

First record of black feathering in a female Red-backed Fairy-wren *Malurus melanocephalus* under natural conditions

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Abstract. During the breeding season, male Red-backed Fairy-wrens *Malurus melanocephalus* can exhibit a spectrum of plumages from wholly black-and-red to entirely brown. By contrast, females generally appear completely brown, although observations of birds in the hand have revealed that some females also develop some red feathers. Here, we document, for the first time, observations of a female Red-backed Fairy-wren that has developed both black and red feathers under natural conditions. We explore possible explanations for this including whether changes to the individual's hormonal milieu could be responsible for the unusual plumage that we observed.

Introduction

Although birds are among the most ornately marked vertebrates, in many species it is often only the male that possesses elaborate feather structures and colourful plumage, and females are generally less conspicuous (Burns 1998; Badyaev & Hill 2003; Dale *et al.* 2015). These differences are often driven by sexual selection, whereby females preferentially mate with males with more prominent secondary sexual characteristics, which differentially affects ornamentation, and lack thereof, in females (Hill 1990; Norris 1990; Sætre *et al.* 1994; Dale *et al.* 2015). As colourful feathers can be costly to produce and maintain, the quality of the ornaments displayed correlates to the fitness of an individual (Andersson 1994; Hanssen *et al.* 2006; McQueen 2019), but empirical evidence suggests that this is not universally the case and fitness trade-offs can be involved (Bókony *et al.* 2008; Rowe *et al.* 2010).

In the Red-backed Fairy-wren *Malurus melanocephalus*, a species that is abundant throughout much of northern and eastern Australia, fully ornamented males typically bear a jet-black bill and an entirely red-and-black plumage during the breeding season, whereas females are wholly brown with a pink bill (Owens & Short 1995; Higgins *et al.* 2001; Newton 2009; see Figure 1). However, secondary sexual characters in the form of darkened bill coloration and red back feathers (Figure 2a), are observed in a small number of females, and it has been shown that females supplied exogenous testosterone produce some black pigmented feathers (Lindsay *et al.* 2016; see Figure 2b). Here, we report the first record of a female Red-backed Fairy-wren observed under natural conditions that has produced both black and red feathers, and suggest possible mechanisms that have led to the production of these atypically pigmented feathers.

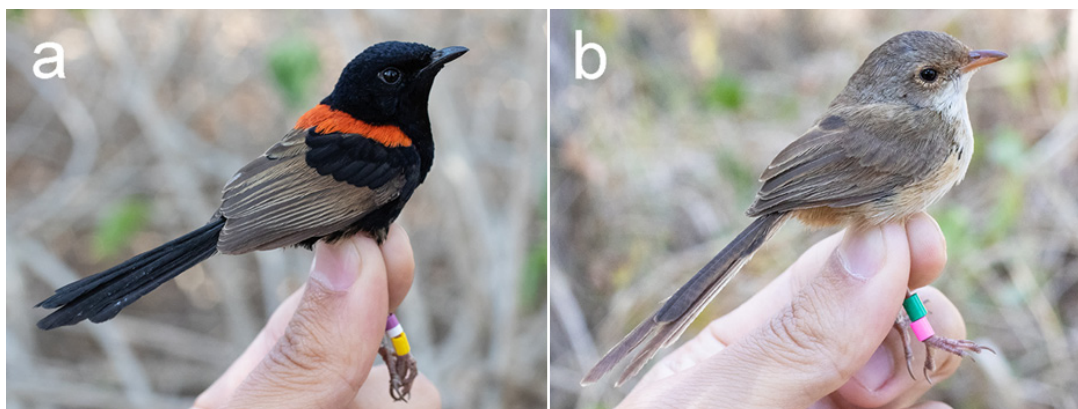


Figure 1. Examples of plumage of Red-backed Fairy-wrens in breeding condition at Lake Samsonvale, Queensland. (a) A fully ornamented male. Note the glossy black body plumage, rectrices and secondary coverts, red scapulars and mantle feathers but retained primary coverts and remiges, and a jet-black bill. (b) An unornamented female. Note the brown body plumage, cream to white underbelly and chin, and pink bill with a dark wash to the upper mandible and tip of lower mandible. Photos: James A. Kennerley

