolus* but less distinctly demarcated in Adelaide Rosellas, traces of orange extending diffusely over the crown. Pale yellow Adelaide Rosellas are usual in the Flinders Ranges population, common in parts of the Mid North but uncommon further south. The fringes of mantle and scapular feathers of such pale Adelaide Rosellas, while yellow, are not as consistently bright as in Yellow Rosellas and may be duller than Smithe's 'cream color', as in many typical orange birds (Figures 4 and 7). The rump in pale Adelaide Rosellas generally shows some orange, unlike the plain lime-tinged rump of Yellow Rosellas, but in the Flinders Ranges and Clare region (DD pers. obs. and Figure 4b) rumps are typically lime-tinged, and any orange in rump plumage is the exception.

Variation in plumage scores across the distribution of the Adelaide Rosella is mapped in Figure 8 and shown as a scatterplot against latitude in Figure 9.

Statistical results

In sequential k-means analyses (k = 2–6) of the partitioning of variation in colour score into geographic areas across eight latitudinal bands (Figure 9), the only statistically significant value was k = 2, i.e. two groups were identified, one occurring south of and one north of -34.5° (Figure 10). In addition, the analyses classified bands south and north of -34.5° as different at all k values. The three bands south of -34.5° were first found different from each other at k = 3, whereas bands to the north were classified as different only when k ≥ 4. Thus, the five northern bands were more alike than the three southern bands. There were statistically significant differences between the frequency of colour scores when samples were pooled into the two groups, south and north of -34.5° ($\chi^2 = 163.1$, df = 6, p = 0.0005). The sign of the adjusted residuals divided the two groups. Rosellas with colour scores ≥ 3 (redder) were over-represented south of -34.5°, whereas rosellas with colour scores of 1 or 2 (yellower) were over-represented to the north (Table 2).

A quadratic equation ($y = 0.0372 + 22.5x + 0.34x^2$) most parsimoniously described the relationship between colour score and latitude. Latitude explained ($R^2 \times 100$ =) 53.4% of the variance in

colour score. Moving from south to north the average colour score declined steeply to about -34° and was virtually flat north of -33.5° (Figure 9).

Variances in colour score between samples were not significantly different south of -34.5° (Levene's statistic = 0.131, p = 0.718) and there was no significant difference in colour score between females (3.36 ± 1.045, n = 64) and males (3.12 ± 1.097, n = 198; $F_{1,260}$ = 2.332, p = 0.128). In contrast, north of -34.5° variances in colour score were significantly different (Levene's statistic = 6.073, p = 0.015) and colour scores were significantly different between the sexes (Mann–Whitney U = 1394, p = 0.002). Females had a higher average colour score and lower variance (1.98 ± 0.69, n = 46) than males (1.56 ± 0.76, n = 87).

DISCUSSION

Fleurieu Peninsula and Flinders phenotypes

Many Adelaide Rosellas on the Fleurieu Peninsula are scarlet but not all (Ashby 1917). We confirm that exceptionally vivid individuals occur there but only a minority are of the reddest hue both above and below and others resemble Adelaide Rosellas elsewhere. Higgins (1999) found less variation in plumage among Fleurieu birds than north of Myponga but recognised a continuous cline in colouration. Some Fleurieu Peninsula residents report both 'Crimson Rosellas' and 'Adelaide Rosellas' in the region after comparing their observations against illustrations in field guides, one commenting on their 'interbreeding', presuming that the variety of intermediately plumaged birds represented 'hybrids' (pers. comm. to AB). While technically incorrect, these are reasonable interpretations of the variety there (AB pers. obs.).

North and east of the Inman and Hindmarsh Valleys, as far as Kuitpo and Meadows (Ashby 1917, 1918; this study), many highly coloured birds can be found among paler individuals. North of -35°, about the latitude of Adelaide and Mount Barker, rosellas are generally orange or orange and yellow. Fully orange birds are rare north of the Barossa, but we found one such example among the large Bundaleer Forest sample (Figure 8).

Table 2. Observed and expected frequencies of seven colour categories in Adelaide Rosellas south and north of -34.5°. Adjusted residuals indicate the magnitude of differences in observed frequencies from random expectations, * p < 0.05, ** p < 0.01. Negative adjusted residuals indicate under-represented cells; positive values indicate over-represented cells.

Colour score	South		North		Total
	Observed number (expected)	Adjusted residual	Observed number (expected)	Adjusted residual	
0	1 (2.6)	-1.7	3 (1.4)	1.7	4
1	11 (48.5)	-10.1**	63 (25.5)	10.1**	74
2	69 (85.2)	-3.6 *	61 (44.8)	3.6*	130
3	87 (67.5)	4.6*	16 (35.5)	-4.6*	103
4	88 (59.7)	7.1**	3 (31.3)	-7.1**	91
5	13 (8.4)	2.7*	0 (4.5)	-2.7*	13
6	9 (5.9)	2.2*	0 (3.1)	-2.2*	9
Total	**278**		**146**		**424**

