Diverse interactions, including hybridisation, between Brown and Inland Thornbills in South Australia

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Abstract

Brown and Inland Thornbills have three zones of contact in South Australia. Two of these involve the Mount Lofty Ranges Brown Thornbill, which hybridises extensively with the Inland Thornbill in coastal shrublands and mangroves of eastern Gulf St Vincent, and which forms an apparently narrow hybrid zone near Meningie with Inland Thornbills of the Upper South-East of South Australia. The third zone involves Brown Thornbills of the South-East of South Australia and the Inland Thornbill, again its Upper South-East population. This is evidently a broad zone of overlap without interbreeding. Closer study of the Gulf St Vincent hybrid zone revealed a variety of hybrid phenotypes but no parental forms. Most of the hybrid phenotypes resemble Inland Thornbills while some resemble Brown Thornbills of the Mount Lofty Ranges or of the South-East of South Australia. Further study could address why Brown and Inland Thornbills show such a diverse range of interactions in South Australia.

INTRODUCTION

The Australo-Papuan thornbills (*Acanthiza* spp.) comprise 12 Australian species (Schodde and Mason 1999) and two now recognised from New Guinea (Nyari and Joseph 2012). In Australia they occur almost continent-wide except across much of the monsoon tropical north. Phylogenetic studies (Nicholls *et al*. 2000; Nicholls 2001; Gardner *et al*. 2010) have established that one clade of thornbills comprises four species: the Brown Thornbill, *A. pusilla*, primarily of wetter south-eastern Australian woodlands and forests; its sister species (closest relative) the Mountain Thornbill, *A. katherina,* of the Wet Tropics rainforests; the Inland Thornbill, *A. apicalis*, widespread across southern and central Australian semi-arid and arid zones and the more mesic south-west of Western Australia; and the Tasmanian Thornbill, *A. ewingi*, endemic to Tasmania and its larger offshore islands.

Though the Brown and Inland Thornbills are not sister species, the nature of interactions between them where they approach each other in several parts of their ranges has long been a contentious area of research (e.g. Mayr and Serventy 1938, Boles 1983, Schodde and Mason 1999). This paper further addresses the issue.

Across their full geographic ranges three major zones of interaction between Brown and Inland Thornbills have been recognised: 1) the Upper South-East of South Australia (SA) and north-western Victoria; 2) the eastern coast of Gulf St Vincent north of Adelaide, SA; and 3) the western slopes of the Great Dividing Range in New South Wales (NSW). Hybridisation between the two species has been reported across all three zones in reviews of geographical variation in either or both species (Boles 1983; Schodde and Mason 1999, Matthew 2002).

Boles (1983) concluded that populations in the South-East of SA and north-western Victoria were intermediate between nominotypical *A. pusilla pusilla* of south-eastern Australia and a subspecies of the Inland Thornbill, *A. apicalis albiventris,* primarily of interior NSW. Schodde and Mason (1999) suggested an alternative view involving a second subspecies of the Inland Thornbill, *A. a. apicalis*, which superficially resembles some populations of Brown Thornbills. They argued that in the north of the Upper South-East of SA these two subspecies of the Inland Thornbill intergrade whereas towards the Lower South-East there is a zone of overlap between Brown and Inland Thornbills without hybridisation.

Possingham and Possingham (2000) reported field observations from the Upper South-East with some birds identified as Brown Thornbills and others as Inland Thornbills, again implying that the two species are sympatric there; none were thought by them to be of hybrid descent. They noted Brown Thornbills in denser habitats, particularly those that included *Melaleuca* shrubs in the understorey, Inland Thornbills being in more open mallee communities.

Black (2015) showed that this major zone involves two separate contact zones, one between Inland Thornbills and South-East Brown Thornbills, *A. pusilla pusilla*, and another between the former and Mount Lofty Ranges Brown Thornbills, *A. pusilla samueli*.

The second major zone of interaction between the two species was defined by Schodde and Mason (1999) as 'the coastal shrubberies of east coast Gulf St Vincent north of Adelaide', Brown Thornbills being on the lower Adelaide Plains north to the Gawler River and Inland Thornbills around the SA gulfs. They concluded that there the two species are locally sympatric and that there are no intermediate forms. Higgins and Peter (2002) agreed although Matthew (2002) recognised a single specimen of intermediate character. Paton, Carpenter and Sinclair (1994) recorded Brown Thornbills in the Mount Lofty Ranges but not on the Adelaide Plains, and Inland Thornbills in coastal habitats north of Adelaide. On the other hand, Black (2015) reported field observations from this area that questioned the presumption that only Inland Thornbills occupy the mangroves of eastern Gulf St Vincent, Brown Thornbills also being reported from them as well as in adjacent habitats, including plantations (Black 2015; see map therein, Figure 1).