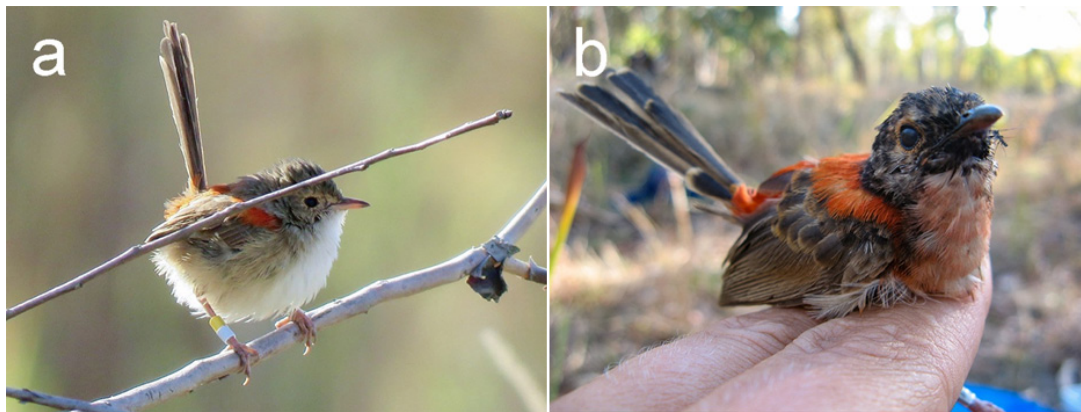


Figure 2. Examples of female Red-backed Fairy-wrens that exhibit secondary sexual characteristics in the form of ornamented plumage. (a) A female observed at Lake Samsonvale under natural conditions. Note the red feathering to the mantle, peachy lores, and a pink bill with a dark wash to the upper mandible and tip of lower mandible. Photo: Hazel H. Carr. (b) The testosterone-implanted female in Lindsay *et al.* (2016) that produced black feathering as well as red feathering. Note black feathering on the chin, tail, and margins of the head feather tract, and orange-pink feathers on the back, chest, and lores, as well as an almost entirely black bill. Photo: Willow R. Lindsay

Methods

Observations were conducted at a study site on the western shores of Lake Samsonvale (27°16'S, 152°51'E), Queensland, between August and December 2019. This location hosts a long-term study into the resident avifauna, with a focus on three fairy-wren *Malurus* species, of which most individuals (>90%) bear a unique combination of leg-bands, allowing them to be identified in the field without need for capture. The bands applied to the birds and discussed hereafter include the colours ivy green (I), dark blue (B), mauve (R), bi-coloured black-and-white (V), and bi-coloured mauve-and-white (Z). In addition, all birds receive a band issued by the Australian Bird and Bat Banding Scheme (S). To maintain long-term monitoring efforts, field technicians and researchers capture and colour-band all unbanded birds at the start of each breeding season, and band each nestling before fledging. Nests are located by following adult birds and the reproductive efforts of each breeding attempt are monitored across the season. Cloacal protuberance and brood-patch of adult birds are scored using the criteria detailed in DeSante *et al.* (2020). The intensive monitoring efforts at Samsonvale have enabled us to make novel observations into the natural habits and behavioural peculiarities of the local avifauna (Feeney *et al.* 2018; Kennerley *et al.* 2019; Poje *et al.* 2019; Richardson *et al.* 2019). The observations presented here were made during standard monitoring of Red-backed Fairy-wrens, for which a stable population of ~70 breeding groups has been monitored since 2010.

Results

The bird of interest (hereafter ISVV, based on colour-band combination) was originally banded at our field site on 10 October 2012 so was at least 7 years old in 2019. When captured in 2012, it was noted to be entirely brown and, as age could not be determined, it was recorded as being of unknown sex as the possibility of a juvenile bird could not be eliminated. However, around the time of capture, ISVV was

observed to be closely associating with a fully ornamented male, suggesting that ISVV was an adult (at least 1 year old) female. ISVV was captured for a second time on 26 November 2013 and a third time on 2 July 2015, when it was recorded as a female because of the entirely brown plumage and knowledge that the bird was at least 3 years old. On 28 June 2017, ISVV was caught and processed again, with no notes on the bird outside of morphometric measurements. ISVV was captured, processed, and photographed most recently on 1 November 2019 by NMR and HHC (Figure 3), and sexed as a female by sex-specific behaviour and physiological characters which are detailed below. On this occasion, ISVV was noted to have several red-orange feathers on the mantle, sparsely and unevenly distributed with more on the left side of the bird's body (Figure 3d). Most notable were several feathers on the crown that were up to 75% black at the centre (Figure 3a) with narrow brown fringes, as well as a few smaller feathers near the lores, eyes, and chin that were entirely black (Figure 3b). The bill was predominantly pale pink, the upper mandible was faintly washed greyish and the tip was slightly darker (Figure 3b). The bird exhibited a brood-patch with a score of '1', meaning that feathers were absent from the lower breast and abdomen and some vascularisation was present, and a cloacal protuberance that was scored as '1', indicating a small but somewhat enlarged and swollen cloaca.

