


New records of hybridisation in Australian Fairy-wrens *Malurus* spp.

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Abstract. Ornithologists have long been fascinated by avian hybrids and this interest has increased in recent years with advances in our understanding of the potential evolutionary consequences of hybridisation. To date there are only four published records of hybridisation between currently recognised species in the Australian fairy-wrens *Malurus* spp., including one involving limited gene flow between two closely related species. Here we present three new records of hybridisation among Australian fairy-wrens and provide further information on a previous report.

Introduction

Hybridisation is increasingly recognised as a common occurrence in animals, including in birds where at least 16% of species are known to hybridise (Ottenburghs *et al.* 2015). Although most hybridisation events likely have little effect on evolution, hybridisation has the potential to influence evolution if hybrid offspring backcross to either of the parent species. In diploid species, such as birds, hybrid offspring inherit genes from both parent species, thus a mating event between a hybrid and a parent species creates an opportunity for genes from one species to move into another (Mallet 2005). In rare instances, this introgression of genes can lead to a species acquiring beneficial traits, such as decorative plumage important in sexual selection (Brumfield *et al.* 2001; Baldassarre *et al.* 2014). In certain circumstances, hybridisation can lead to the evolution of new species (reviewed in Ottenburghs 2018), the loss of existing species (Rhymer & Simberloff 1996; Seehausen 2006; Seehausen *et al.* 2008), or to the mitochondrial DNA of one species taking over that of another (Kearns *et al.* 2014; Andersen *et al.* 2021; Joseph 2021). Thus, documenting even apparently anomalous hybridisation has become an important component of understanding the evolution of birds (Ottenburghs *et al.* 2015).

Although hybridisation has been documented between many bird species, observations of hybrids in nature are not common for multiple reasons. First, hybridisation is rare relative to most species' population sizes, meaning

obvious first-generation (F1) hybrids are rarely observed in nature (Justen *et al.* 2020; Justyn *et al.* 2020; Ottenburghs & Slager 2020). Second, detection of individuals descended through successive generations after an initial hybridisation event is often impossible: for example, hybrids of several Australian birds were phenotypically indistinguishable from one of the parent species and were detected only through genetic analyses (Joseph & Moritz 1993; Toon *et al.* 2012; Shipham *et al.* 2015, 2019). This loss of phenotypic traits may occur in only a few generations of backcrossing to a parent species (Joseph & Moritz 1993), meaning that observations of F1 hybrids offer important yet fleeting insights into how evolution may be influenced by hybridisation.

Many environmental and behavioural processes are thought to increase the likelihood of hybridisation among related species. Environmental processes can lead to hybridisation when changing environments, such as altered fire regimes (Toon *et al.* 2012), result in change and blurring of previously sharp habitat boundaries, allowing species that were separated by geographical and habitat barriers to make secondary contact (Joseph *et al.* 2019; Shipham *et al.* 2019). Behavioural processes encourage hybridisation when pre-zygotic (pre-mating) species-recognition mechanisms break down (Joseph & Moritz 1993), or when individuals disperse outside of their species' typical habitat (Hubbs 1955). The latter exemplifies 'Hubbs' principle' or the 'desperation hypothesis' in which individuals outside their species' normal range have

Table 1. List of eBird checklists that contain additional photographs of each new hybrid fairy-wren record presented in this paper.

Hybrid	Location	Date	Checklists
Red-backed × Superb Fairy-wren	Brisbane, Queensland	19 Dec. 2006	https://ebird.org/checklist/S93501762/
		20 Dec. 2006	https://ebird.org/checklist/S93509508/
		5 Jan. 2007	https://ebird.org/checklist/S93510802/
		15 Jun. 2007	https://ebird.org/checklist/S93512684
		4 Jul. 2007	https://ebird.org/checklist/S93513054
	Gladstone, Queensland	16 Feb. 2020	https://ebird.org/checklist/S64542440
		22 Feb. 2020	https://ebird.org/checklist/S64837308
		18 Jan. 2021	https://ebird.org/australia/checklist/S79516817
		18 Jan. 2021	https://ebird.org/australia/checklist/S79520763
		21 Jan. 2021	https://ebird.org/australia/checklist/S79627863
White-winged × Superb Fairy-wren	Oakey, Queensland	3 Oct. 2020	https://ebird.org/australia/checklist/S82597438
		23 Oct. 2020	https://ebird.org/australia/checklist/S82600402
		23 Oct. 2020	https://ebird.org/australia/checklist/S82600655
		14 Nov. 2020	https://ebird.org/australia/checklist/S82599512
		27 Dec. 2020	https://ebird.org/australia/checklist/S82597963
	Thunder Swamp, Victoria	11 Feb. 2021	https://ebird.org/australia/checklist/S82598726
		16 Nov. 2014	https://ebird.org/checklist/S20587915
		27 Nov. 2014	https://ebird.org/checklist/S20699530

difficulty finding a suitable mate (Randler 2002). Such hybridisation events in birds (McCracken & Wilson 2011) are thought to be especially likely at the limits of species' ranges (Short 1969; Ford 1987).

The fairy-wrens are one such clade where hybridisation across species occurs but is rarely observed. At present, the genus *Malurus* includes 12 species and 26 named subspecies that occupy nearly every type of habitat in the Australo-Papuan region (Winkler *et al.* 2020). Putting aside some subspecies' hybrid zones, including the Splendid Fairy-wren *M. splendens* (Kearns *et al.* 2009) and Purple-backed Fairy-wren *M. assimilis* (Ford & Johnstone 1991), we note that only two currently recognised *Malurus* species are in contact through anything like a hybrid zone, albeit with limited gene flow. Purple-backed Fairy-wrens and Variegated Fairy-wrens *M. lamberti* appear to have diverged relatively recently between 62,000 and 312,000 years ago (McLean *et al.* 2017a) and show introgression of mitochondrial genes where their ranges meet (McLean *et al.* 2017b). Otherwise, only three records of hybridisation between currently recognised species have previously been reported for *Malurus* fairy-wrens. In 1980, Malcom Wilson and colleagues described a probable hybrid between a Red-backed Fairy-wren *M. melanocephalus* and a Superb Fairy-wren *M. cyaneus* near Bowenville, Queensland (Wilson 1983), in 2008 PS photographed a probable hybrid of the same two species in Brisbane, Queensland (Low 2014), and in 2014, Peter Haines described up to three probable hybrids between White-winged Fairy-wrens *M. leucopterus* and Superb Fairy-wrens at Hart Lagoon near Waikerie, South Australia (Haines 2014).