The third major zone of interaction is on the western slopes of the Great Dividing Range in northern, central and southern NSW. Norman (1987; not accessed - see Schodde and Mason 1999 and Matthew 2002), using allozymes as well as phenotypic data, found evidence of hybridisation across three east-west transects in this region. Phenotypically intermediate specimens were found within only a short segment of each transect. Genetic introgression was limited but occurred over distances of between 30 km in the north and 200 km in the south. Norman (1987) found that the integrity of both species was maintained by habitat choice: eucalypt forest by the Brown Thornbill, and *Callitris* and mallee scrub by the Inland Thornbill.

Matthew (2002) examined most Australian material of the two species, including that available to Boles (1983), Norman (1987) and Schodde and Mason (1999). He could not confirm Norman's finding of intermediate forms on her three transects but identified three putative hybrid specimens, one from each of the major zones of interaction just discussed here.

Clearly, then, there are alternative views on how Brown and Inland Thornbills interact where their ranges come into contact. Accordingly, the aim of this paper is to review specimen evidence to clarify the nature of these interactions but the scope is restricted to two zones of contact in South Australia (Meningie area and east Gulf St Vincent). Specifically, we ask whether these closely related and similar but not sister species (Nicholls *et al.* 2000, Nicholls 2001, Gardner *et al.* 2010) occur sympatrically with little or no hybridisation, or whether there is intergradation between them, either from secondary contact and hybridisation, or as a primary cline.

Short (1969) outlined two kinds of zones of secondary contact between differentiated populations: the zone of overlap and hybridisation, and the hybrid zone, with a strategy for distinguishing them. He defined the former as containing both parental phenotypes as well as a variety of intermediate forms and, because it suggested a degree of reproductive isolation, he argued that it characterises interactions between distinct species. The latter contains intermediate individuals showing progressive variation across the zone and implies a degree of reproductive compatibility between the interacting populations. Distinguishing the two is rendered problematic when differences between parental forms are subtle and hybrids are difficult to recognise as a consequence. Endler (1977) on the other hand used the term hybrid zone for the former and cline for the latter and stressed that clines might be steep or gentle, stepped or smooth, narrow or broad, no matter whether primary or secondary intergradation was involved. Hewitt (1989) referred to clines between parapatric subspecies as hybrid zones. There are thus many variations in the terminology and definitions applied to the subject of hybridisation and hybrid zones. Short (1969) regarded very gradual intergradation across a broad zone as a primary cline and not a region of secondary contact.

If Brown and Inland Thornbills hybridise as a result of secondary contact we anticipate finding a narrow zone containing a diversity of intermediate phenotypes as well as parental forms. If their interaction represents a primary cline of differentiation we expect a broad zone of progressive intergradation between one parental type and the other.

MATERIALS AND METHODS

The following abbreviations will be used for geographical regions in South Australia: EP – Eyre Peninsula; GSV – Gulf St Vincent; KI – Kangaroo Island; MLR – Mount Lofty Ranges; MM – Murray Mallee; MN – Mid North; SE – South-East; USE – Upper South-East; YP – Yorke Peninsula.

We examined a total of 232 specimens of both species in the South Australian Museum, Adelaide (SAMA), including those in the S. A. White Collection held there but not seen by Black (2015), and Australian National Wildlife Collection, CSIRO, Canberra (ANWC). This included all SAMA material of both species from throughout most of their ranges (*A. pusilla*: Queensland (n = 3), NSW (5), Victoria (11), SE (35), MLR (31); *A. apicalis*: south-western Australia (18), EP and Gawler Ranges (38), YP (13), MN (7), Flinders Ranges (5), inland SA (10) and MM/USE (32)) and the following from the two contact zones of focal interest: Meningie area (n = 9; eastern margin of Lake Albert) and east GSV (n = 15; Outer Harbor and St Kilda to Port Gawler and the Light River). The broader SAMA and ANWC material included specimens of both species from immediately adjacent populations in the MLR, USE, MN and YP.