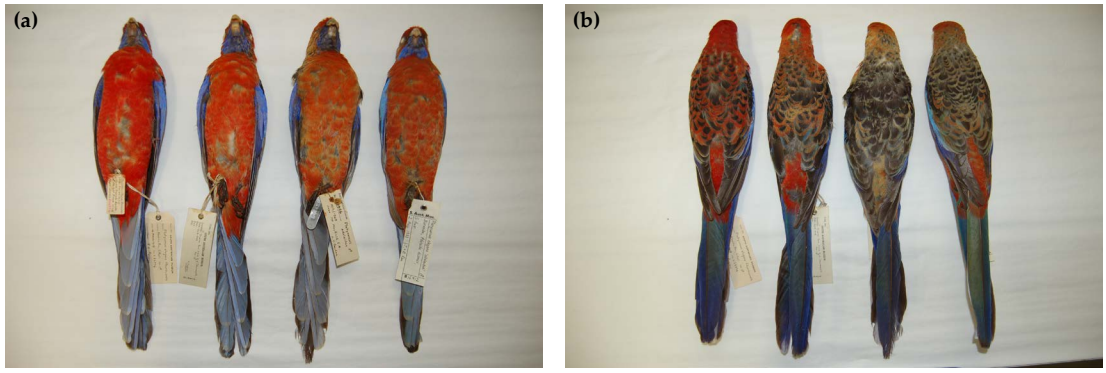

Figure 2. (a) Ventral view of some darker Adelaide Rosellas, all males. From left to right: SAMA B22774 Cape Jervis, SAMA B19716 8 km S of Delamere, SAMA B23956 Mt Hayfield, all Fleurieu Peninsula, SAMA B16912 Burnside, suburban Adelaide. Note subtle variation in tone among Fleurieu birds and the strongly coloured Burnside bird. **(b)** Dorsal view of the same specimens and in the same order. Variation is more evident among Fleurieu birds. From left to right, they were scored 6, 5, 3 and 4 respectively. Images P. Horton

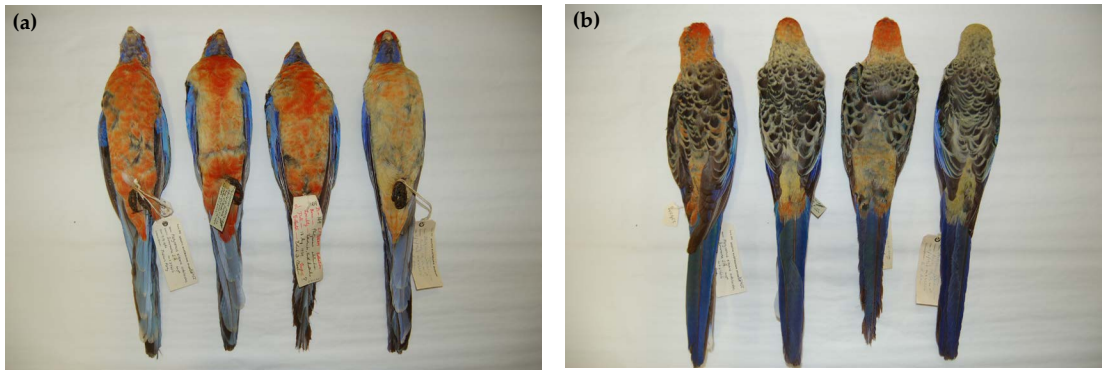

Figure 3. (a) Ventral view of some orange Adelaide Rosellas, all males. From left to right: SAMA B27636 Gumeracha, SAMA B22767 Chain of Ponds, both Mount Lofty Ranges, SAMA B22235 Sutherlands, SAMA B23852 Brady Creek west of Robertstown, both Mid North. Despite much variation, all show some orange on vent and undertail plumage. **(b)** Dorsal view of same specimens in same order. All show some orange in rump plumage. From left to right, they were scored 3, 2, 3 and 1 respectively. Images P. Horton

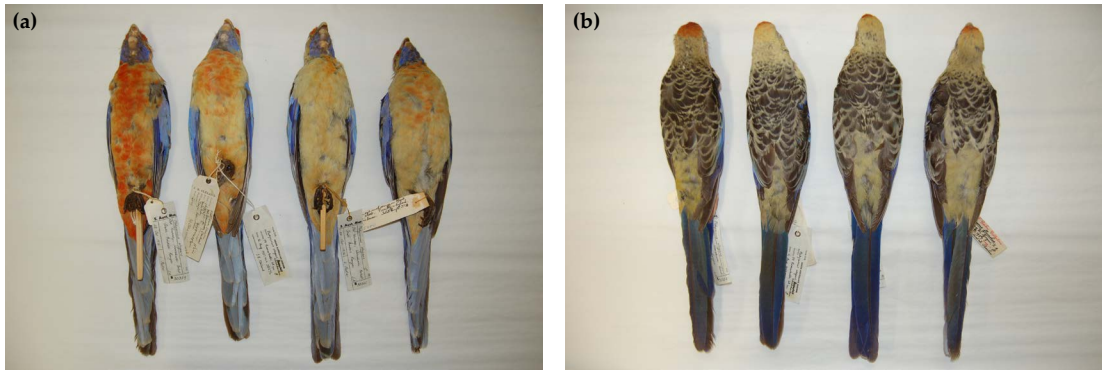

Figure 4. (a) Ventral view of some paler (yellow) Adelaide Rosellas, all males. From left to right: SAMA B30359 Wirrabara Forest, SAMA B28276 Mount Remarkable, SAMA B30360 Wirrabara Forest, all Flinders Ranges, SAMA B25080 Morgan, labelled *flaveolus*. The Morgan specimen shows traces of orange on vent and undertail plumage, an Adelaide Rosella trait. **(b)** Dorsal view of same specimens. Note traces of orange on the crown but absence of any orange in rump plumage. From left to right, they were scored 2, 1, 0 and 1 respectively. Images P. Horton