Here we present three further records of probable hybridisation among fairy-wren species, including one

between Red-backed Fairy-wrens and Superb Fairy-wrens and two between White-winged Fairy-wrens and Superb Fairy-wrens. We also provide further background on the probable Red-backed × Superb Fairy-wren hybrid from Brisbane listed above (Low 2014). We describe the atypical plumages of the putative hybrids and their distinction from potential parental species and suggest why hybridisation is the most likely explanation for these observations. We present these records in chronological order of their discovery.

Observations

Probable hybrid fairy-wrens in Brisbane, Queensland. December 2005–June 2009

In late 2005, GN identified a brown-plumaged, locally uncommon, Red-backed Fairy-wren visiting a nest at Moorhen Flats Recreation Area in Brisbane, Queensland (27°29'30"S, 153°02'49"E) (Table 1). A single offspring fledged from this nest in December and only the single brown-plumaged bird was seen at or near the nest or attending the fledgling. A year later, on 19 December 2006, GN observed a male fairy-wren with atypical plumage accompanied by a brown-plumaged Red-backed Fairy-wren near where the nest was found in 2005. Both individuals were carrying small food items to a nest in long grass. The atypical male exhibited a black bill, blue forecrown and small blue cheek-patches on the black head, red-orange scapulars, black mantle and lower back, blue-black tail, black throat, white belly, and a light-brown vent (Figure 1a, Table 2: Videos 1 and 2). On 20 December 2006, nestling begging calls were heard coming from the



Figure 1. Photographs of the probable Red-backed \times Superb Fairy-wren hybrids from Brisbane, Queensland. (a) The probable hybrid male on 19 December 2006. (b) A fledgling fairy-wren in the hybrid male's group on 5 January 2007. (c) A fairy-wren in atypical non-breeding plumage (reddish bill and blue-grey tail) on 15 June 2007. (d) The more-ornamented male in breeding plumage on 17 October 2007. (e) The less-ornamented male in breeding plumage on 17 October 2007. (f) A probable hybrid male on 8 August 2008. (a)–(c) video frames: Greg Nye; (d)–(f) photos: Petr Sramek

Table 2. List of videos of the probable Red-backed × Superb Fairy-wren hybrids from Brisbane, Queensland. All videos were recorded by Greg Nye.

Video	Date	Link
1	19 Dec. 2006	https://macaulaylibrary.org/asset/362660451
2	20 Dec. 2006	https://macaulaylibrary.org/asset/362689021
3	5 Jan. 2007	https://macaulaylibrary.org/asset/362700721
4	5 Jan. 2007	https://macaulaylibrary.org/asset/362700541
5	5 Jan. 2007	https://macaulaylibrary.org/asset/362697541
6	5 Jan. 2007	https://macaulaylibrary.org/asset/362698371
7	5 Jan. 2007	https://macaulaylibrary.org/asset/362699341
8	15 Jun. 2007	https://macaulaylibrary.org/asset/362710771
9	4 Jul. 2007	https://macaulaylibrary.org/asset/362716721

nest, and on 5 January 2007, GN sighted two fledglings out of the nest (Figure 1b, Table 2: Video 3), one of which was allopreening with the brown Red-backed Fairy-wren (Table 2: Video 4). On 5 January 2007, the atypical male exhibited some brown feathers on its head (Table 2: Videos 5–7). On 15 June 2007, an individual was observed that resembled a brown Red-backed Fairy-wren except that it had light-brown lores and a blue-grey tail (Figure 1c, Table 2: Video 8). A bird with similar plumage was observed allopreening with a brown Red-backed Fairy-wren on 4 July 2007 (Table 2: Video 9).

Over the following 3 years, PS and BM observed several male fairy-wrens with atypical plumage at Moorhen Flats Recreation Area: two individuals on 17 October 2007, and a minimum of three on 7 August 2008 and 12 June 2009. At least two were photographed in 2007. One was more ornamented than the other and resembled the description of the male seen by GN the previous year, as given above (Figure 1d). The less-ornamented male exhibited some brown on its head, body, and tail, and had fewer red-orange scapulars (Figure 1e). A male in atypical plumage was also photographed in 2008 and exhibited more extensive breeding plumage than seen in the previous year, with blue extending onto its belly (Figure 1f; previously published in Low 2014). Red-backed, Superb, and Variegated Fairy-wrens occur in and around Brisbane, but the plumages of these males were distinct from each of these species.

Moorhen Flats was established in 1994 as a 4-ha bushcare site. Superb Fairy-wrens have always been common, whereas Red-backed Fairy-wrens have been uncommon there. From at least early 2005 until July 2007, only a single brown-plumaged Red-backed Fairy-wren was seen by GN, and none were recognised between then and when the atypical males were last seen in June 2009 by PS and BM. There are subsequent eBird records of Red-backed Fairy-wrens between 2012 and 2020, but always fewer than Superb Fairy-wrens [eBird (2021) Basic Dataset, eBird hotspot <https://ebird.org/hotspot/L2560514>]. Moorhen Flats is still visited by GN and other observers but no probable hybrid fairy-wrens have been observed there after 2009.

Probable hybrid fairy-wrens at Thunder Swamp, Victoria. November 2014

In November 2014, GL observed two male fairy-wrens with atypical plumage at Thunder Swamp, north of Bendigo, Victoria (36°26'07"S, 144°16'36"E) (Table 1). Each exhibited a blue crown and blue cheeks separated by a black eye-stripe, blue, black, and grey scapulars, a blue mantle, blue-and-black lower back, blue tail, blue throat, and a mostly blue belly and vent (Figure 2). White-winged, Purple-backed, and Superb Fairy-wrens all occur in this region, but the plumages of these atypical males were distinct from each of these species. Thunder Swamp is still regularly visited by GL and others, but no probable hybrid fairy-wrens have been observed there since.