We assessed the variation of colour and tone of skin specimens, as shown by Schodde and Mason (1999) and/or Higgins and Peter (2002) to vary among subspecies of Brown and Inland Thornbills. Colour perception and description without a method such as reflectance spectrophotometry pose significant problems. They can then be highly subjective and, unlike Black (2015), we did not use Smithe's (1975) colour chart because we have found that it produces neither objective nor consistent results when used by different observers. Our examination was essentially comparative if subjective but we are confident that trends can be discerned and are worth reporting. In particular we viewed concurrently all known specimens from the target regions alongside representatives from adjacent populations. We noted the colours/tones of the frontal feather bases and scalloping, the upperparts (crown, mantle, back), rump, underparts generally and flanks. We noted the breadth of the subterminal tail bar but, because of its irregular form, did not believe it practical to attempt an objective measurement. We looked for the presence of pale or white tipping to outer tail feathers. Finally we reviewed the colour of feet (tarsi and toes), which Schodde and Mason (1999) found distinguished the two species reliably.

RESULTS

Plumage variation

Table 1 summarises variation in plumages within and between populations of Brown and Inland Thornbills. All Brown Thornbills, whether in fresh or worn plumage, showed olive toning, whereas Inland Thornbills showed little or none. All Inland Thornbills (and Brown Thornbills from Queensland but not from SA) showed substantial white patches on the inner vanes of outer tail feathers (not shown in Table 1). In Brown Thornbills such patches, where observed, were pale but not truly white. Worn plumage will affect the size, whiteness and visibility of these patches.

Inland Thornbills on EP, YP and in the MN, all assigned to the nominate subspecies *A. apicalis apicalis*, closely resemble those from south-western Australia. The south-westernmost specimens (not shown in the Table) are browner and in other respects are the most *pusilla*-like. Eastern SA populations from the MM and USE are alike, being intergradient between the nominate subspecies and the reddish rumped *A. apicalis albiventris* of the interior of NSW.

The feet (tarsus and toes) of Inland Thornbills are very dark, almost or actually black, while those of Brown Thornbills show pinkish tinting. Though generally consistent, we did encounter exceptions in SA populations and in specimens of *A. apicalis apicalis* from south-western Australia, which had pinkish tinted *A. pusilla*-like feet. That character and the breadth of the subterminal tail band were also excluded from Table 1, the latter being of variable shape and definition. Generally, the subterminal tail band was broader in Inland Thornbills but there was overlap between species and variability within, specimens from south-western Australia in particular having tail bands across the range from narrow to broad.

In populations considered here, MM and USE Inland Thornbills showed stronger tonal contrast

Table 1. Plumages traits among populations of Inland Thornbill (upper three rows) and Brown Thornbill (lower two rows).

Population	Upperparts	Frontal feather bases	Frontal feather scalloping	Underparts	Flanks
Inland Thornbill South-western Australia *A. a. apicalis*	Grey brown	Grey brown	Buff to brown	Pale cream	Pale brown
Inland Thornbill EP, YP and MN *A. a. apicalis*	Grey brown	Grey or with slight brown wash	Whitish to pale buff	White to fawn white	Pale brown
Inland Thornbill MM and USE *A. a. apicalis/ albiventris*	Grey brown	Grey to grey brown	Pale buff	Whitish	Pale brown
Brown Thornbill SE SA *A. p. pusilla*	Pale olive grey brown	Grey brown to brown	Brown to buff	Pale cream	Pale olive brown
Brown Thornbill MLR *A. p. samueli*	Olive brown	Moderate to rich brown	Brown to buff	Cream	Olive brown

between the rump and dorsum than YP and MN Inland Thornbills, while Brown Thornbills showed only moderate contrast.

Inland Thornbills from the arid interior *A. apicalis whitlocki* and Flinders Ranges (intergrades of *A. a. apicalis, A. a. whitlocki* and *A. a. albiventris*) are paler and greyer with white underparts and will not be further considered in this comparative study.

Description of thornbill specimens from the contact zones of focal interest

Meningie-Lake Albert region
1. SAMA B22644, [near] Meningie, October 1923, considered to be of intermediate phenotype by Matthew (2002): similar to MM *A. apicalis* (greyer than SE *A. pusilla*) with white tail tipping and similar rump contrast but with pinkish feet, slightly cream belly, paler flanks and browner frontal feathers and scalloping.

2. SAMA B22645, [near] Meningie, October 1923: similar to SAMA B22644 but with only very slightly cream underparts; frontal features as in *A. apicalis*.

3. SAMA B22651, [near] Meningie, October 1923: as SAMA B22645.

4. SAMA B22657, [near] Meningie, October 1923: close to *A. apicalis* but with slightly pinkish feet.

5. SAMA B53239, Lallawa Station [on the stem of Narrung Peninsula due west of Meningie], 27 September 1894: resembles SE *A. pusilla* with brown frons and scalloping, pinkish feet and lacks white in the tail.

