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Regional variation in iris colour of the White-browed Scrubwren *Sericornis frontalis* complex in digital photographs

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Abstract. A large sample (*n* = 590) of location-tagged digital photographs was examined to assess regional or subspecific variation in iris colour of the White-browed Scrubwren *Sericornis frontalis* complex, which may be a diagnostic character misrepresented in the literature. The irides of the western/Spotted Scrubwren group (*maculatus, balstoni, mellori, ashbyi*) were found to be consistently more blue-green in colour compared with the remainder of the complex; this difference approached criteria for diagnosability and matched reported taxon boundaries. Lack of variation within the western group suggests a genetic rather than an ecophenotypic basis. Since juveniles of both groups have similar irides, this difference probably represents the acquisition of yellow-orange pigmentation with maturity in eastern but not western birds.

Introduction

Taxonomic treatment of the White-browed Scrubwren *Sericornis frontalis* (Vigors & Horsfield, 1827) complex has varied historically to include one, two, three or up to four species. Under the recently prevailing, but not universal, arrangement (e.g. Higgins & Peter 2002; Christidis & Boles 2008; del Hoyo *et al*. 2016; BirdLife Australia 2017; Clements *et al.* 2018), this species complex excludes the Tasmanian (Brown) Scrubwren *S. humilis* (including *S. h. tregallasi*), but includes three principal groups formerly recognised as full species: the south-eastern nominate *frontalis* group (including *rosinae*, *harterti*, *flindersi*, *tweedi*), the western *maculatus* group (including *balstoni*, *mellori*, and *ashbyi*) and north-eastern *laevigaster* (Clements *et al.* 2018). Of these, the *maculatus* group is arguably the most distinct morphologically, leading to its recognition as 'Spotted Scrubwren' *S. maculatus* Gould, 1847 in several major taxonomic lists (Mayr & Traylor 1986; Dickinson & Christidis 2014) and recent elevation to species in the IOC checklist (Gill & Donsker 2019).

A recently published phylogenetic study (Norman *et al.* 2018) showed *maculatus* as basal to *frontalis, humilis*, and the Atherton Scrubwren *S. keri* from Bayesian analysis of mitochondrial (*ND2*) DNA, and again recommended recognition of *S. maculatus* as a full species. In recent online discussion around this finding, it was remarked (attributed to Graeme Chapman, Jeff Davies *in litt.*; see also Chapman n.d.) that individuals of the *maculatus* group consistently have bluish or greenish irides, in contrast with the yellowish irides of eastern birds, and that this difference is readily confirmed from photographs. If true, this has largely escaped attention in published field guides and reference works, which either fail to mention subspecies differences in eye colour, or incorrectly present the iris of western birds as yellow in either written descriptions (Slater 1974; Serventy & Whittell 1976; Storr & Johnstone 1985; Higgins & Peter 2002) or colour plates (Simpson & Day 1993; Pizzey & Knight 2007; Slater *et al.* 2009). However, Johnstone & Storr (2004, p. 64) noted the eye colour of *maculatus* as "white, greyish white or greyish green", and Peter Marsack's plates in both Higgins & Peter (2002) and Menkhorst *et al.* (2017) depict grey-green eyes in some western forms. Higgins & Peter (2002, p. 180) noted that iris colour "varies greatly" and suggested (without fully resolving) subspecies differences, noting a higher proportion of "pale-orange or pinkish" irides in *laevigaster* and "off-white or pale-greyish" irides in *balstoni* and *mellori* but rarely *maculatus*, suggesting an ecophenotypic effect by which the "iris tends to be paler in drier habitats of coastal w. WA and SA, and more orange or pinkish in wetter habitats". If true, such an effect may drive a broader difference, since the *maculatus* group is known to inhabit a broader range of habitats including more open and drier thickets (Macdonald 1979; Pizzey & Doyle 1980). Eye colour is further complicated by age, with the iris of juveniles noted as "light greyish …, light brownish-grey … or bluish grey" by Higgins & Peter (2002, p. 180), and in immatures (of *frontalis*) as "dull grey rapidly changing to cream" by Rogers *et al.* (1986, p. 71).