Probable hybrid fairy-wrens in Gladstone, Queensland. February 2020-ongoing

Between February 2020 and June 2021, several observers, including MR, TW, AN and DW, intermittently observed two atypical male fairy-wrens near Police Creek in Gladstone, Queensland (23°51'55"S, 151°14'13"E) (Table 1). The first (Figure 3) was seen in February 2020, and from May 2020 to March 2021, this male exhibited a black bill, a blue forecrown and small blue cheek-patches on the blue-and-black head, red-orange scapulars, a blue-black mantle and lower back, blue-black tail with some white-tipped feathers, blue-black throat, a blue-and-grey belly, and grey vent (Figure 3a, 3b). In April 2021, this individual mostly exhibited non-breeding plumage with only a few blue crown and cheek feathers, brown scapulars, mantle, and lower back, a fawn-white throat, belly and vent, and blue-brown tail (Figure 3c). On 14 May 2021, it was moulting (Figure 3d) and by 28 May 2021 it was in full breeding plumage, showing even more blue plumage on the belly and more white tips on its tail-feathers than previously (Figure 3e, 3f). The second, less-ornamented male, first observed in September 2020, had a smaller blue forecrown, smaller blue cheek-patches, fewer red-orange mantle feathers, and a black-and-brown throat and tail (Figure 4a, 4b). This male was in breeding plumage in February 2021 but was moulting in March 2021 (Figure 4c). In April 2021, it was in a partial non-breeding plumage

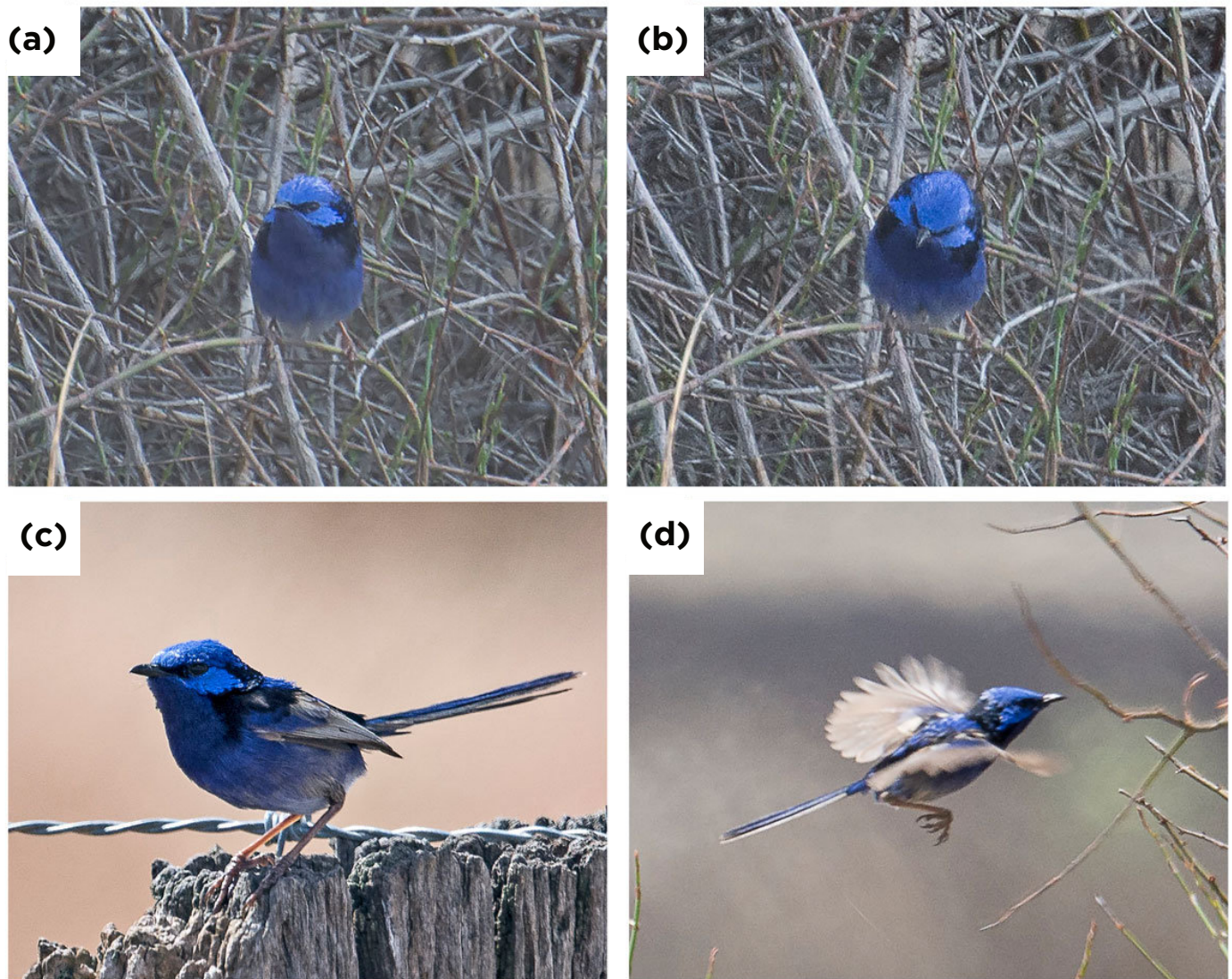


Figure 2. Photographs of the probable White-winged \times Superb Fairy-wren hybrids from Thunder Swamp, Victoria. (a)–(c) Breeding plumage on 16 November 2014. (d) Breeding plumage on 27 November 2014. Photos: Greg Licence

similar to the other bird, but with a black-and-pink bill, and a black-and-brown tail (Figure 4d). In June 2021, this male was beginning to moult back into breeding plumage (Figure 4e). Red-backed and Variegated Fairy-wrens occur in the Gladstone region, whereas Superb Fairy-wrens, whose plumages these atypical males partly resembled, are rare (see below). Behavioural observations indicate that both the atypical males paired with female Red-backed Fairy-wrens (Ross & Briggs 2022).

Previous observations of Superb Fairy-wrens in Gladstone provide background to these hybrid males. On 7 May 2012, HB and AN identified a female Superb Fairy-wren allopreening with a male Red-backed Fairy-wren in breeding plumage (Figure 5a; eBird checklist S16713687) within 100 m of where the atypical males were discovered 8 years later. On 1 June 2013, HB and AN observed a female Superb Fairy-wren with a male Red-backed Fairy-wren in the same location, accompanied by a third individual that had the overall appearance of a female Superb Fairy-wren but with less distinct lores and eye-ring (Figure 5b; eBird checklist S16621661). To date, these are the only sightings of presumed Superb Fairy-wrens in the Gladstone area reported in eBird or Birddata, the nearest sighting in Birddata coming from Tannum Sands, ~16 km

to the south, and the nearest sighting in eBird coming from Dumgree, ~80 km to the south-east (eBird checklist S75508635).