6. SAMA B53230, Albert Hill [north of Meningie], November 1917: close to *A. apicalis* but with pinkish feet; probably similar to SAMA B22645 but no recognisable cream on underparts perhaps because of exposure.

7. SAMA B53241, Albert Hill [north of Meningie], November 1917: similar to SAMA B53230.

8. SAMA B53242, Albert Hill [north of Meningie], November 1917: similar to SAMA B53230 but no white seen in the tail.

9. SAMA B 53243, Albert Hill [north of Meningie], November 1917: close to *A. apicalis*, feet almost black.

Examples of the above population are shown in Figures 1 and 2.

Eastern Gulf St Vincent region
10. SAMA B19409, Buckland Park, 22 May 1916: appearance intermediate between *A. p. samueli* and *A. apicalis apicalis* of YP and MN; dorsum paler olive brown than the former and not as grey as the latter, rump colour richer, closer to latter, ventrally intermediate with slight cream and olive toning, brown flanks also intermediate in tone and brown area more extensive than in YP and MN *A. a. apicalis*. Feet slightly pink, outer tail feathers tipped with white and frontal plumage as in YP and MN birds.

11. SAMA B19410, St Kilda, 21 October 1915: similar to SAMA B19409.

12. SAMA B22656, St Kilda, 9 April 1917: similar to SAMA B19409.

13. SAMA B23107, Lower Light, 5 June 1919: similar to SAMA B19409 but frontal plumage very slightly browner.

14. SAMA B53244, St Kilda, 24 April 1913: similar to SAMA B23107.

15. SAMA B53249, St Kilda, 24 April 1913: similar to SAMA B19409.

16. SAMA B53250, Outer Harbor, June 1911: similar to SAMA B23107.

17. ANWC B17821, Port Gawler, 22 January 1975: similar to SAMA B19409, dorsum slightly greyer but frontal plumage slightly browner as in SAMA B23107; ventral area damaged, feet black.

Figure 1. Inferred Meningie hybrids (central two), compared with MLR Brown Thornbill (left) and MM Inland Thornbill (right). Dorsal view of specimens: SAMA B33723 *Acanthiza pusilla samueli*, Kuitpo Forest, MLR; SAMA B22644 *Acanthiza pusilla-apicalis* hybrid, near Meningie; SAMA B22645 *Acanthiza apicalis*-resembling hybrid, near Meningie; SAMA B19141 *Acanthiza apicalis apicalis/albiventris*, Karoonda, MM. Note greyer tones in the hybrid and Inland Thornbill specimens. Pertinent frontal plumage features are not visible. Image Peter Gower

Figure 2. Inferred Meningie hybrids. Ventral view of specimens as in Figure 1. Note slight cream tones and pinkish-tinted legs in the hybrid specimens. Image Peter Gower

18. ANWC B40368, Saltfields north of St Kilda, 30 September 1985: similar to ANWC B17821 but frontal plumage as in YP birds; ventrally as in SAMA B19409.

19. ANWC B40372, Saltfields north of St Kilda, 30 September 1985: similar to ANWC B40368.

20. ANWC B40381, Saltfields north of St Kilda, 30 September 1985: similar to ANWC B40368 but with frontal plumage very slightly browner, similar to SAMA B23107, feet only slightly pink.

21. SAMA B22648, Buckland Park, 22 May 1916, considered to be of intermediate phenotype by Matthew (2002): similar to SAMA B19409 but frontal plumage browner and with stronger cream and olive brown tones ventrally, the appearance approaching that of *A. p. samueli*.

22. ANWC B40392, Saltfields north of St Kilda, 3 October 1985: dorsum paler and greyer than skins 10-21 with some olive resembling SAMA B22648, frons similar to 10-20; ventrally similar to 10-20 but with stronger olive and cream tones yet paler and not as brown as in SAMA B22648 and so closer to SE *A. p. pusilla*; a small area of pure white in the tail, feet pinkish.

23. ANWC B40393, Saltfields north of St Kilda, 3 October 1985: similar to ANWC B40392 but no white seen in the tail.

24. ANWC B40394, Saltfields north of St Kilda, 3 October 1985: similar to ANWC B40393.

Features of the above 15 specimens (nos. 10-24) are summarised in Table 2 and compared with those of adjacent thornbill populations. They are illustrated in Figures 3 to 6.