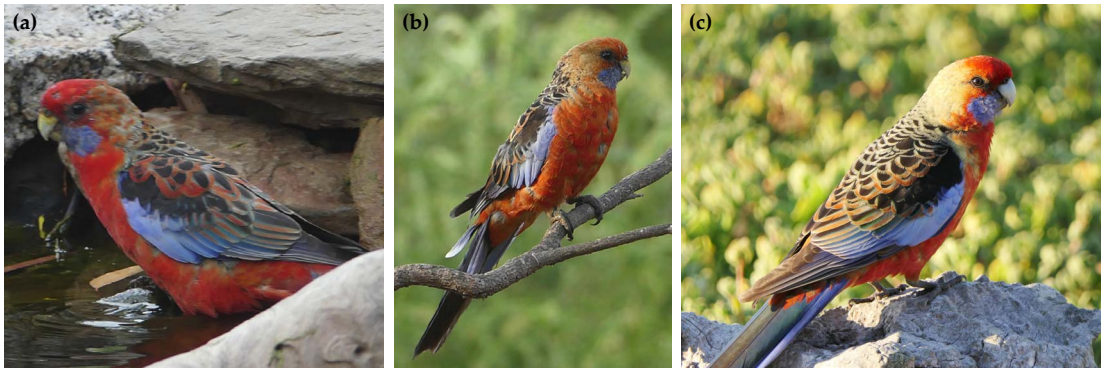

Figure 5. (a) A scarlet Adelaide Rosella, Victor Harbor. Image G. Dare
(b) A more typical Adelaide Rosella, Victor Harbor. Image G. Dare
(c) A pale Fleurieu Peninsula Adelaide Rosella, Waitpinga. Image E. Steele-Collins

Figure 6. (a) A brightly plumaged Adelaide Rosella, Scott Conservation Park. Image R. Daly
(b) A typical Adelaide Rosella, Burnside. Image G Dare
(c) A pale Adelaide Rosella, Barossa Valley. Image G. Dare

Figure 7. (a) A Flinders Ranges Adelaide Rosella, Telowie Gorge. Image G. Dare
(b) Male (above) and female Flinders Rosellas. Image B. Haase
(c) A yellow Adelaide Rosella, Clare. Image D. Donato

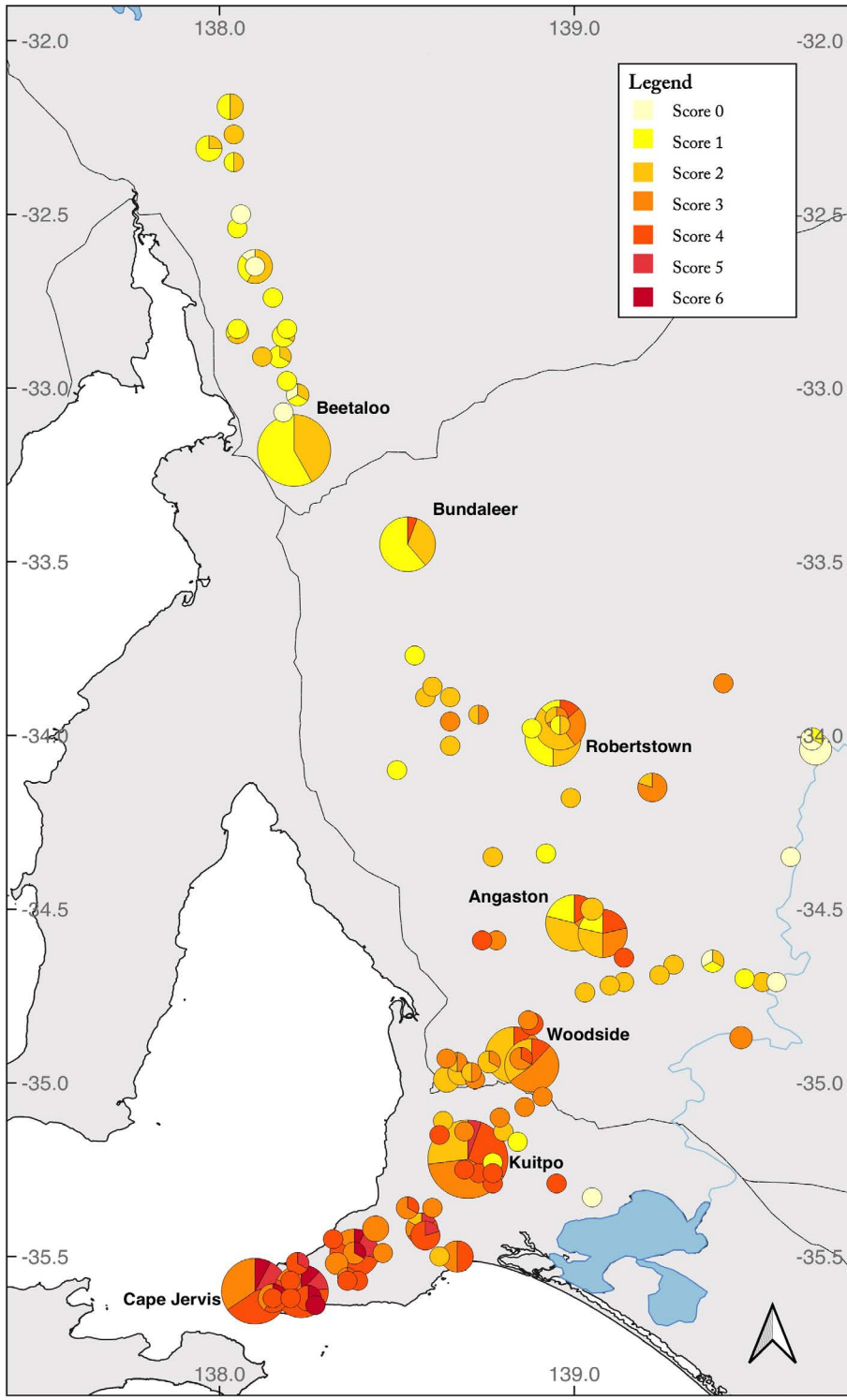

Figure 8. Map showing plumage scores for all Adelaide Rosella specimens examined, together with Yellow Rosella specimens from Morgan and downstream. The smallest circles represent single specimens.