Probable hybrid fairy-wren in Oakey, Queensland. October 2020-ongoing

From October 2020 through June 2021, GR and KR observed an atypical male fairy-wren near Oakey, Queensland (27°25'21"S, 151°43'30"E) (Table 1). In early October 2020, this male exhibited a blue crown and blue cheeks separated by a black eye-stripe, white scapulars, a blue mantle, blue-and-black lower back, blue tail, blue-and-black throat, blue-and-white belly, and a white vent (Figure 6a). By late October, he had begun to moult into non-breeding plumage as grey feathers began to appear amongst his breeding plumage (Figure 6b, 6c). By mid November 2020, the blue face feathers had mostly been replaced with grey, but the back of his head remained ornamented, and his white scapulars and blue-and-black throat were still visible (Figure 6d). In February 2021, a black patch on the back of his head and limited black and blue on his belly were all that remained of his breeding plumage (Figure 6e). His tail remained blue in non-



Figure 3. Photographs of the more-ornamented probable Red-backed × Superb Fairy-wren hybrid from Gladstone, Queensland. (a) Breeding plumage on 5 October 2020. (b) Breeding plumage on 19 February 2021. (c) Non-breeding plumage on 16 April 2021. (d) Molt into breeding plumage on 14 May 2021. (e)–(f) Breeding plumage on 1 June 2021. Photos: (a), (c) Martin Ross; (b), (d) Deb Walker; (e)–(f) Tracey Welburn

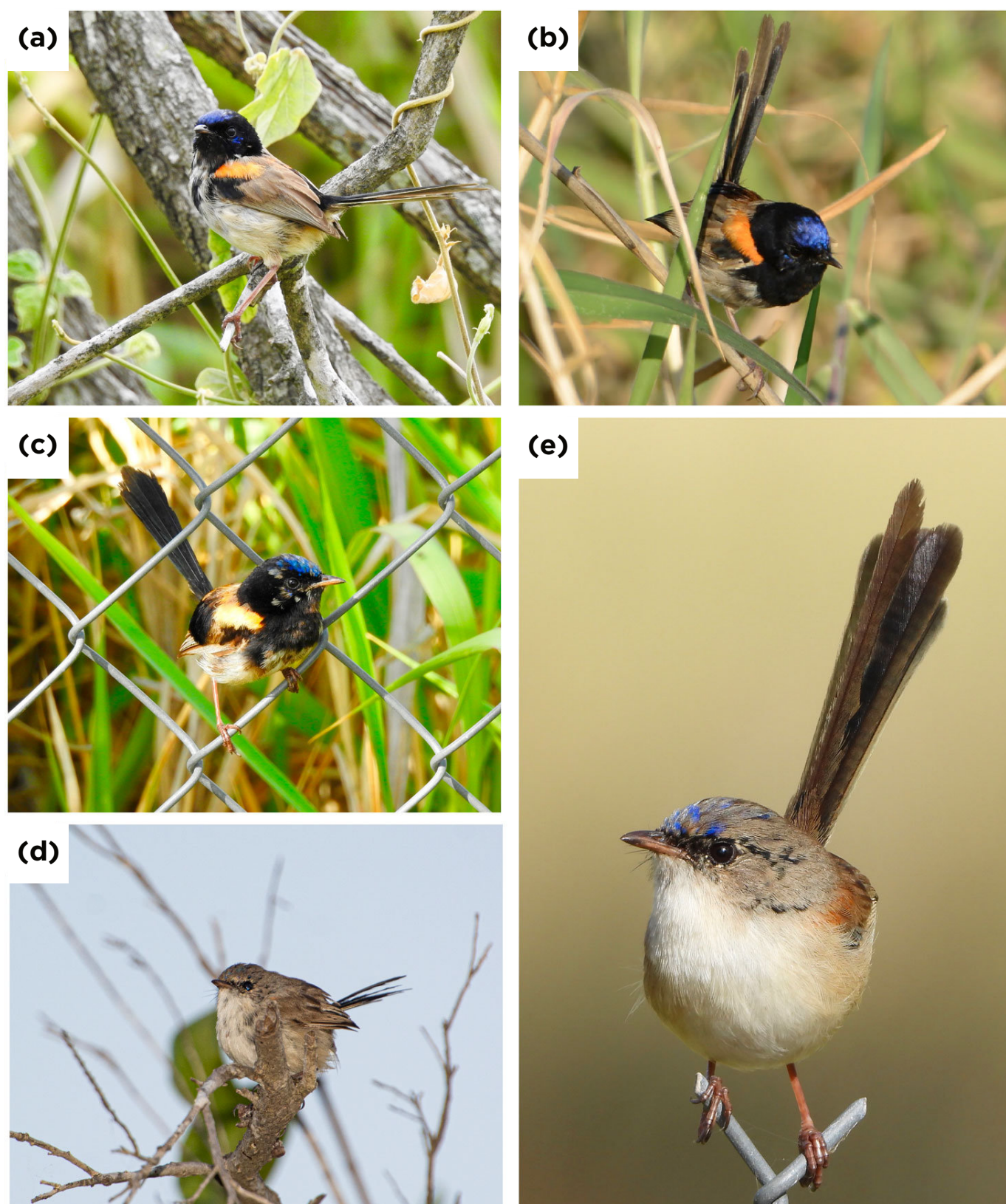


Figure 4. Photographs of the less-ornamented probable Red-backed × Superb Fairy-wren hybrid from Gladstone, Queensland. (a) Molt into breeding plumage on 23 September 2020. (b) Breeding plumage on 2 October 2020. (c) Start of molt into non-breeding plumage on 24 February 2021. (d) Non-breeding plumage on 16 April 2021. (e) Molt into breeding plumage on 23 June 2021. Photos: (a), (c), (e) Tracey Welburn; (b), (d) Martin Ross