DISCUSSION

The aim of this study has been to examine the relationship between Brown and Inland Thornbills in two major zones of interaction in SA, including whether hybridisation occurs more than occasionally, as might be inferred from previously published material. We have found that hybridisation is not exceptional and is common in one of the two zones. An additional question is whether the occurrence of intergradient individuals is consistent with secondary contact between species or represents a primary cline.

In the Meningie-Lake Albert area we confirmed Matthew's (2002) view that SAMA B22644 (specimen no. 1) shows traits intermediate between those of the Brown and Inland Thornbill. In addition we found that from two to five (nos. 2, 3 and perhaps 6-8) of the other eight specimens from the Meningie area show more subtly intermediate features, some showing more olive tones and their feet not being as black as in most USE specimens of *A. apicalis* (Figures 1 and 2). The locality of these probable hybrid specimens, well north of the distributional limit of SE Brown Thornbills, suggests that their parental populations are MLR Brown and USE Inland Thornbills (Black 2015).

Two specimens, nos. 4 and 9, appear closer to the Inland Thornbill phenotype and no. 5, the only specimen known to have been taken on the Narrung Peninsula, resembles a SE Brown Thornbill *A. pusilla pusilla*. Because that specimen and the Albert Hill specimens from the S.A. White collection (nos. 6-9) are 'foxed' from exposure, however, they appear paler and browner. Therefore, it is indeterminate in our view whether the identity of the Narrung Peninsula specimen might alternatively be *A. pusilla samueli* or of hybrid origin. Sight records from the Narrung Peninsula are few and of uncertain identity. East and south of Lake Albert recent field observations have been of presumed Inland Thornbills (Black 2015).

In the east GSV area we have found evidence of a population of intermediate phenotypes. Of 15 such specimens there are 11 (nos. 10-20) that are phenotypically close to Inland Thornbills from YP and the MN (Table 2), ten having some pure

Table 2. Varied plumages among Inland and Brown Thornbills and inferred hybrids in and near the eastern Gulf St Vincent area.

Population	**(A)** **YP and MN** ***A. apicalis apicalis***	**(B)** **Eastern GSV** ***A. apicalis*-like hybrids (nos. 10-20)**	**(C)** **Eastern GSV** ***A. pusilla pusilla*-like hybrids (nos. 22-24)**	**(D)** **Eastern GSV** ***A. pusilla samueli*-like hybrid (no. 21)**	**(E)** **MLR** ***A. pusilla samueli***
Upperparts	Grey-brown	Grey-brown, slightly browner than (A).	Olive grey-brown, relatively pale	Grey-brown with olive cast; slightly browner than (B), not as olive as (E).	Olive-brown
Frontal feather bases	Grey or with slight brown wash	Slight to moderate brown wash	Slight to moderate brown wash	Moderate brown wash	Moderate to rich brown wash
Scalloping	Whitish to pale buff	Whitish to warm buff	Whitish	Pale brown	Warm buff to pale brown
Rump (contrast with mantle and back, and colour)	Slight to moderate, rarely strong, chestnut or rufous-chestnut	Moderate, rufous-chestnut	Slight, olive-chestnut	Moderate, rufous-chestnut with olive cast	Slight to moderate, olive-rufous-chestnut
Underparts	White to fawn-white	Whitish to fawn-white	Whitish-cream	Fawn-white with cream cast	Cream
Flanks	Fawn to very pale brown	Pale to mid brown	Olive-grey	Olive-grey-brown	Rich olive-brown
Black subterminal tail band	Medium to broad	Medium	Medium to narrow	Medium	Narrow
White tail tips	Present	Present but often duller or reduced	Little or none	Present, reduced	None

Figure 3. Inferred Gulf St Vincent hybrids 1 (central two), compared with MN Inland Thornbill (left) and MLR Brown Thornbill (right). Dorsal view of specimens: ANWC B18685 *Acanthiza apicalis apicalis*, Tothill Range, MN; SAMA B22656 *Acanthiza apicalis*-resembling hybrid, St Kilda, GSV; SAMA B22648 *Acanthiza pusilla samueli*-resembling hybrid, Buckland Park, GSV; SAMA B22642, *Acanthiza pusilla samueli*, Cape Jervis, MLR. Note progressive left to right change in tone of upperparts from paler grey brown to darker olive brown. Image Peter Gower

Figure 4. Inferred Gulf St Vincent hybrids 1. Ventral view of specimens as in Figure 3. Note extensive flank coloration in the hybrids and white in the tail with progressive left to right increase in olive brown tone. Image Peter Gower