Other evidence hints that iris colour may have potential taxonomic utility as a phenotypic marker. In particular, Norman *et al.* (2018) found that the *ashbyi* form of Kangaroo Island unexpectedly aligned with the eastern *frontalis* group on Bayesian *ND2* analysis, flagging inconsistency between this molecular data and its plumage, which clearly aligns with the western plumage type. Noting the possibility of introgression, incomplete lineage sorting or other complex evolutionary history as an alternative to plumage convergence, they recommended leaving *ashbyi* within the western group pending further study. Since *ashbyi* is also noted as having a "pale bluish-grey" eye by Baxter (2015, p. 470), iris colour may provide further evidence of its alignment. The adjacent mainland form *rosinae* of the southern Mount Lofty Ranges and Fleurieu Peninsula has itself been regarded as an intermediate between *mellori* and nominotypical *frontalis* (Mayr 1937; Condon 1951; Ford 1970; Christidis & Schodde 1991; Schodde & Mason 1999). Similarly, populations in southernmost Victoria (*harterti*) and Flinders Island (*flindersi*) have been discussed as sharing characters with *S. humilis* (Cooper 1975; Schodde & Mason 1999), and the *tweedi* form occupies a zone of phenotypic and genetic intergradation between *frontalis* and *laevigaster* (Mayr 1937; Christidis & Schodde 1991; Schodde & Mason 1999).

Geographic comparison of iris colour requires broad sampling with reliable colour determination. However, iris colour is not routinely recorded in banding schemes involving live birds, and is not always noted (e.g. on specimen tags) during preparation of museum skins. Even where recorded, human perception of colour is subjective and influenced by light conditions, even when standardised colour charts are used for comparison (Bortolotti *et al.* 2003). Since they must be in contact with the measured surface, digital colorimeters cannot be used on irides (Villafuerte & Negro 1998). Analysis of digital photographs offers one solution for measurement of iris colour. Bortolotti *et al.* (2003) successfully measured RGB colour from digital photographs of live American Kestrels *Falco sparverius* to quantify differences in iris colour undetectable to the naked eye, using standardised flash lighting and greyscale reference cards. Although not collected under such standardised conditions, the ever-increasing availability of high-quality, location-tagged digital bird photographs on the internet may potentially allow for similar analysis of colours of the bare parts. Accordingly, the aim of this study was to assess regional and subspecific variation in iris colour in the White-browed Scrubwren complex from digital photographs, relative to known morphologic and genetic diversity as outlined above.

Method

Images were obtained for this research purpose (by download or image capture) from a variety of searchable image databases including Flickr (www.flickr.com), eBird/Macaulay Library (www.ebird.org), Feathers and Photos (www.featherandphotos.com.au), HBW Alive/The Internet Bird Collection (www.hbw.com/ibc/), iNaturalist (www.inaturalist.org), BirdLife Photography (www.birdlifephotography.org.au), Bird Forum (www.birdforum.net/gallery) and various other websites (including www.pbase.com, www.bushpea.com, www.alamy.com). Photographs were also obtained from Facebook (www.facebook.com) groups including Australian Bird Photography, Australian Bird Identification, Western Australian Birds, and South Aussie Birding, and the public galleries of several individual photographers (see Acknowledgements). The search strategy focused on gaining adequate representation of each taxon, full geographic coverage across the species' ranges, and particularly on maximal sampling within Western Australia and South Australia. Criteria for image inclusion included high resolution (i.e. sufficient pixels within the iris), reliable location data (usually from a stated location or map coordinates), adequate lighting on the eye, and natural colour (i.e. without any apparent tint or colour cast).

Eye images were processed in Adobe Photoshop CS6 (v. 13.0 x64, Adobe Systems Inc., 2012) to derive average iris colour. Using the *Lasso* tool, the brightest, central parts of the iris were manually delimited (typically a crescent centred within the lower two-thirds of the central iris) and the values of all included pixels were averaged (*Filter*/*Blur*/*Average*). The $L^*a^*b^*$ colour values of this average was determined using Digital Colour Meter (v. 5.11, Apple Inc., 2017). In this three-axis colour system, the L^* (lightness) axis spans from white to black, the a^* axis from green to red, and the b^* axis from blue to yellow, with true neutral grey at (50, 0, 0); the a^*b^*-defined colour hue is considered independent of L^*-defined luminance. Additionally, the apparent colour of the outer rim of the iris was noted (i.e. grey, red, red-brown, brown) where contrasting with the core iris colour.