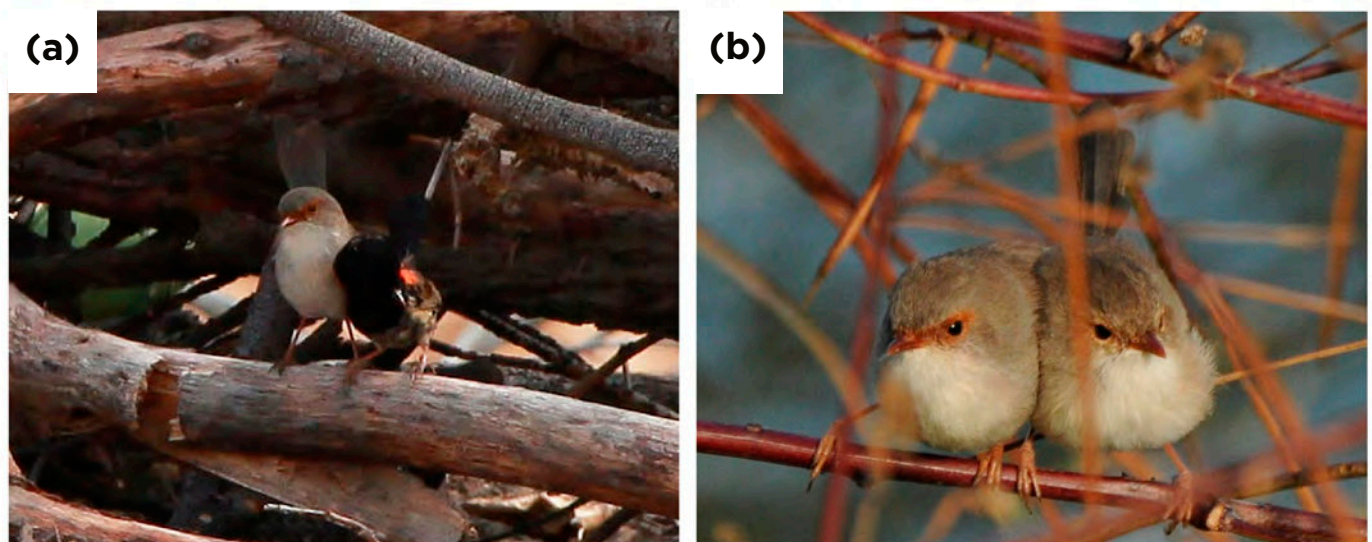


Figure 5. Photographs of fairy-wrens from Police Creek in Gladstone, Queensland. (a) The first female Superb Fairy-wren (left) with a male Red-backed Fairy-wren in breeding plumage (right) on 7 May 2012. (b) Female Superb Fairy-wren (left) and a second female or juvenile Superb Fairy-wren, or hybrid Red-backed \times Superb Fairy-wren (right) on 1 June 2013. Photos: (a) Alicia Newport; (b) Hannah Busch

breeding plumage. By June 2021, the male appeared to have moulted into nearly the same plumage as in October 2020 except that the scapulars were grey-brown instead of white (Figure 6f). White-winged, Superb, Red-backed, Purple-backed, and Variegated Fairy-wrens all occur in the Oakey region, but the plumage of this atypical male was distinct from each of these species. From October 2020 through May 2021, this male was seen moving and foraging with both White-winged and Red-backed Fairy-wrens, including a male Red-backed Fairy-wren in breeding plumage for part of that time.

Discussion

Red-backed \times Superb Fairy-wren hybrids

We propose that the atypical male fairy-wrens from Brisbane and Gladstone, Queensland, are the result of hybridisation between Red-backed and Superb Fairy-wrens. Each showed clear plumage characteristics of a male Red-backed Fairy-wren in breeding plumage, specifically the red-orange scapulars and mostly black head (Figure 7a). None of the other species in these areas exhibit these traits. Breeding male Variegated Fairy-wrens have blue plumage on the head that is continuous between the crown and the cheek feathers. The presumed hybrid males had a blue crown and cheeks separated by a black eye-stripe, consistent with Superb Fairy-wren plumage (Figure 7b). The throat of the bird in Figure 2 resembles the throat of a male Superb Fairy-wren in breeding plumage (Figure 7b), being blue or black (or a mix of blue and black depending on the light angle), whereas male Variegated Fairy-wrens exhibit a black throat with purple patches at each edge. Notably, the plumages of these atypical males closely match the description provided by Malcom Wilson and colleagues in the first report of hybridisation between these species: “It can be most easily visualised if one imagines a bird with the head of a Superb Fairy-wren and the body of a Red-backed Fairy-wren, except that the apparent hybrid had two shoulder patches of orange-gold” (Wilson 1983, p. 38).

Although these atypical males are all likely hybrids, in both Brisbane and Gladstone, one was more ornamented than the other. This variation may be due simply to genetic variation among offspring, or the more-ornamented individuals might have been older, as younger male fairy-wrens sometimes exhibit intermediate breeding plumages (Webster *et al.* 2008; Peters *et al.* 2013). Another explanation is that the less-ornamented males were backcrosses between a hybrid and an individual of one of the parent species, as different ratios of parental genes may lead to plumage variation. Further observations of these hybrids will be insightful to determine whether this is a true plumage difference or merely variation because of age.

Origins of the Red-backed \times Superb Fairy-wren hybrids

We may be able to trace the two Red-backed \times Superb Fairy-wren hybrid lineages back to their initial breeding events. In Brisbane in 2005, GN observed a brown-plumaged Red-backed Fairy-wren attending a nest at a site where Red-backed Fairy-wrens are rare but Superb Fairy-wrens are common. Although both females and young male Red-backed Fairy-wrens occur in brown plumage (Welklin *et al.* 2021), this first brown-plumaged individual was likely a female based on evidence from the following year. Red-backed Fairy-wrens near Brisbane are very site-faithful across years, often nesting very close (<20 m) to where they did in the previous year (JFW pers. obs.). Therefore, the brown-plumaged individual observed in 2005 was likely the female that paired with the hybrid male and nested in nearly the same location in 2006. The hybrid male might have been the fledgling fairy-wren from the 2005 nest, as a male Red-backed Fairy-wren will sometimes pair with his mother if dispersal opportunities are limited by a lack of available females or if no other male is around to pair with the female (Karubian *et al.* 2011). If this was a mother–son pairing, it is unlikely that the hybrid male sired any offspring with this female. When mother–son pairings occur in Red-backed Fairy-wrens, females nearly always seek extra-