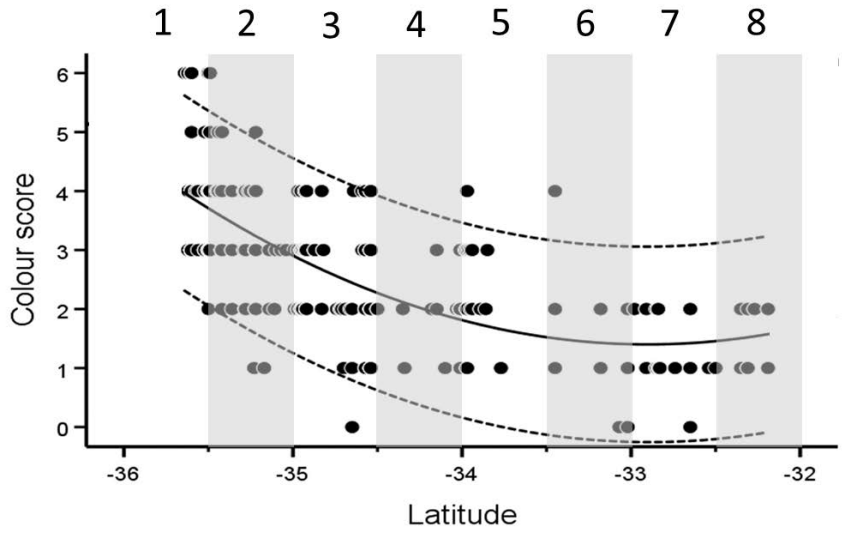

Figure 9. Scatterplot showing the relationship between colour score and latitude in decimal degrees for 424 Adelaide Rosellas. The solid line shows a quadratic regression between the two variables ($R^2 = 0.534$). Dashed lines indicate 95% confidence intervals. Alternating white and grey vertical bands indicate the 0.5° bands into which skins were placed for k-means analysis. These bands are numbered from 1 in the south to 8 in the north.

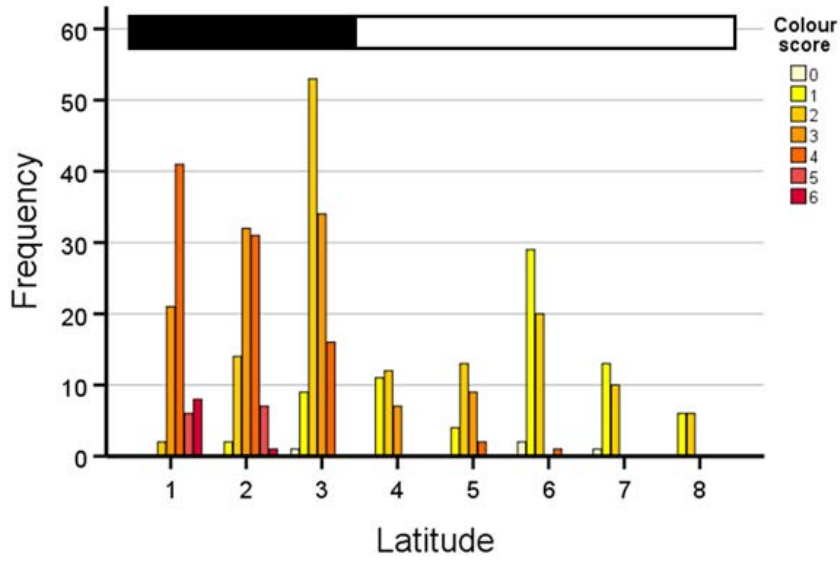

Figure 10. Frequency of colour scores across eight 0.5° latitudinal bands running from south (1) to north (8) for 424 Adelaide Rosellas. The horizontal bar above the graph indicates the division of the latitudinal bands into two groups as determined by k-means analyses.

The largely isolated South Flinders Ranges population is pale and mostly yellow. Morgan (in North 1912: 120) first questioned its treatment as a Yellow Rosella while living at Laura between 1893 and 1897 (Horton *et al.* 2018), observing that some birds there had such 'a great deal of red about them' that they resembled Adelaide Rosellas. We confirm such variation. While some exhibit limited orange on breast, vent and undertail, a few as little as Yellow Rosellas, others are more extensively orange below. This population is separated by about 30 km from the population of rosellas near Bundaleer, and about 50 km from those north of Bungaree, the consequence of intervening naturally treeless *Lomandra* tussock grasslands (Specht 1972). Plumages on either side of those discontinuities are however generally similar (Ashby 1917; DD pers. obs.; L. Pedler pers. comm.; this study). Thus, pale yellow birds with limited orange extend south through the Clare district, and rosellas with fully orange underparts are not seen there. These predominantly yellow Adelaide Rosellas have the same lime-coloured rumps as Yellow Rosellas, with few and minor exceptions, whereas many elsewhere in the Mid North show some orange in rump plumage.

Sexual dimorphism

Condon (1941), Lendon (1973) and Hutchins and Lovell (1985) referred to the male rosella's larger head and bill, which may be evident in the field (DD and GJ pers. obs.). Higgins (1999) noted differences in dorsal and underwing plumage. Lendon (1968, 1973), Forshaw (1969, 1981) and Hutchins and Lovell (1985) reported sexual dichromatism in paler populations, with females showing more orange plumage than males. It is the experience of DD in the Clare district that only males are of the yellowest form and that females may have more extensively orange underparts. Our data confirm the presence of sexual dichromatism in populations (see Figure 7) north of but not south of -34.5°, the latitude of Angaston.