Figure 5. Inferred Gulf St Vincent hybrids 2, from left to right: MN Inland Thornbill, GSV hybrid, SE Brown Thornbill and MLR Brown Thornbill. Dorsal view of specimens: ANWC B18687 *Acanthiza apicalis apicalis*, Tothill Range, MN; ANWC B40393 *Acanthiza pusilla*-resembling hybrid, St Kilda saltfields, GSV; SAMA B26812 *Acanthiza pusilla pusilla*, Naracoorte, SE; SAMA B22642 *Acanthiza pusilla samueli*, Cape Jervis, MLR. Note dorsal tone of the hybrid specimen is intermediate between that of the Inland and Brown Thornbills. Image Peter Gower

Figure 6. Inferred Gulf St Vincent hybrids 2, as in Figure 5. Ventral view of specimens: ANWC B18687 *Acanthiza apicalis apicalis*, Tothill Range, MN; ANWC B40392 *Acanthiza pusilla*-resembling hybrid, St Kilda saltfields, GSV; SAMA B26812 *Acanthiza pusilla pusilla*, Naracoorte, SE; SAMA B22642 *Acanthiza pusilla samueli*, Cape Jervis, MLR. Note cream and olive tones in the hybrid specimen, more closely resembling SE Brown Thornbill than MLR Brown Thornbill. Image Peter Gower

white on the tips of tail feathers. Nevertheless, all of those 11 have more extensively brown and darker flanks than those Inland Thornbills, a character state approaching that of MLR Brown Thornbills, *A. p. samueli,* though with less cream or olive toning (Figures 3 and 4). Some have other intermediate features, including pinkish *pusilla*-like feet; their dorsal tone and frontal plumage vary. Four specimens, no. 21 (SAMA B22648, previously identified as hybrid) and nos. 22-24 (presumably those given by Mathew (2002) as *pusilla* but since relabelled *apicalis*), show more olive and cream toning in their plumages but not as strongly as is seen in Brown Thornbills (Table 2). Of these, no. 21 is overall a more olive-brown toned skin, closer to *A. p. samueli* (Figures 3 and 4), while nos. 22-24 are paler olive-grey and lack the warm brown toning, thus more closely resembling SAMA skins of SE *A. p. pusilla* (Figures 5 and 6).

Schodde and Mason (1999) and Higgins and Peter (2002) found that Inland and Brown Thornbills were sympatric in the eastern GSV mangroves and shrublands north of Adelaide and that intermediate phenotypes were absent or rare (Matthew 2002). We found three broad phenotypes as described above but stress our conclusion that none corresponded fully with that of the adjacent MLR Brown Thornbill (Figure 7) or the Inland Thornbill of the MN and YP (Figure 8). Two of the three phenotypes, together with skins of Inland and MLR Brown Thornbills are shown (as above) in Figures 3 and 4 and the third phenotype is shown with SE and MLR Brown Thornbills in Figures 5 and 6.

Perhaps inevitably, recent field records from Torrens Island and St Kilda, north to Port Wakefield, provide at best equivocal evidence for the occurrence of both species. AB has observed birds resembling Inland Thornbills in mangroves at St Kilda, Port Gawler and Middle Beach, and others resembling Brown Thornbills in *Casuarina* trees at Buckland Park Lake and in plantations near the Dry Creek estuary. Derek Carter (pers. comm. to AB) and others have recorded what appeared to be Brown Thornbills in wetlands of the lower Little Para River and in mangroves of the Light River and at Port Wakefield. Graham Carpenter (pers. comm. to AB) questioned the identity of thornbills seen in mangroves between Torrens Island and Parham (Figures 9 and 10) after failing to observe tail cocking, a distinctive

Figure 7. Mount Lofty Ranges Brown Thornbill, *Acanthiza pusilla samueli.* Photographed at Stirling, MLR. Image Les Peters

Figure 8. Yorke Peninsula Inland Thornbill, *Acanthiza apicalis apicalis*. Photographed at Price, YP. Image Kent Treloar

behavioural characteristic of the Inland Thornbill but seen infrequently in the Brown Thornbill (Higgins and Peter 2002 and references therein, Black 2015). However, near the head of the gulf, Paul Taylor (pers. comm. to AB) has observed tail cocking by Inland Thornbills at Bald Hill Beach 10 km south of Port Wakefield over many years. Carter has seen tail cocking in thornbills at Port Wakefield but has not recorded it south of there, nor has AB. Mangroves extend from the head of the gulf at Port Wakefield west and south to Price where Inland Thornbills typical of the YP population are present (Kent Treloar pers. comm. to AB; Figure 8).