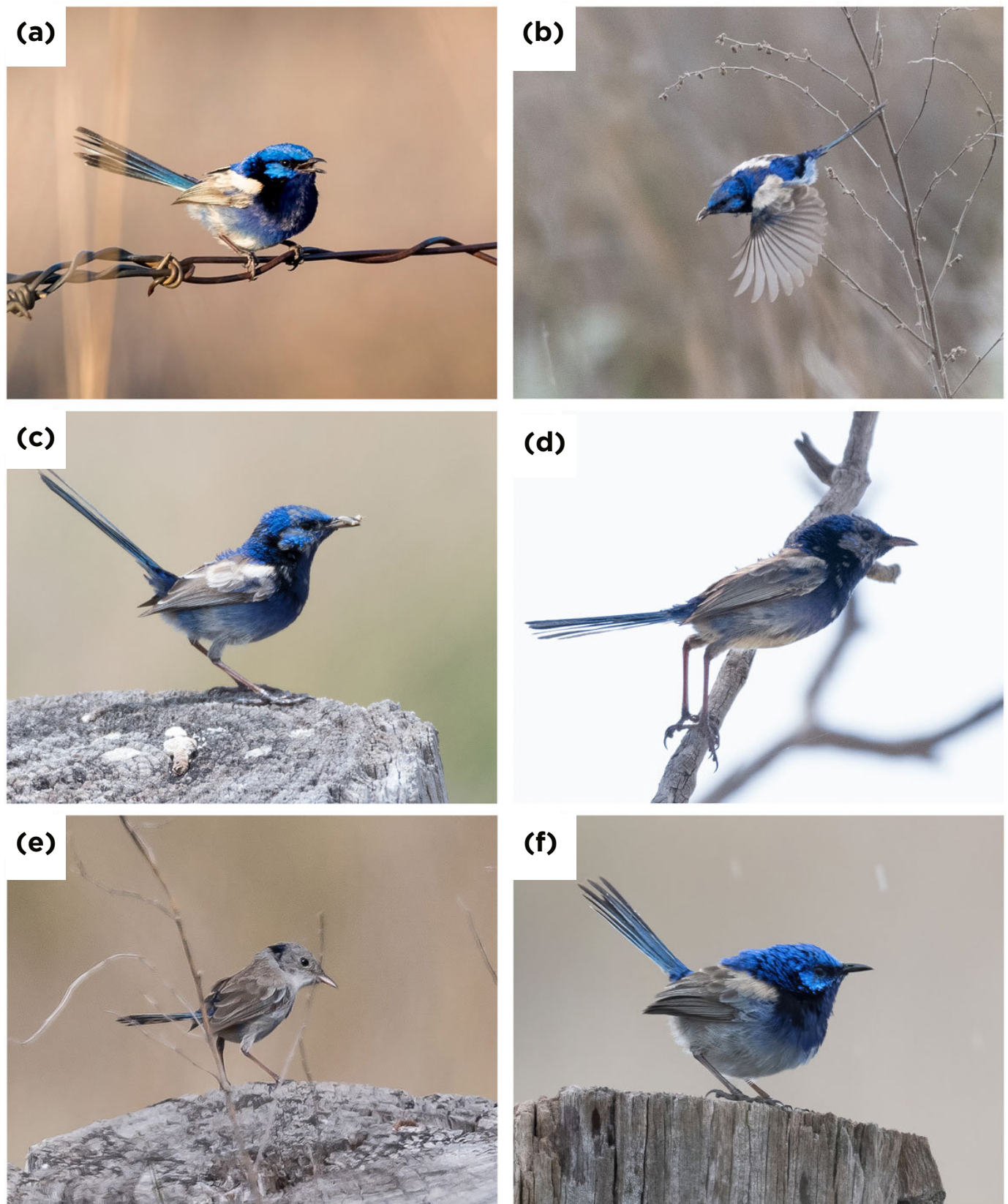


Figure 6. Photographs of the probable White-winged \times Superb Fairy-wren hybrid from Oakey, Queensland. (a) Breeding plumage on 3 October 2020. (b)–(c) Beginning of moult into non-breeding plumage on 23 October 2020. (d) Moult into non-breeding plumage on 14 November 2020. (e) Non-breeding plumage on 11 February 2021. (f) Breeding plumage on 14 June 2021. Photos: Glenn Roman

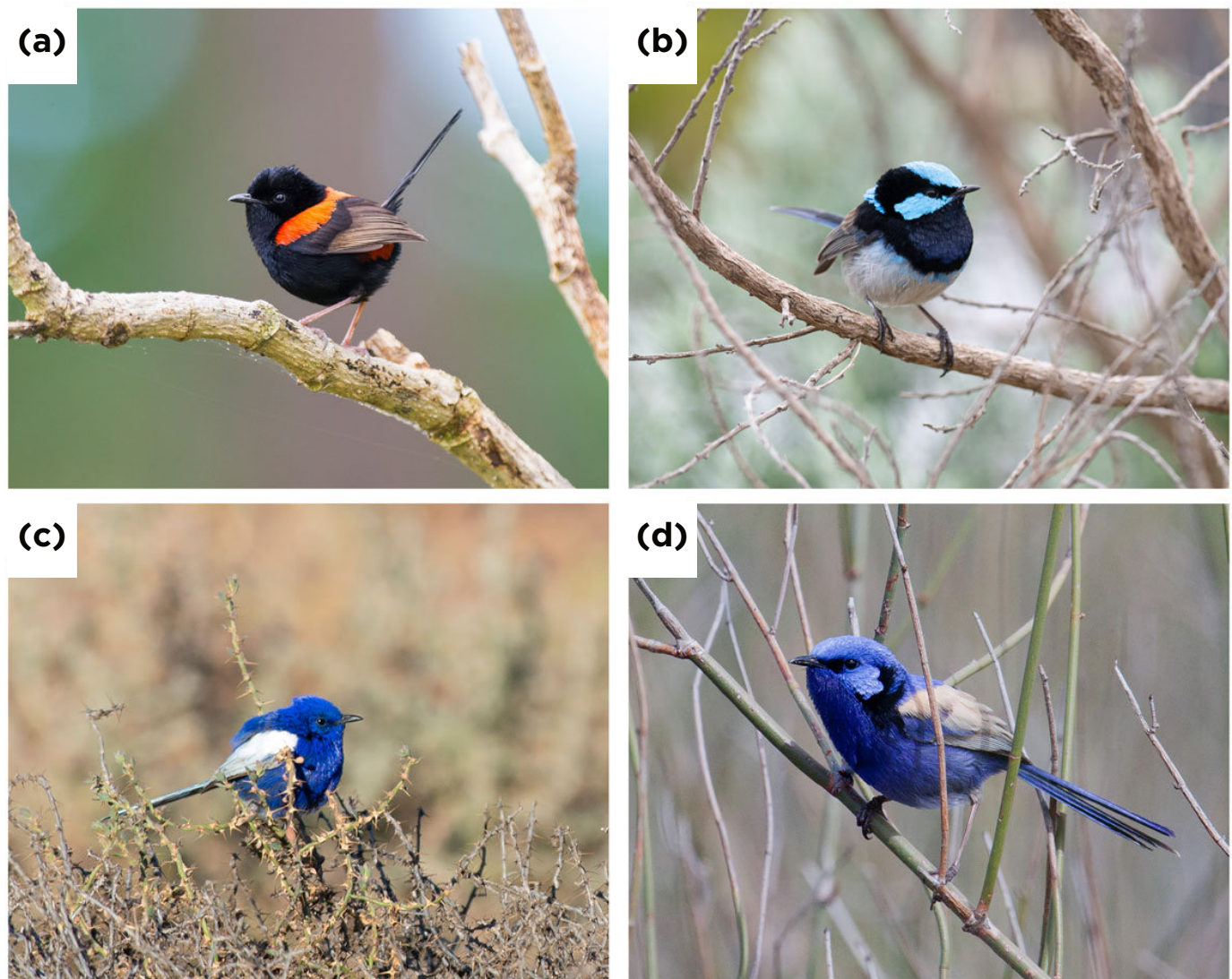


Figure 7. Probable parent species of the reported hybrid fairy-wrens and a previously reported hybrid for comparison. (a) Male Red-backed Fairy-wren in breeding plumage, Samsonvale, Queensland. (b) Male Superb Fairy-wren in breeding plumage, Port Campbell, Victoria. (c) Male White-winged Fairy-wren in breeding plumage, Cunnamulla, Queensland. (d) Probable White-winged \times Superb Fairy-wren hybrid, Hart Lagoon, South Australia, September 2013, previously reported in Haines (2014). Photos: (a)–(c) Joseph F. Welklin; (d) Peter Haines

pair copulations with neighbouring males instead of mating with their sons (Varian-Ramos & Webster 2012).