As far as was possible, the photographed birds were sexed and/or assigned to age classes (juvenile, immature, adult) using the plumage descriptions in Higgins & Peter (2002). In particular, the retention of juvenile (buff-tipped) outer greater secondary coverts was taken to indicate immaturity. Principal component analysis (PCA) using a rotated covariance matrix (SPSS Statistics, v.22, IBM) was used to derive a single variable (*pc1*) representing the main vector of a^*b^*-defined colour hue variation. Mean differences in *pc1* and L^* between groups (eastern/western group, taxon) and within groups (sex, age class) were tested by independent *t*-test or by one-way Analysis of Variance and Fisher's Least Significant Difference *post-hoc* ($P < 0.05$).

Results

The image sample included 590 White-browed/Spotted Scrubwrens (n = 386 eastern/*frontalis* group, 204 western/*maculatus* group; n = 431 adults, 100 immatures, 59 juveniles) plus 75 Tasmanian Scrubwrens *S. humilis*. Overall, the irides of western/*maculatus* group adults were found to be significantly more blue-green (i.e. lower *pc1*) in photographs compared with the eastern/*frontalis* group [$t(429) = 18.72$, $P < 0.001$; effect size (Cohen's d) = 1.93]. There was only partial overlap between groups in a^*b^* colourspace (Figure 1) as well as in *pc1* (Figure 2), such that a *pc1* threshold including 85% of western group birds excluded 85% of the eastern sample, or alternately a lower threshold including 75% of the western group excluded 93% of eastern group (see Figure 2). The irides of western birds were also darker compared with the eastern group (L^* 55.7 ± 14.9 vs 69.3 ± 11.5, $t(429) = 10.66$, $P < 0.001$).

Sex and age class had an effect on iris colour hue only in the eastern/*frontalis* group. Age class significantly affected *pc1* [$F(2) = 10.66$, $P < 0.001$] such that the irides of eastern immatures and juveniles were both significantly more

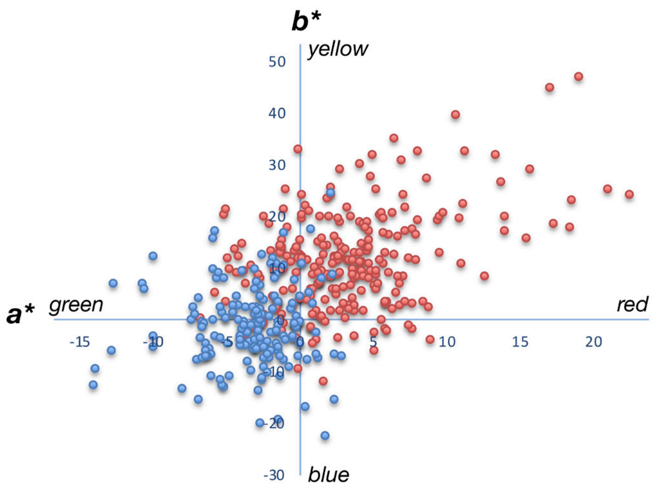

Figure 1. *X-Y* plot of iris colour as the a^* and b^* dimensions of $L^*a^*b^*$ colour, in adults of the eastern/*frontalis* group (red circles) and western/*maculatus* group (blue circles) of White-browed Scrubwrens.