Having examined the relevant specimen material from the GSV, we are mindful of the difficulty, inherent in field observations such as those just cited, of observing and reporting subtly varying key character states like those that distinguish these thornbills. Accordingly, we consider that the observations cited above of birds resembling Brown Thornbills, Inland Thornbills and thornbills of uncertain identity do not reject and are generally consistent with our interpretation of the specimen evidence showing a range of intermediate thornbill plumages occurring in the mangroves and coastal shrublands of eastern GSV. Habitat data attached to one Inland-resembling hybrid specimen referred to mangrove and nitrebush flats. Habitat notes on other specimens of each phenotype referred to samphire with scattered shrubs or small trees but selective habitat occupation by phenotype, as suggested by field observations, cannot be confirmed. On the other hand, images of living birds (Figures 9 and 10) show that Inland-resembling thornbills do occupy mangroves in the area. Particularly noteworthy are six ANWC specimens, nos 18-20 and 22-24, all adult birds collected from the saltfields at St Kilda in September-October 1985. Three (18-20) are Inland-like while the other three (22-24), collected only four days later, are noticeably different, more closely resembling SE Brown Thornbills.

The recognition of hybridisation between Brown and Inland Thornbills may challenge but does not negate their status as separate species, especially as they are non-sister species. Further, maintenance of divergence despite ongoing gene flow has long been an active area of research in population biology (Endler

Figure 9. Probable *Acanthiza apicalis*-resembling hybrid thornbill in mangroves at St Kilda saltfields, GSV. Note pale grey-brown above, very pale below and limited area of flank coloration (less than in all examined specimens) but distinctly brown frontal feather bases.
Image Colin Rogers

Figure 10. Probable *Acanthiza apicalis*-resembling hybrid thornbill in mangroves on Garden Island (south-east of Torrens Island), GSV. Note grey-brown dorsum, white tail tip and strong rump contrast of apicalis but distinctly brown frontal plumage. Image © Kym Murphy 2014 (www.birdlife.org.au)

1977; Pinho and Hey 2010) and ornithology is no exception (Joseph and Moritz 1993; Rheindt and Edwards 2011; Kearns *et al*. 2014). Moreover, genetic introgression between taxa does not necessarily disprove that they represent independent evolutionary lineages (Gill 2014, Rheindt and Edwards 2011). Nevertheless, species delimitation studies have long involved assessments of zones of contact for evidence of hybridisation (Short 1969), and Carstens *et al*. (2013) observed that determining such delimitations is complicated when either taxon is polytypic, as is the case with both species discussed here.

The nature of the zone of interaction on the western slopes of the Great Dividing Range in NSW, which has not been a focus here, might be interpreted as a narrow hybrid (or clinal) zone having demonstrated introgression, or as a zone of overlap and hybridisation if both parental forms and hybrids can be found within it. The evidence is conflicting, Norman (1987) but not Matthew (2002) recognising hybrids. That interaction, which warrants further study, occurs between *A. pusilla pusilla* and *A. apicalis albiventris*. In the USE we found that Inland Thornbills there and those in the MM were alike, forming an [intraspecific] intergradient population *A. apicalis apicalis/albiventris*. We thus differed from Schodde and Mason (1999) who assigned USE Inland Thornbills to the nominotypical subspecies *A. apicalis apicalis* and not to the intergradient MM population. The absence of any evidence of interspecific hybrid birds (i.e. between those Inland Thornbills and the pallid SE Brown Thornbill *A. pusilla pusilla*) suggests that that region is a broad zone of overlap between the two species and this may be the only region where they occur sympatrically. On the other hand, at the western extremity of this region we have shown that the same Inland Thornbill population has hybridised to an unknown extent with (presumably) the MLR Brown Thornbill, *A. pusilla samueli*.

The evidence is of only limited hybridisation but not of progressive intergradation and suggests restricted secondary contact between populations of the two species. This inference is provisional, being based largely on field observations together with a small number of specimens, many of which are old and imperfectly preserved. Because of the extent of habitat loss in that area, there are limits to which this region of hybridisation can be analysed further. There is an opportunity, however, to examine the contrastingly and apparently extensive USE overlap zone between the species, employing ecological, behavioural and genetic methods. It is also observed that there is no specimen material from within that area of presumed sympatry.