In Gladstone in 2012, HB and AN observed a single presumed female Superb Fairy-wren interacting with a male Red-backed Fairy-wren in an area where Red-backed Fairy-wrens are common but Superb Fairy-wrens are exceedingly rare. This female might have been a progenitor of either hybrid identified in this population, in view of the scarcity of sightings of Superb Fairy-wrens in the area and the limited distances between where this female was observed and the much later observations of the probable hybrids. The second brown-plumaged fairy-wren in 2013 might have been the first hybrid offspring or a juvenile Superb Fairy-wren that dispersed into the population. This individual's indistinct lores and eye-ring could point towards either possibility. Juvenile Superb Fairy-wrens have duller lores than in adult females (Schodde 1982), but brown-plumaged hybrids may be expected to show plumage characteristics that are intermediate between Superb and Red-backed Fairy-wren plumages. Female and male Red-backed Fairy-wrens in brown plumage lack the distinct red-brown lores and eye-ring of Superb Fairy-wrens.

White-winged \times Superb Fairy-wren hybrids

We propose that the atypical male fairy-wrens at Thunder Swamp, Victoria, and Oakey, Queensland, are the result of hybridisation between White-winged and Superb Fairy-wrens. These individuals exhibited plumage characteristics of both Superb and White-winged Fairy-wrens. The white scapulars of the male observed near Oakey, although not as extensive, clearly resemble those of a male White-winged Fairy-wren in breeding plumage (Figure 7c), and the crown and cheek-patches of individuals from both locations resemble those of a male Superb Fairy-wren in breeding plumage (Figure 7b). The individuals at Thunder Swamp had less white in their scapulars, but the probable hybrid at Oakey also had more grey-brown scapulars in his 2021 breeding plumage, suggesting that this trait could change with age. The individuals at Thunder Swamp more closely resemble male Superb Fairy-wren breeding plumage, but the very blue throat and extensive blue on the belly are unlike typical male Superb Fairy-wren breeding plumage. The lack of any purple in the mantle feathers and chestnut in the scapulars suggest that it is unlikely that one of the

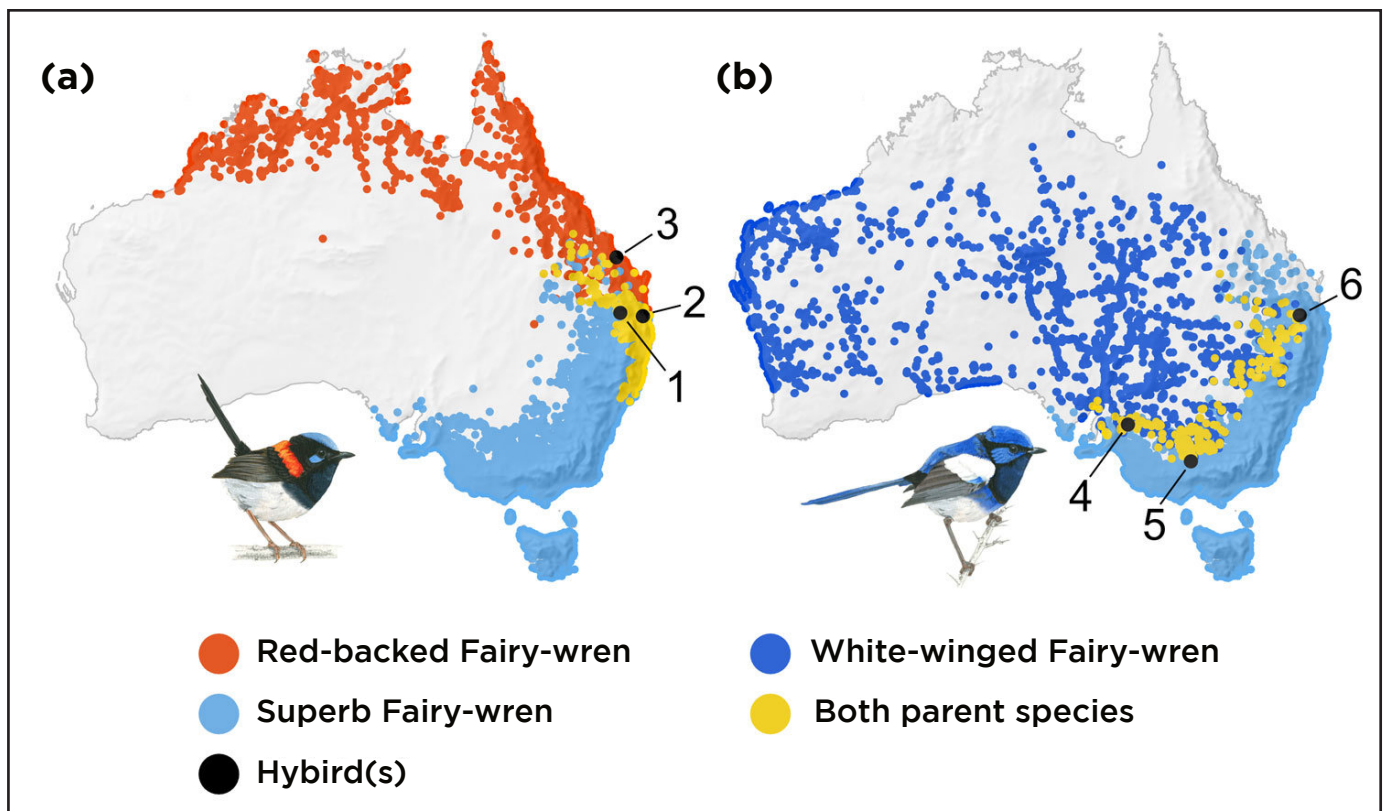


Figure 8. Locations of hybrid fairy-wrens in relation to where each parent species has been seen. Each point shows the location of an eBird checklist reporting one or both parent species from January 2000 through January 2021. (a) Red-backed and Superb Fairy-wren sighting locations and a drawing of a potential Red-backed \times Superb Fairy-wren hybrid. Point 1—location of the probable hybrid reported by Malcom Wilson in 1980 near Bowenville, Queensland. Point 2—location of the probable hybrids reported here from Brisbane, Queensland. Point 3—location of the probable hybrids reported here from Gladstone, Queensland. (b) White-winged and Superb Fairy-wren sighting locations and a drawing of a potential White-winged \times Superb Fairy-wren hybrid. Point 4—location of the probable hybrids reported by Peter Haines in 2014 at Hart Lagoon, South Australia. Point 5—location of the probable hybrids reported here from Thunder Swamp, Victoria. Point 6—location of the probable hybrid reported here from Oakey, Queensland. Species location data from eBird (2021) Basic Dataset. Fairy-wren illustrations: Allison E. Johnson, modified by Joseph F. Welklin