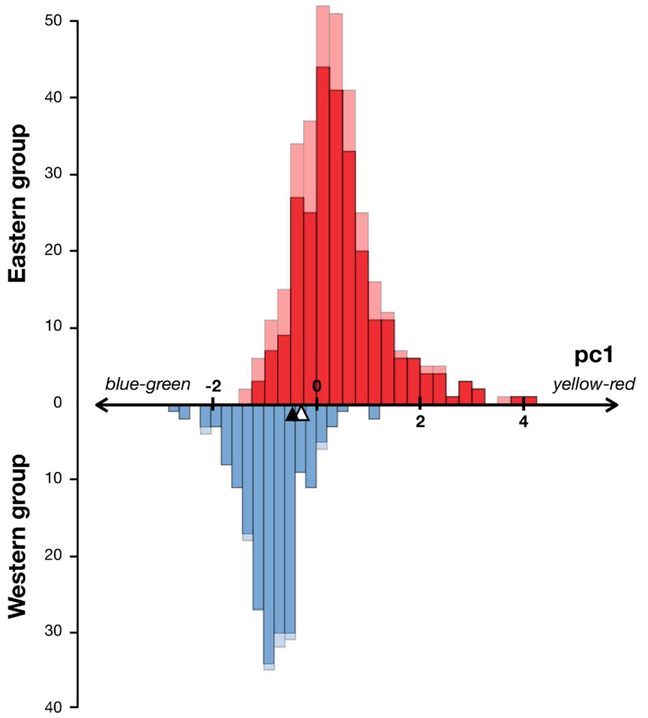

Figure 2. Frequency histogram of iris colour in White-browed Scrubwrens as *pc1* variable, representing the main vector of *a***b** colour hue difference within the sample. Red/upper bars, eastern/*frontalis* group; blue/lower bars, western/*maculatus* group; solid bars, adults; paler bars, adults and immatures. White triangle indicates nodal point separating 85% of each population; black triangle indicates the point separating 75% of western and 93% of eastern [i.e. approximating Donegan's (2018) Level 3 (75%/99%) diagnosability criteria].

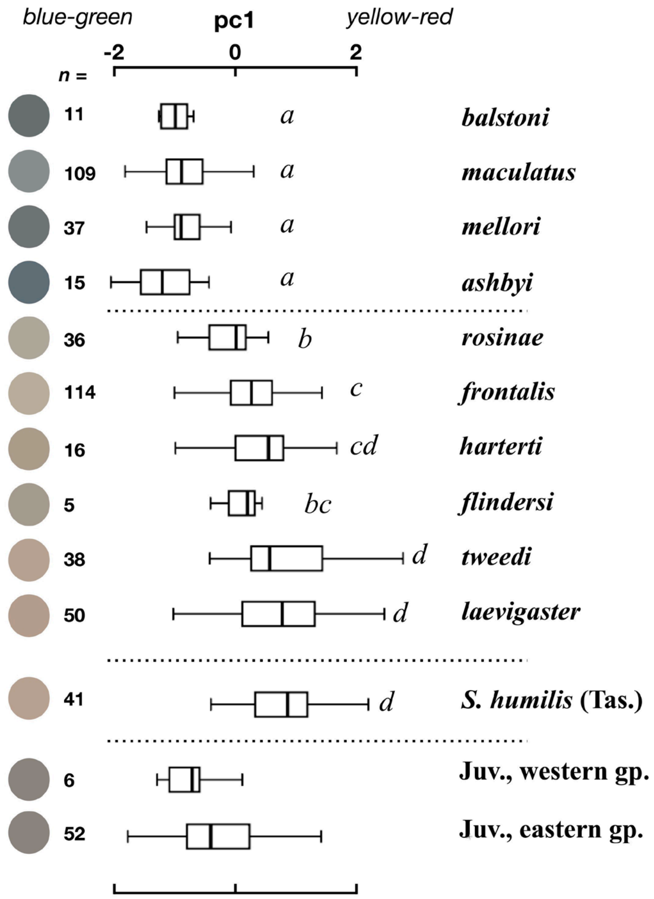

Figure 3. Box plots of iris colour in White-browed Scrubwren taxa as *pc1* (i.e. principal axis of *a***b** colour variation), within each taxon of the western group (*maculatus*, *balstoni*, *mellori*, *ashbyi*) and of the remaining eastern group, juveniles (juv.) of each group (gp), and Tasmanian Scrubwren *S. humilis*. Sample sizes are indicated by *n*. Boxes indicate median and interquartile range, bars indicate upper and lower range. Letters indicate statistically significant differences between taxa; the means of groups that do not share a letter are different. Coloured circles represent the average photographic iris colour, as predicted from mean *a** and *b** value in a taxon.