Interaction between Yellow and Adelaide Rosellas

A century ago, Adelaide and Yellow Rosellas were said to meet at Mannum, where W. A. [= W. T.] Angove 'took their [= Adelaide Rosella] eggs ... in October 1907' (North 1912: 118), and at Schuetze Landing, a little upstream of Mannum (E. Ashby in Mathews 1917). Ashby (*loc. cit*.) believed that the two forms merged there but residents considered each was separately represented. Further north, Lendon (1973) observed both on the lower Marne River and collected a Yellow Rosella (SAMA B24749) about three kilometres upstream of Wongulla; he too believed that they remained separate. Other authors have assumed that interbreeding occurs through contact along the Marne (Cain 1955; Condon 1968; Forshaw, 1969, 1981; Hutchins and Lovell 1985; Schodde 1997; Eckert 2000) and surrounding mallee lands (Forshaw 1981; Schodde 1997). Some have suggested that this also occurs along Burra Creek to its entry into the Murray at Morgan (Condon 1968; Hutchins and Lovell 1985) or across the Mount Mary Plains east of Sutherlands (Boehm 1954, though retracted 1959; Schodde 1997). Recent records, including specimens (Figure 1), indicate an uninterrupted distribution between Yellow and Adelaide Rosellas through Wongulla and the Marne River. A more tenuous connection is shown downstream from Wongulla to Mannum and along Reedy Creek (Figure 1) and the minor drainages nearby of Saunders and Shepherd Creeks (AB pers. obs.), records being sparse in the region otherwise (SAOA 1977; Paton *et al.* 1994). Lendon (1968) and Cox (1973) found Yellow Rosellas to be rare south of Wongulla and Cox (1973) saw Adelaide Rosellas only occasionally nearby at Reedy Creek during 28 months residence at Mannum, suggesting a change since the beginning of the 20th century. Recently, Adelaide Rosellas are reliably reported along Reedy Creek and on both banks of the Murray at Mannum (AB pers. data).

Joseph *et al.* (2008) found Yellow and Adelaide Rosellas to be genetically distinct and, in their

supplementary material, drew attention to the meagre specimen record and imperfect identification of pale rosellas within the potential contact zone between Morgan and Mannum. In particular they questioned the holotype locality of the presently unrecognised *P. flaveolus innominatus* Mathews, 1912 reportedly taken by Ashby at Mannum (AMNH 627551) (Figure 11). We have examined a second *flaveolus* skin from 'near Mannum' according to its original label, SAMA B52248, collected by S. A. White in November 1913. Among 11 skins labelled *P. e. flaveolus* from south of Morgan, we detected Adelaide Rosella traits, the presence of orange in undertail plumage, in three: SAMA B25080 from Morgan (1957; see Figure 4), SAMA B52247 (1913) from between Morgan and Blanchetown and Lendon's specimen SAMA B24749 (1956) from west of Wongulla and thus on the Marne. Of eleven other specimens from the Marne River or from near Cambrai, which is on the Marne, seven are typical Adelaide Rosellas but four are very pale, suggesting intergradation, with two, ANWC 11806 and ANSP 191255, close to the *flaveolus* phenotype but with faint orange over the crown and in undertail plumage (Figure 11).

Figure 11. Ventral and dorsal views of the holotype of *P. flaveolus innominatus* Mathews, 1912, AMNH 622751 Mannum (left in each) and Marne River specimen ANSP 191255. Note only a trace of orange on the upper breast of the former and widespread, orange-tinged feathers on underparts and crown of the latter. Compare the latter with SAMA 30360 from Wirrabara Forest in Figure 4. Image L. Joseph

Eckert (2000) reported possible sight records of Yellow Rosellas north-east of Strathalbyn and obtained a specimen south of Langhorne Creek in December 1995 (SAMA B57121) that he found identical to that form. We accept his identification but suspect an escaped cage bird, since a Yellow Rosella specimen obtained by Eckert on an unstated date (SAMA B57120) is from a nearby aviary.

The degree to which Yellow and Adelaide Rosellas have been in contact historically, while confidently and frequently asserted, remains unclear. Enzyme electrophoresis (Joseph and Hope 1984) provided evidence of introgression but DNA data (Joseph *et al.* 2008) demonstrate their genetic distinction despite low within- and between-population diversity among all south-east Australian populations. At the eastern end of the Yellow Rosella's range, Cain (1955) could not confirm contact with the Crimson Rosella; he postulated that they were terminal components of a 'ring species' in which two reproductively isolated populations are connected by serial intergrading populations, and that 'Casuarina' woodlands represented a habitat barrier. Joseph *et al.* (2008) found the hypothesis unsupported by their data, which revealed genotypic and phenotypic discordances and multiple genetic discontinuities. On the other hand, they did not reject that a continuous circular distribution had been involved in the evolutionary history of the southern Crimson Rosella group.

Clearance of 'Casuarina' woodlands might explain records first documented by Martindale (1974) of Adelaide-like rosellas between Wagga Wagga and Gundagai, New South Wales (Schodde 1997; Higgins 1999; Joseph *et al.* 2008). These intergrades are now readily encountered in both New South Wales and Victoria and specimens are held in North American museums and ANWC (L. Joseph pers. comm.). The clearance of mallee in South

Australia might similarly have disturbed the purported separation of Yellow and Adelaide Rosellas. Because few relevant specimens have been taken since the holotype of *innominatus*, reports of Yellow Rosellas south of Morgan and particularly south of Wongulla might include birds of intergradient phenotype. Observations of Adelaide Rosellas near the river at Mannum, as above, and of rosellas with extensively orange underparts near Weston Flat east of Morgan in November 2018 (AB pers. obs.) and by Roger Schmitke since around 2010 (pers. comm. and photos to AB) provide evidence that the two forms are presently and perhaps increasingly in reproductive contact.