Observations made during August through December 2019 by HHC indicated that ISVV was a typical female Red-backed Fairy-wren because of what, at a distance, appeared to be a wholly brown plumage and female-specific behaviour, including ISVV being paired with and copulating with its social mate, a fully ornamented male (denoted RSBZ, by colour combination), in the female position, as well as copulating with an unornamented and unbanded male, on 11 September. Throughout September and October, HHC also observed a neighbouring fully ornamented male (denoted XSBZ, where X denotes a missing colour band) conducting courtship petal displays, which appeared to be directed at ISVV. HHC later



Figure 3. The focal female Red-backed Fairy-wren with colour-band combination ISVV, on 1 November 2019 at Lake Samsonvale. (a) Note black feathering on the base of crown feathers with narrow brown fringes. (b) Note the entirely black feathers near the base of the bill, eyes, and chin, and peachy lores. The bill is predominantly pale pink, the upper mandible faintly washed greyish, and the tip slightly darker. (c) There is little to no red or orange feathering on the bird's right side. (d) Note the red-orange feathering on the scapulars and back on the bird's left side. Photos: Nicole M. Richardson

observed ISVV nest building on 23 and 27 September. The nest was completed by 30 September, but no eggs were laid. ISVV was not observed building another nest or caring for chicks thereafter and no previous nesting attempts have been recorded for ISVV since the bird was banded in 2012. It should also be noted that in the spring of 2019 it was unusually hot and dry, with a mean daily maximum temperature of 27.0°C and total rainfall of 73.4 mm recorded in Brisbane (Bureau of Meteorology 2019), which led to the least productive breeding season recorded at the study site for this 10-year project.

Discussion

No black feathering was observed in ISVV's plumage, either in the field or on any of the four occasions that ISVV was captured before 2019, when a very small cloacal protuberance (a typically male physiological character) was also noted. Over 8 years of observations, ISVV was observed paired with two different fully ornamented colour-banded males, exhibited female-specific traits (i.e. brood-patch), and was observed performing female-specific behaviours (i.e. nest building and copulating in female position), indicating that this individual was a female Red-backed Fairy-wren bearing some black and red feathers.

Under natural conditions, female Red-backed Fairy-wrens do not bear the ornamented black-and-red plumage typical of males in breeding condition (Figure 1a), although

it is not uncommon for females of some species of passerine to be ornamented like their male counterparts including the *moretoni* subspecies of the White-shouldered Fairy-wren *Malurus alboscapulatus*, which is a resident of New Guinea and a close congener to the Red-backed Fairy-wren (Rowley & Russell 2020). Sexually dimorphic plumage is often explained by constraints because of natural selection as it is only the females that build nests, incubate eggs, and brood young, thus muted coloration minimises the risk of nest depredation (Martin & Badyaev 1996; Higgins *et al.* 2001; Medina *et al.* 2017), although recent studies suggest that factors other than predation play a role in the evolution of female plumage colour (Dale *et al.* 2015; Medina *et al.* 2017; Cain *et al.* 2019). Unlike males, female Red-backed Fairy-wrens typically do not undergo seasonal shifts in plumage coloration, although they do grow shorter tail-feathers during the breeding season (Higgins *et al.* 2001). Interestingly, this species is unusual in displaying reverse sexual dimorphism in tail-length, such that during the breeding season, females possess longer tails than males (Swaddle *et al.* 2000).