blue-green than those of eastern adults [P = 0.016 and P <0.0001, respectively). Irides of immature eastern males (n = 29) were significantly more blue-green [$t(75)$ = 2.15, P = 0.034] than immature eastern females (n = 46). In both eastern and western groups, age class affected lightness L^* [$F(2)$ = 10.62, P <0.001], such that juveniles, but not immatures, had significantly darker irides compared with adults (54.8 ± 16.5 vs 63.9 ± 14.5, P <0.001). The irides of young fledglings were very dark grey or blackish.

Comparison of mean iris colour across all taxa (Figure 3) showed that the average colour in Kangaroo Island form *ashbyi* in photographs was a greyish blue-green colour, similar to *maculatus*, *balstoni* and *mellori*. The irides of Mt Lofty Ranges subspecies *rosinae* were found to be significantly more yellow-red than the *maculatus* group, yet significantly more blue-green than the more buffy irides of nominate *frontalis* (i.e. somewhat intermediate). The irides of north-eastern *tweedi* and *laevigaster* were a more orange-buff colour, similar to *S. humilis*. The irides of eastern-group birds often (44%) showed a reddish, brown, or reddish-brown outer rim (Figure 4); significantly fewer (20%; P <0.001) western-group birds showed a darker rim to the iris, typically dark greyish in colour when present. Bill colour was also incidentally noted to differ across taxa (*pace* Jeff Davies *in litt.*), with a pinkish-buff tone to the bill base, especially in the lower mandible, in most (76%) western-group birds but only a few (15%) of the eastern birds.

Geographic variation of iris colour across South Australia (Figure 5) showed that the transition in iris colour from greenish blue to buff occurred between the gulf coast north of Adelaide and the Mt Lofty Ranges to the south-east, corresponding to the recognised distribution of *mellori* and *rosinae*. A few adult birds in the Adelaide Hills region showed light-green irides in photographs. In Western Australia (Figure 6), there was no discernible regional variation in iris colour from north to south, or between dry coastal or inland regions compared with wetter forested areas.

Discussion

The plumage and morphometric variation of the White-browed Scrubwren complex has been studied in detail (Mayr 1937; Ford 1970, 1985), but subspecific or geographic variation in eye colour has apparently passed almost unreported until recently. The present study confirms a distinct east–west difference in iris colour, which even under uncontrolled photographic conditions (which should be expected to have a much greater error than