A variable entity

Our results show that Adelaide Rosella plumages vary in a latitudinal cline and individually throughout their range, with red birds predominating in the south and yellow birds in the north. As shown in the Crimson Rosella complex more broadly (Ribot *et al.* 2019), this is consistent with Gloger's (1833) ecophenotypic rule in which heavily pigmented forms occupy more humid portions of a species' range, and lightly pigmented forms the more arid. There has been uncertainty, however, in defining the geographic extent of the cline. Ashby (1925: 89) suggested that there was 'a complete gradation' across all populations and, while Condon (1941) and Cain (1955) appeared to support that view, Forshaw (1981) and Schodde (1997) found that it occurred largely within the central population. Higgins (1999) described a cline with local variation involving southern and central populations but relatively consistent plumage in the South Flinders population. Lendon (1973) and Hutchins and Lovell (1985) held similar views. Variation is present nonetheless in the South Flinders population and latitudinal change within it has not been addressed.

Our regression analysis shows that plumage variation exists as a cline in relation to latitude as far north as the Bundaleer sample at around -33.3° (Figures 8 to 10, Gazetteer), beyond which the curve flattens, and no cline is evident.

The Fleurieu Peninsula contains the scarlet *fleurieuensis* phenotype, but Lendon (1968, 1973) observed paler birds there and rejected Ashby's subspecies. Mathews (1930, 1931) had placed *fleurieuensis* in synonymy and Collar (1997) omitted it. Ashby himself (1917: 43) did not claim that all Fleurieu Peninsula Rosellas were of the scarlet form, only 'a quota of highly coloured birds' being seen in their stronghold between Normanville, Second Valley and Cape Jervis. The scarlet form is represented north to Kuitpo Forest, beyond which most Adelaide Rosellas in the Mount Lofty Ranges and adjacent plains are either fully orange or orange and yellow. Regression studies of plumage score versus latitude reveal no disjunction through this part of the Adelaide Rosella's range.

The *subadelaidae* phenotype of the Flinders Ranges population is of pale largely yellow birds with lime coloured rump and patchy orange restricted chiefly to the breast, vent and undertail. A similar phenotype predominates in the Clare and Bundaleer regions, with orange-rumped birds in a small minority. More extensively orange individuals with orange in the rump are more common immediately to the west near Blyth and to the east south of Burra (DD pers. obs.).

Joseph *et al.* (2008) considered that the Adelaide Rosella is more likely to have resulted from Pleistocene secondary contact between Crimson and Yellow Rosellas than to have evolved independently in isolation but that in either case its present cline developed subsequently as a result of strong selective pressure across an environmental gradient. Alternatively, R. Schodde (*in litt.* to AB) suggested that during Pleistocene arid periods, Fleurieu Peninsula, Mount Lofty Ranges and Flinders Ranges populations contracted into isolates, expanding and intergrading during warmer pluvials, accounting therein for the Adelaide Rosella's

present plumage diversity. Earlier, Ford (1977) had suggested that subspecies *flaveolus* had differentiated as a Mount Lofty Ranges isolate before moving northwards to the Flinders Range and eastwards to Murray River woodlands. Joseph *et al.* (2008) found no support for Ford's (1977) hypothesis and inferred that the two yellower subspecies, *flaveolus* and *subadelaidae* evolved independently. While we did not distinguish a small number of *subadelaidae* specimens from Yellow Rosellas quantitatively, subtle plumage differences between the typical phenotype of each supports the independence of these two forms. Furthermore, Higgins (1999) showed that *P. e. flaveolus* is significantly smaller on average than *P. e. subadelaidae* in wing, tail, bill and tarsus length, and weight. There are also differences in juvenile and immature plumages. In young Adelaide Rosellas from throughout its range much of the body plumage is olive green but young Yellow Rosellas more closely resemble adults and are yellow with a pale greenish wash (DD pers. obs.). Lendon (1973) observed that young Yellow Rosellas were generally dull yellowish green, young Adelaide Rosellas being olive green, and Hutchins and Lovell (1985) wrote that some young Yellow Rosellas leave the nest as a dull version of the adult. The successional plumages of maturing birds among members of the Crimson Rosella complex are worthy of further study.

The pronounced diversity in plumage colours among Adelaide Rosellas is uncommon in a natural population. Bocalini and Silveira (2015) and Lima *et al.* (2020) addressed similar taxonomic questions in studies of *Forpus* parrotlets and *Picumnus* piculets respectively in north-eastern South America. Among 518 specimens of the four then named subspecies of *Forpus xanthopterygius*, Bocalini and Silveira (2015) found variation in plumage (scored 0–5) throughout their combined distributions with duller individuals predominating in more humid and brighter in drier habitats respectively. Lima *et al.* (2020) examined two named species (alternatively subspecies) of *Picumnus* piculets where phenotypic intermediates had been reported and another subspecies named. They applied a plumage score (1–5) to 66 museum specimens and 284 photographs of wild birds. Each method produced a similar result, clinal change across the total distribution following Gloger's rule and phenotypic diversity throughout. Those authors argued that the described patterns of plumage diversity represented a single polymorphic species with clinal variation. They revised existing taxonomy, naming a single species with synonyms but no subspecies. Both studies' findings closely parallel ours and, since all Adelaide Rosellas are combined in a single genetically coherent group (Joseph *et al.* 2008), a single name might similarly be applied to that entity.

Yet, while clinal change is present in plumage from the Fleurieu Peninsula through the Mount Lofty Ranges and Mid North, the cline ceases through the Flinders population, where limited diversity of plumage appears consistent throughout. Its relative homogeneity is evident in the map (Figure 8) and in regression studies (Figures 9 and 10), there being negligible latitudinal change north of -33.5°. That population is essentially isolated by tussock grasslands to the south and east and in both these respects our findings differ from those of the above authors. Another allopatric and unvarying population assigned to the same microsatellite cluster as the Adelaide Rosella is the Kangaroo Island Crimson Rosella *P. e. melanopterus* (Joseph *et al.* 2008), whose consistency of plumage and isolation by a sea barrier have hindered its recognition as an integral component of the Adelaide Rosella complex.