On the eastern coast of GSV we have found a broad zone of at least 30 km occupied by a variety of hybrid thornbills. We found no progressive variation through the zone to indicate a cline and recognised no parental forms within it. We suggest that further research might test the hypothesis that this hybrid population be regarded as a hybrid swarm (Cockayne and Allan 1926, Short 1969, Freed *et al.* 2015).

A characteristic of hybrid swarms that distinguishes them from simple hybrid zones is that the populations within them show relatively higher reproductive isolation from one or both parental forms, a circumstance that appears consistent with the evidence here for the eastern GSV hybrid population.

Relevant to this is first that only three records have been attributed to either species from between Bald Hill Beach and the Light River estuary (SAOA 1977, Paton, Carpenter and Sinclair 1994, Atlas of Living Australia, www.ala.org.au, Birds SA database, Brian Blaylock pers. comm.), a 30 km gap in which mangroves are sparse and discontinuous.

Second, historical records of Brown Thornbills on the Adelaide Plains are few (Black 2015). The Atlas of Living Australia (www.ala.org. au) showed only three , the earliest in March 1924, evidently from Mellor (1924) but it was not among Mellor's frequent observations at Fulham but from Stirling MLR (*c.f.* Black 2015). There were two others, apparently from the city of Adelaide itself, dated 1951-1960 and 1.1.2009. The former has not been sourced but the latter is from a composite list that includes several species that are restricted to the forested ranges. Otherwise there are none in that database from suburban Adelaide except those from the Barker Inlet and in coastal localities north to Middle Beach. Higgins and Peter (2002) cited only one observation from suburban Adelaide, a report by R. J. Whatmough of two in scrub near the River Red Gum lined Torrens River at Levi Caravan Park, Vale Park on 13 December 1975 (Reid 1976).

The Brown Thornbill is unlisted among surveys and other records of Adelaide's parklands and lower sections of the Torrens (Anon. 1915, White 1919, Glover 1953, Paton 1976, Whatmough, van Weenen and Tan 2013, David and Penny Paton pers. comm.). There is no other record from the Adelaide suburbs in the Birds SA database (Brian Blaylock pers. comm.). Even woodlands of the foothills may not have regularly supported Brown Thornbills, the Crompton brothers failing to report them at Stonyfell over a thirty year period (Crompton 1915). Beyond those woodlands, to the north and west of the city, lay a belt of mallee and extensive grasslands (Kraehenbuehl 1996). It appears therefore that Brown Thornbill habitat has been limited at best on the Adelaide Plains since European settlement. Even in River Red Gum woodland associated with the Torrens River we find only one reliable record and none from its lower reaches. Whether the species occurred within similar woodlands along Dry Creek and the Little Para and Gawler Rivers is conjectural.

The existence of a broad zone occupied by what might be regarded as a hybrid swarm was unanticipated but, with specimens taken over a century ago, it appears to be of reasonably long standing. Added to that is the evidence of limited potential contact between Inland and MLR Brown Thornbills through narrow riverine woodland corridors, a circumstance unlikely to have driven extensive hybridisation unless MLR Brown Thornbills and hybrids held a powerful selective advantage over Inland Thornbills (see Endler 1977). Population expansion in one or both species is the most plausible explanation for how secondary contact originated and led to development of a hybrid zone. Pending molecular data bearing on the deeper evolutionary histories of all of these populations, we note that past distributional patterns and zones of interaction between the two species are of course unknown but feasibly may have been very different from those of the present day.

We predict that the GSV hybrid population that we have identified here will be found to have existed for much longer than a hundred years, more probably of the order of thousands of years. Populations derived from hybridisation between long diverged species are of evolutionary interest, having the potential to develop into new species of hybrid origin (Brelsford, Borja and Irwin 2011).

Accordingly, the GSV hybrid thornbill population demands further study. First, its northern limit has not been defined so more detailed study will be needed within the mangroves and other habitats of the area, extending north to Port Wakefield. Second, as we have concluded, the hybrid specimens described here show a range of phenotypes between one that closely resembles the Inland Thornbill and others that are more like Brown Thornbills of either the MLR or SE subspecies. But we have not yet determined whether Brown Thornbills reported from wooded wetlands of the lower Little Para River are of parental or intergradient phenotype. Finally, there is a need for genetic data relating to this complex interspecific interaction.

In both South Australian zones of contact (Meningie area and east GSV) the specimen evidence is consistent with a hypothesis of secondary contact between populations of independent evolutionary lineages (species) rather than with the alternative hypothesis of a primary cline of intergradation. We find much scope for further research into the relationships between the two species.

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