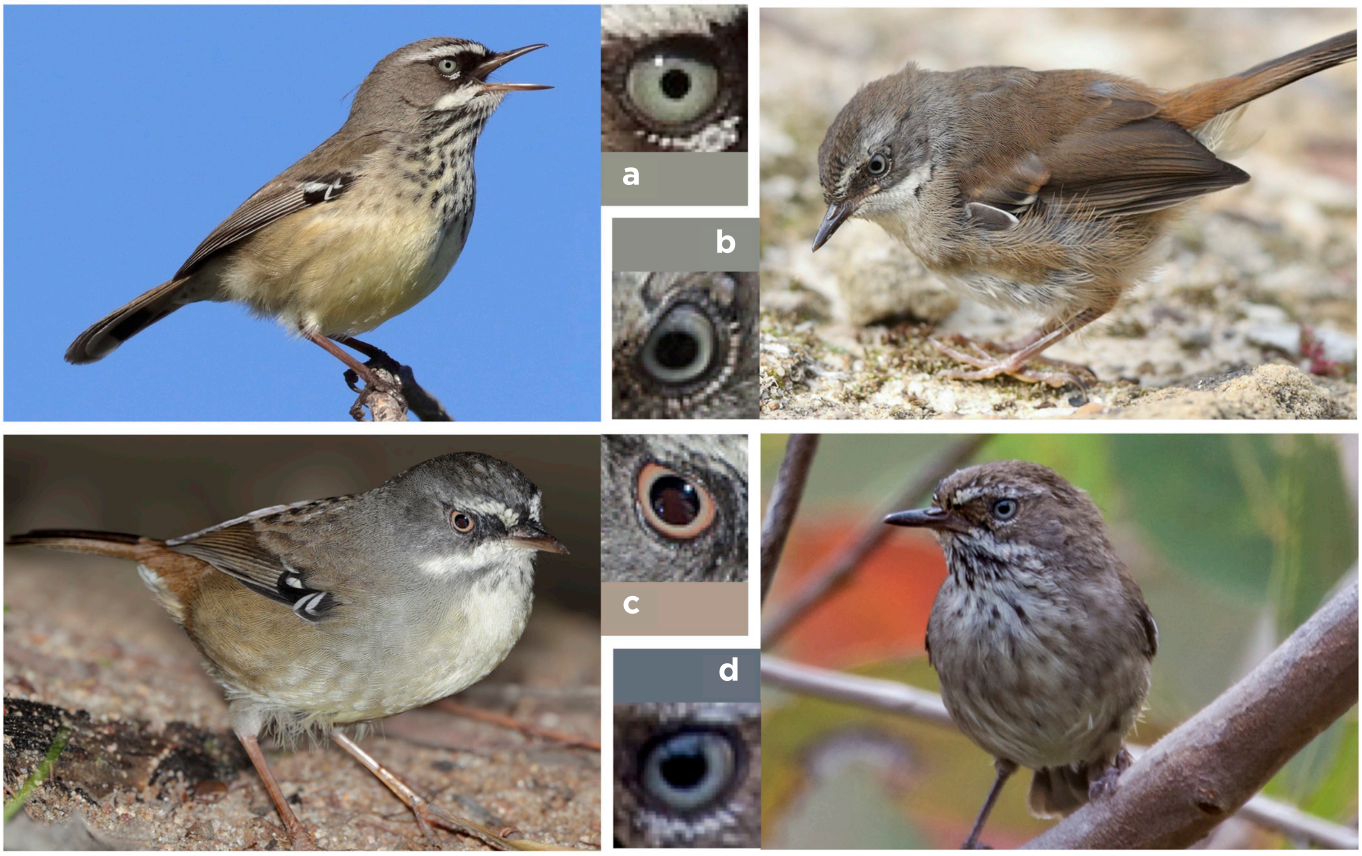

Figure 4. (a) Adult male *maculatus*, Mullaloo Beach, Perth, Western Australia. Photo: William Betts. Note pinkish-buff bill base, and indistinct greyish rim to grey-green iris. (b) Immature female *frontalis*, Australian National Botanic Gardens, Canberra, Australian Capital Territory. Photo: Con Boekel. Note several buff-tipped greater secondary coverts indicating immaturity. (c) Adult male *frontalis*, Selby Bushland Reserve, Victoria. Photo: Ian Wilson. Note distinct reddish rim to yellow-brown iris. (d) Adult female *ashbyi*, Flinders Chase, Kangaroo Island, South Australia. Photo: Julius Simonelli. Averaged central iris colour of each bird is indicated in coloured rectangles (see Method).