The significance of -34.5°

Our analyses (Figure 10 and Table 2) divided latitudinal colour variation into two natural groups, one south of and one north of -34.5°. This latitude was defined by our methods but is not the point of division between the two groups

because the cline in colour score continues through it. The latitude reflects a change between wetter mainly hilly localities of the Mount Lofty Ranges in the south and drier mainly plains localities north of the Barossa. It is possible also that it represents an approximate boundary between the influences on plumage colours through introgression from *subadelaidae* in the north and *melanopterus* in the south. The former is most evident in Bundaleer and Clare Valley populations which are clearly intergradient, the latter on Fleurieu Peninsula as long recognised.

Taxonomic implications

Here we turn to the four patterns of plumage variation offered as alternative hypotheses. We reject patterns 2 and 4 because our results provide no basis for recognising Fleurieu Peninsula rosellas as a subspecies, since they merge with the main central population in a cline that extends through the Mount Lofty Ranges and Mid North. Pattern 1 is also rejected, because the South Flinders Ranges population is not part of the cline. Pattern 3 is represented by our data and we consequently recognise two geographically definable subspecies within the Adelaide Rosella. They are (1) the clinally and individually variable central + southern populations, and (2) the less varied, geographically restricted and essentially allopatric northern population of the South Flinders Ranges. For the former, the name *Platycercus elegans adelaidae* Gould, 1840 has priority over *P. e. fleurieuensis* Ashby, 1917. We acknowledge that evidence favours a hybrid origin for this entity. The pattern of colour variation could be explained by local adaptation, secondary admixture of previously differentiated populations, or some combination of the two. Spectrophotometric analysis of colour variation and additional genetic data will be required to test to what extent the variable plumages in Adelaide Rosellas reflect these alternative evolutionary processes.

In summary, we find a cline in adult plumage colour within the Adelaide/Kangaroo Island Rosella lineage (Joseph *et al.* 2008) between uniformly red *P. e. melanopterus*, through variable red, orange and yellow *P. e. adelaidae,* to primarily yellow *P. e. subadelaidae*. The cline is within *P. e. adelaidae* alone, and extends between the two more consistently plumaged populations, separated in the south by Backstairs Passage, the 14 kilometres of sea that isolated *P. e. melanopterus* on Kangaroo Island most recently 8,900 years ago (Belperio and Flint 1999), and in the north across almost treeless grasslands separating Beetaloo, Bundaleer, the Bungaree Hills and Burra. Genetic data suggest that the Adelaide/Kangaroo Island Rosella lineage diverged from other components of *P. elegans* prior to the disjunction of island from peninsula (Joseph *et al.* 2008). Despite the close resemblance of some *P. e. subadelaidae* and *P. e. flaveolus* they belong to separate lineages (Joseph *et al.* 2008).

In accordance with our findings, we identify three subspecies within the Adelaide Rosella complex:

Platycercus elegans melanopterus Kangaroo Island Rosella,
P. e. adelaidae (including *P. e. fleurieuensis* in synonymy) Adelaide Rosella,
P. e. subadelaidae Flinders Rosella.

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APPENDIX
Early taxonomy of the Adelaide Rosella

Gould

Gould (1840) described the Adelaide Rosella *Platycercus adelaidae* from specimens obtained during his visit to South Australia in 1839 when he collected from the Adelaide Plains, Mount Lofty Ranges and 'Belts of the Murray' (western Murray Mallee) (Carpenter and Black 2015). His illustration of the parrot (Gould 1840–48: Plate 22) was of two distinctly different birds (Figure 12). The body of one is an almost evenly coloured orange, including all underparts, crown, posterior neck, lower back, rump and the fringes of black-centred mantle feathers, scapulars and tertials. The other bird is paler, mostly yellow but with patches of reddish orange, including a frontal bar with diffuse extension over the crown, and on the throat, upper breast, vent and undertail coverts.

Gould expressed 'considerable perplexity from its close similarity in some stages of its plumage' to the Crimson Rosella *Platycercus elegans* but failed adequately to describe the diversity of plumage that his artists figured so strikingly. He wrote that the paler bird was 'an immature bird in the course of change from the green plumage to adult dress' but both are adults. We now understand Gould's 'perplexity' at the similarities of Adelaide and Crimson Rosellas and are accustomed to the great variation in Adelaide Rosella plumage.

Mathews, Ashby and others

Mathews's (1912) 'Reference-list to the birds of Australia' introduced to Australian ornithology the naming of geographically partitioned differentiated populations as subspecies. He interpreted Gould's 'perplexity' in that context, recognising the Adelaide Rosella as a subspecies of the Crimson Rosella with the scientific name *Platycercus elegans adelaidae.* Even more astutely, he named S. A. White's almost yellow rosella from near Port Augusta as *Platycercus elegans*

subadelaidae, appreciating its similarity to the Adelaide Rosella but differing in its 'less brilliant underparts and reduced red over the crown.' When Mathews (1913) published a further 'List', he had relegated his recently described subspecies *subadelaidae* to synonymy in *P. e. adelaidae* but reinstated it as a separate subspecies in *The Birds of Australia* (Mathews 1916–1917).

Shortly afterwards, Ashby (1917) described a scarlet variant *Platycercus elegans fleurieuensis* from specimens he and Frank Parsons had collected on the Fleurieu Peninsula (Schodde *et al*. 2021). Although he named it as a subspecies of the Crimson Rosella, his preference then (Ashby 1917) was to place both *fleurieuensis* and *flaveolus*, in which he included Flinders and Mid North populations, as subspecies of the Adelaide Rosella. Ashby (1925) further promoted the Adelaide Rosella as a species, explicitly rejecting Mathews's placement of it as a subspecies of *elegans* but conceded that two species might be 'more correct', in which case *adelaidae* and *fleurieuensis* should be subspecies of *flaveolus*. In this indecisive and self-contradictory interpretation, he overlooked or ignored Mathews's insightful treatment of *subadelaidae* and continued to include Flinders and Mid North populations in the Yellow Rosella. Mathews (1920) added Ashby's subspecies *fleurieuensis* in a Supplement to *The Birds of Australia* but, perhaps influenced by Ashby, included *subadelaidae* within the Yellow Rosella as *P. flaveolus subadelaidae*.