parent species was a Purple-backed Fairy-wren for any of these individuals. The plumages of these individuals also closely resemble the probable White-winged \times Superb Fairy-wren hybrids reported by Peter Haines at Hart Lagoon, South Australia (Haines 2014; Figure 7d).

Locations of hybrid fairy-wrens

We have presented four records of probable hybridisation among fairy-wren species. As seen in some other bird species (McCracken & Wilson 2011), most of the fairy-wren hybridisation events reported here and those reported previously occur on the edge of or beyond a species' normal range, where conspecific mates are infrequent or non-existent (Wilson 1983; Haines 2014). The probable Red-backed \times Superb Fairy-wren hybrids from Gladstone, Queensland, are on the edge of the Superb Fairy-wren range (Figure 8a), and the hybrid reported by Malcom Wilson and colleagues is on the edge of the Red-backed Fairy-wren range (Figure 8a). The probable White-winged \times Superb Fairy-wren hybrids reported here, and the hybrids observed by Peter Haines, are on the edge of the White-winged Fairy-wren range (Figure 8b). The reasons why these individuals dispersed beyond their species' typical range are unclear, but could be associated with altered

habitat regimes as hypothesised for other Australian and Papuan hybrids (Toon *et al.* 2012; Joseph *et al.* 2019; Shipham *et al.* 2019).

Exceptions to this association with range edges are the probable Red-backed \times Superb Fairy-wren hybrids from Brisbane, Queensland, a location within both species' ranges (Figure 8a). Moorhen Flats Recreation Area is an urban park near the centre of Brisbane where Superb Fairy-wrens are common, but Red-backed Fairy-wrens were locally rare at the time when the hybrid was discovered (GN, PS, BM pers. obs.). Thus, it is possible that a Red-backed Fairy-wren in the city centre was unable to find a conspecific mate, resulting in hybridisation. This observation might suggest that human-induced habitat change and the creation of microhabitats that are suited to one species but not the other may also lead to hybridisation. Females are the dispersing sex in fairy-wrens, whereas males rarely settle far from their natal territory (Mulder 1995; Rowley & Russell 1997). Thus, at least some hybridisation events in fairy-wrens are likely initiated by females dispersing outside of their species' typical range, a hypothesis supported by the observations of at least one female Superb Fairy-wren in Gladstone before the discovery of hybrid males.

Consequences of hybridisation in fairy-wrens

Hybridisation events have great evolutionary potential (Ottenburghs 2018) but tracking the impact of a single event on the evolution of either parent species is difficult (Grant & Grant 1992). The inevitable question that arises is: Are the hybridisation events reported here important for the evolution of fairy-wrens? Six examples of hybridisation among fairy-wren species have now been recorded, in addition to the limited hybridisation and gene flow between Purple-backed and Variegated Fairy-wrens (McLean *et al.* 2017b). Two of these reports remain under observation, with hybrid individuals active in early 2022. There have been no recent reports of hybrids from the other four locations, only possibly Bowenville, Queensland (Wilson 1983), still not commonly visited by observers. From this limited sample size, we can generate a few hypotheses: (1) the outcomes of *Malurus* fairy-wren hybridisation are probably short-lived, as most of these occurrences were documented for <4 years. Fairy-wrens are year-round residents, suggesting that these hybrid individuals likely died rather than migrated (Rowley & Russell 1997). Therefore, we also hypothesise that (2) there may be strong pre-zygotic (e.g. mate choice) or post-zygotic (e.g. genetic incompatibility) selection against hybrid fairy-wrens backcrossing with a parent species because few additional atypically plumaged birds followed the initial sightings. Both probable hybrid males in Gladstone associated and maybe even paired with a female Red-backed Fairy-wren (Ross & Briggs 2022), suggesting that selection may not act on pre-zygotic forces, such as mate choice, but rather may come from post-zygotic selection, such as hybrid infertility (Price & Bouvier 2002). However, a further possibility is that neither pre- nor post-zygotic selection is at play but, through backcrossing to a parent species, the phenotypic evidence of hybridisation disappears within a few generations (Joseph & Moritz 1993).

The impact of the hybridisation records described here will ultimately depend on whether any of the hybrids were able to reproduce and whether any genes transferred between species extended any benefit to the survival or reproduction of their offspring. Further observations of breeding success and further work investigating whether a genomic signature of past hybridisation remains in these populations would be a fascinating line of research, as it has been in other Australian taxa (Joseph & Moritz 1993; Toon *et al.* 2012; Shipham *et al.* 2015, 2019). Studies on the population genetics of fairy-wrens have not reported evidence of past hybridisation (Kearns *et al.* 2009; McLean *et al.* 2012; Skroblin *et al.* 2012, 2014; Walsh *et al.* 2021), except the limited gene flow between Purple-backed and Variegated Fairy-wrens (McLean *et al.* 2017b), although, because the main focus of most of these studies did not appear to be identifying signatures of past hybridisation, caution should be taken when drawing conclusions from a lack of reported evidence for past hybridisation.

Further scrutiny and observation of fairy-wren behaviour at species' range limits might help to better understand how these events are initiated. We encourage birders and photographers to look for more hybrid fairy-wrens across Australia, and those who visit locations near a species' range limit or at habitat boundaries should be especially vigilant for potential hybrids or females outside their typical range. As humans continue to disrupt past habitat boundaries that

once separated species, we may expect to see increased hybridisation at these boundaries. Birders who live in urban areas should also keep being vigilant for the presence of non-typical urban species occurring in natural areas surrounded by urban environments. Given the vastness of the Australian continent, it is likely that many more hybrid fairy-wrens exist than those we have reported, and citizen science offers an opportunity to document these events in a way that no one individual or organisation could hope to accomplish.

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