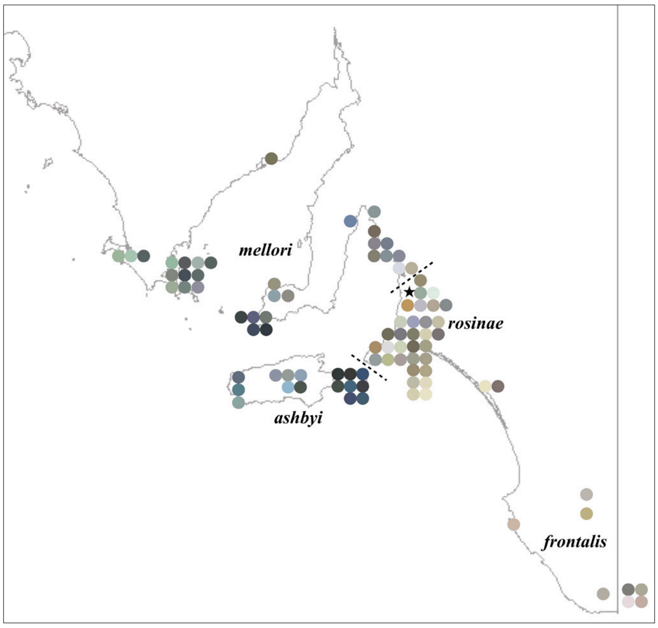

Figure 5. Adult iris colour in photographs of the White-browed Scrubwren complex in southern South Australia, including the *maculatus* group west of dashed lines (subsp. *mellori* of mainland north-west of Adelaide (★) and *ashbyi* of Kangaroo Island), and the *frontalis* group to the east (including subsp. *rosinae* of the Mt Lofty Ranges and Fleurieu Peninsula, and nominate *frontalis* further east). Note the sudden transition from more blue-green to more yellow-brown iris hues, corresponding to taxon boundaries.

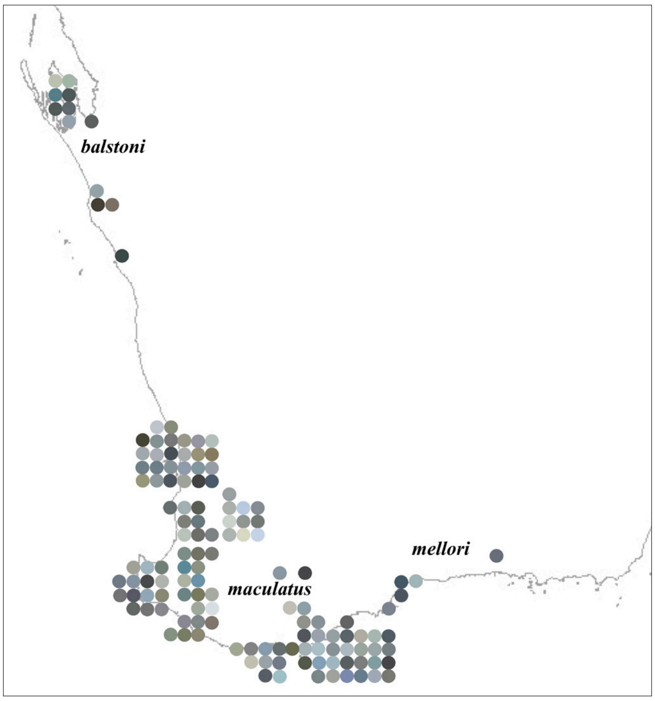

Figure 6. Adult iris colour in photographs of the White-browed Scrubwren complex in Western Australia. Note lack of regional variation between the drier northern/inland regions and the wetter, more forested south-western region of the state.

standardised photographic or direct measurement) comes close to achieving Level 3 diagnosability criteria (i.e. 75%/99% separation) as defined by Donegan (2018). Iris colour thus provides another consistent, if not necessarily diagnostic, morphologic difference separating those taxa comprising the 'Spotted Scrubwren' *S. maculatus* group from the remainder of the White-browed Scrubwren complex. Notably, based on iris colour this western *maculatus* group should include the potentially disputed Kangaroo Island form *ashbyi*, which aligns differently on mitochondrial DNA (Norman *et al.* 2018). Also of note, though based on a very small sample, the irides of *flindersi* are closer in colour to southern *frontalis* forms than to *S. humilis*, which is closer in eye colour to the more northern forms *tweedi* and *laevigaster*.