Because the naming of subspecies had not yet become established in Australia, the Australian Checklist (RAOU 1926) included them only as synonyms for named species. Adelaide and Yellow Rosellas were listed as species with *subadelaidae* a synonym of the Yellow Rosella and *fleurieuensis* a synonym of the Adelaide Rosella.

Mathews's next listings (1930, 1931) relegated *fleurieuensis* to synonymy in *P. e. adelaidae*; he continued to name the Flinders population as *P. flaveolus subadelaidae*.

Figure 12. Strikingly different plumage patterns in Gould's Adelaide Rosellas.

While Mathews equivocated, Parsons advised Neville Cayley that he believed his co-collector Ashby was 'in error in stating that *Pl. flaveolus* extends through the Flinders Ranges' (Cayley 1938: 155–156). In Parsons's view Flinders birds represented the yellow extreme among Adelaide Rosellas and '*Pl. flaveolus* in South Australia is only found along the Murray'.

Condon (1941) recognised the Yellow Rosella as a subspecies and the Adelaide Rosella as a cline of three subspecies, *fleurieuensis*, *adelaidae* and *subadelaidae*. Cain (1955) followed Condon but was undecided how to represent the cline taxonomically. Both authors implied that all four subspecies interbred.

In his final 'working list', Mathews (1946) named *adelaidae* and *fleurieuensis* as subspecies of *elegans* but was unable to categorise *subadelaidae*. He wrote of it as a 'form (that) may connect [species] *flaveolus* and [species] *elegans'*, thus implying cross-species hybridisation but without elaborating on the implications of such

a suggestion. Hybridisation between species, let alone the existence of hybrid populations, was a contested topic until well after Mayr's mid-twentieth century elucidation of the 'biological species concept' (Mallet 2005).

Gazetteer of South Australian localities

Locality	Latitude/Longitude	Locality	Latitude/Longitude
Adelaide	34° 56′ S, 138° 36′ E	Marne River (source)	34° 40′ S, 139° 07′ E
Angaston	34° 30′ S, 139° 03′ E	Meadows	35° 11′ S, 138° 45′ E
Beetaloo (Reservoir)	33° 11′ S, 138° 13′ E	Morgan	34° 02′ S, 139° 40′ E
Blanchetown	34° 21′ S, 139° 37′ E	Mount Barker	35° 05′ S, 138° 52′ E
Blyth	33° 51′ S, 138° 29′ E	Mount Compass	35° 21′ S, 138° 37′ E
Bordertown	36° 19′ S, 140° 46′ E	Mount Hayfield	35° 31′ S, 138° 20′ E
Brady Creek	33° 58′ S, 139° 00′ E	Mount Mary	34° 06′ S, 139° 26′ E
Brookfield Conservation Park	34° 21′ S, 139° 31′ E	Mount Remarkable	32° 48′ S, 138° 08′ E
Buckaringa	32° 02′ S, 138° 03′ E	Murray Bridge	35° 07′ S, 139° 16′ E
Bundaleer (Forest)	33° 17′ S, 138° 34′ E	Myponga	35° 23′ S, 138° 28′ E
Bungaree (Hills)	33° 43′ S, 138° 33′ E	Normanville	35° 27′ S, 138° 19′ E
Burnside	34° 57′ S, 138° 40′ E	Port Elliot	35° 32′ S, 138° 41′ E
Burra	33° 40′ S, 138° 55′ E	Quorn	32° 21′ S, 138° 03′ E
Cambrai	34° 39′ S, 139° 17′ E	Reedy Creek	34° 55′ S, 139° 11′ E
Cape Jervis	35° 36′ S, 138° 06′ E	Robertstown	33° 59′ S, 139° 05′ E
Chain of Ponds	34° 49′ S, 138° 50′ E	Salt Creek	36° 07′ S, 139° 39′ E
Clare	33° 50′ S, 138° 37′ E	Schuetze Landing	34° 52′ S, 139° 27′ E
Crystal Brook	33° 21′ S, 138° 12′ E	Scott Conservation Park	35° 25′ S, 138° 44′ E
Delamere	35° 34′ S, 138° 12′ E	Second Valley	35° 32′ S, 138° 13′ E
Florieton	33° 51′ S, 139° 26′ E	Strathalbyn	35° 16′ S, 138° 54′ E
Gumeracha	34° 49′ S, 138° 53′ E	Sutherlands	34° 09′ S, 139° 13′ E
Hindmarsh Valley	35° 30′ S, 138° 37′ E	Telowie Gorge	33° 02′ S, 138° 07′ E
Inman Valley	35° 29′ S, 138° 28′ E	Waitpinga	35° 36′ S, 138° 32′ E
Jamestown	33° 12′ S, 138° 36′ E	Weston Flat	34° 02′ S, 139° 49′ E
Keith	36° 06′ S, 140° 21′ E	Wirrabara Forest	33° 03′ S, 138° 13′ E
Kuitpo Forest	35° 13′ S, 138° 41′ E	Wongulla	34° 42′ S, 139° 34′ E
Langhorne Creek	35° 18′ S, 139° 02′ E	Victor Harbor	35° 33′ S, 138° 38′ E
Laura	33° 11′ S, 138° 18′ E	Yankalilla	35° 28′ S, 138° 21′ E
Mannum	34° 55′ S, 139° 18′ E		