Plumage colour in birds is typically produced in two ways: tissue structural coloration that typically appears as green and blue hues as well as iridescence, or with use of pigments. Commonly found pigments include porphyrins (which produce a range of hues, including reds, browns and greens), carotenoids (which produce red hues), and melanins (which produce black, grey, and brown hues, with eumelanin producing blacks and darker browns and

pheomelanin producing lighter reddish-brown colours) (Brush 1978; Durrer 1986). Carotenoid- and eumelanin-based plumage pigmentation acquisition in male Red-backed Fairy-wrens has been found to be positively correlated with levels of circulating androgens, including testosterone, with elevated levels of androgens during the pre-alternate moult (Lindsay *et al.* 2009, 2011). By experimentally implanting testosterone into female Red-backed Fairy-wrens, it has been shown that females have the capacity to produce both black and red pigmented feathers, thus demonstrating that females have a similar hormonally regulated mechanism to produce secondary sexual characteristics as their male counterparts (Lindsay *et al.* 2016). However, these black pigmented feathers were produced to a limited capacity; of four females implanted with testosterone, Lindsay *et al.* (2016) observed three to grow orange feathers on the back and one individual to grow black feathers on the chin, tail, and margins of the head feather tract in addition to orange-pink feathers on the back and chest (Lindsay *et al.* 2016; Figure 2b). In addition, we have observed females with red feathering on the back and shoulders under natural conditions at our field site (Figure 2a).

Past studies have suggested that female fairy-wrens are mechanistically constrained in their ability to produce black melanin-pigmented feathers. For example, Boersma *et al.* (2020) found that some female White-shouldered Fairy-wrens of the subspecies *lorentzi*, which naturally lacks ornamentation, do not produce black feathers when supplied endogenous testosterone whereas others do. Similarly, Peters (2007) found that when treated with endogenous testosterone, female Superb Fairy-wrens *Malurus cyaneus* begin a prenuptial moult but the resulting feathers lack the blue and black structural coloration typical of males. In each case, the results suggest that circulating testosterone is only partially responsible for the production of male-like plumage characters. Lindsay *et al.* (2016) suggested that such a constraint in females to produce melanic feathers may be because of the presence of the hormone estradiol, which has been found to inhibit production of male-typical feather coloration in other avian orders (Kimball 2006; Kimball & Ligon 1999), including the melanisation of feathers in Mallards *Anas platyrhynchos* (Haase *et al.* 1995). It may also be responsible for inhibiting melanin production in some female Passeriformes (Witschi 1961; Perlut 2008). Estradiol is also required for successful egg formation (Çiftçi 2017). It is, therefore, possible that ISVV experienced decreases in estradiol levels, which promoted development of secondary sexual characters and resulted in the failure to lay eggs.

In one notable example of a female bird expressing male-like secondary sex characters, Perlut (2008) documented a female Bobolink *Dolichonyx oryzivorus* bearing typical female plumage one breeding season, and male-like plumage the following year. In the first year, she produced a viable clutch of eggs and young fledged, and in the following year, in addition to male-like plumage, her eggs were infertile. With respect to ISVV, we observed a similar correlation whereby male-like plumage was associated with probable infertility (absence of documented young and no eggs laid despite nest building in 2019). Infertility was not confirmed, however, and further research is warranted.

Lindsay *et al.* (2016) noted that expression of secondary sexual characteristics by females, including the male-like

darkened bill coloration and red back feathers in Red-backed Fairy-wrens, is positively associated with age. Similar observations have been made in other species including the Red-winged Blackbird *Agelaius phoeniceus*, whereby older females develop brighter-red epaulettes, a character typically associated with male plumage (Blank & Nolan 1983). Considering that ISVV was at least 7 years old in 2019, a relatively old age for a Red-backed Fairy-wren (Feeney & Webster unpubl. data), our observations are in line with the findings of Lindsay *et al.* (2016) that it is usually older females that show more-prominent secondary sexual characters, such as red feathers. Given past research, we suggest that the erosion of sexual dimorphism that we observed with ISVV was most likely age-related and hormonally driven, involving increases in androgen levels and decreases in estradiol levels.

Conclusion

Our findings show that there is more natural variation in female plumage of the Red-backed Fairy-wren than previously documented and is especially relevant to older birds. The black plumage expressed by ISVV highlights the importance of careful observations of individually colour-marked birds, without which it is reasonable that such variation is missed. This is especially pertinent since it is unknown at what age hormonal mechanisms may begin to erode that could result in secondary sexual characters being expressed in female Red-backed Fairy-wrens or the onset of infertility, and whether such a condition could be inherited, or whether pathogenic infection could be responsible for the breakdown of hormonal mechanisms. Although past research has shown that females of some bird species can acquire more-prominent secondary sexual characteristics through changes in hormonal milieu, the female-specific mechanism underlying sexual dichromatism remains an area worthy of further research attention.

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