Though a few examples of regional variation in iris colour are known from Australia (e.g. Masked Booby *Sula dactylatra*, Brown Quail *Synoicus ypsilophora*, Pacific Gull *Larus pacificus*, Little/Western Wattlebird *Anthochaera chrysoptera/A. lunulata*), this is perhaps a feature of more prominent taxonomic significance elsewhere, separating for example subspecies of Eastern Towhee *Pipilo erythrophthalmus* (Dickinson 1952) and Boat-tailed Grackle *Quiscalus major* (Stevenson 1978), and otherwise largely cryptic species such as Campbell Albatross *Thalassarche impavida*, Chivi Vireo *Vireo chivi* (Johnson & Zink 1985), Streak-eared Bulbul *Pycnonotus conradi* (Garg *et al.* 2016) and Cream-eyed Bulbul *P. pseudosimplex* (Shakya *et al.* 2019), and Willard's Sooty Boubou *Laniarius willardi* (Voelker *et al.* 2010). In questioning how the distinct blue-grey eyes of the last species were overlooked until so recently, Voelker *et al.* (2010) suggested low light conditions of its forest habitat and lack of attention to museum labels as possible factors. Although the same question may be asked for the White-browed Scrubwren, details recorded on museum specimen tags are apparently less consistent than the findings of the present study, since they failed to resolve regional differences when specifically reviewed for this purpose (Higgins & Peter 2002). Perhaps the most likely reason for this discrepancy is that these records were never accurate, since human perception of colour is notoriously subjective even when standards are used (Bortolotti *et al.* 2003; McKay 2013), and is influenced by multiple variables including light conditions, contrast against adjacent colours, and individual (human) variation.

An alternative explanation may be post-mortem changes in iris colour. The mechanisms of iris coloration in birds are complex and poorly understood, including pigmentation from melanin, carotenoids, purines and pterins (Bortolotti *et al.* 2003; Hill & McGraw 2006). It is feasible that stromal pigment granules may be obscured or lysed after death. Reddish colours can also be generated by haemoglobin; for example, iris colour has been observed to change from red to yellow in handled Red-billed Oxpeckers *Buphagus erythrorhynchus*, presumably because of the effect of stress on irideal blow flow (Raijmakers & Ellmer 2009), and increased irideal redness has been reported in handled Noisy Friarbirds *Philemon corniculatus* (Longmore 1990). Vascular mechanisms may conceivably account for the reddish irideal rim of many *frontalis*-group birds, which was striking in some individuals in the present study.

Given that irides of western scrubwrens were similar to juveniles of both groups, the predominant difference appears to be the acquisition of yellow-orange pigmentation with maturity in eastern but not western birds. Maturation from dull-eyed juveniles is a typical feature of bright-eyed birds and has been hypothesised as a mechanism for signalling the reproductive maturity of potential mates (Bortolotti *et al.* 2003; Craig & Hulley 2004), and iris colour has been implicated in reproductive isolation of several cryptic species of bulbul (Garg *et al.* 2016; Shakya *et al.* 2019). The lifelong retention of the juvenile iris hue in the western group of White-browed Scrubwrens may conceivably represent a mechanism contributing to their reproductive isolation in parapatry. Although females typically have slower maturation of maximal iris colour in bright-eyed species (Bortolotti *et al.* 2003), the present study instead suggested slower transition in eastern-group males (alternatively, this result may be an artefact of greater difficulty in separating immature and adult females from single photographs).

Conclusions

The findings of this study remain subject to the overarching caveat that colour in digital photographs is prone to multiple technical artefacts, and may no more represent the 'true-life' colour than subjective sight or museum records. This is particularly so given uncontrolled photographic conditions, where camera settings (e.g. white balance) and image post-processing might have altered true colour. This study does, however, demonstrate the ease of collating a large sample of high-quality, location-tagged digital images from public sources (for common species at least), and their objective measurement to detect subtle colour differences that until recently have apparently eluded the naked eye.

Subject to this caveat, this study suggests that a statistically significant and consistent, possibly even diagnostic, difference in iris colour should be included among morphological criteria separating the western taxa split by some authorities as Spotted Scrubwren *S. maculatus* (including Kangaroo Island form *ashbyi*) from the remainder of the White-browed Scrubwren complex (Dickinson & Christidis 2014; Gill & Donsker 2019). This difference is probably driven by acquisition of yellow-orange pigmentation (and often a reddish irideal rim, suggesting possible vascular mechanisms) with maturity in eastern birds, versus retention of the juvenile iris hue in adult *maculatus*. Although some geographic (or subspecific) differences were present among eastern taxa, there was no evidence between or within western taxa to support ecophenotypic variation as suggested in Higgins & Peter (2002). Given that iris changes are thought to signal maturity in bright-eyed species, this difference may speculatively represent a potential isolating mechanism contributing to their divergence.

Acknowledgements

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