

Pelage variation in dingoes across southeastern Australia: implications for conservation and management

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Abstract

How to manage hybridization and introgression in wild animals is controversial. Wildlife managers and researchers may often rely upon phenotypic variables such as coat colour to inform on ground management decisions. In Australia, dingoes are typically believed to be ginger in colour, and unusual coat colours such as brindle or sable are widely posited to be evidence of contemporary domestic dog hybridization. We carried out microsatellite-based genotyping on 1325 wild canids from southeastern Australia of known coat colour to estimate the extent of domestic dog introgression. A key aim of our study was to examine the relationship between coat colour and ancestry in wild dingoes. We observed that 27.4% of our samples were dingoes with no evidence of domestic dog ancestry whilst 72.6% were dingoes with some domestic dog ancestry. Our data confirm that feral dogs, domestic dogs with no dingo ancestry, are rare in the wild, representing less than 1.5% of the population. There was no coat colour that could distinguish dingoes with or without dog ancestry from each other. Contrary to popular belief, colours such as brindle and patchy were positively associated with dingoes with no dog ancestry and were less common in dingoes of mixed ancestry. A key finding of this work is that coat colour should not be used to assess ancestry in dingoes. Further research is needed to uncover the antiquity, origin and potential adaptive value of these genomic regions. It is possible that this is a similar example of adaptive introgression as has been observed in North American wolves with black coat colour. These data add perspective to global debates about how to manage and conserve enigmatic animal populations in the presence of modern or historical introgression.

Introduction

Hybridization is a threat to many wildlife species and often arises due to human modification of animal distributions allowing previously allopatric species, sub-species or populations to interbreed (Simberloff, 1996; Rhymer & Simberloff, 1996; Allendorf *et al.*, 2001). This has led to debate about the role of adaptive introgression, blurring species boundaries and how introgression should be managed for conservation (vonHoldt *et al.*, 2018; Supple & Shapiro, 2018; Muhlfeld *et al.*, 2014; Murphy *et al.*, 2018; Mable, 2019; Macdonald *et al.* 2010). Genetic introgression resulting from hybridization can be a driver of phenotypic variation (Anderson *et al.*, 2009; Jones *et al.*, 2018; Schweizer *et al.*, 2018; vonHoldt & Aardema, 2020). Consequently, phenotypic characteristics are often used

in management programmes to identify hybrids from non-hybrids (Kitchener *et al.*, 2005; Daniels *et al.*, 1998; Macdonald *et al.* 2010; Elledge *et al.*, 2006; Corbett, 2001a; Fleming *et al.* 2001; Galov *et al.*, 2015). However, discriminating hybrid and non-hybrid forms on the basis of their phenotype requires a sound understanding of the range of phenotypic variability possible in both forms.

Dingo-dog hybridization is a controversial topic in Australia. The domestication status of the dingoes' ancestor is unclear and has sparked debate about the taxonomic status of dingoes. Crowther *et al.* (2014) and Smith *et al.* (2019) suggest that dingoes represent an early or pre-domestication dog lineage that is distinct from modern domestic dogs, positing the nomenclature *Canis dingo*. Jackson *et al.* (2017, 2019) argue that dingoes are a feral domestic dog (*Canis familiaris*).

Regardless of taxonomy, dingoes are a wild living canine that has been present in Australia for at least 3500–8000 years according to molecular and archaeological evidence (Cairns & Wilton, 2016; Fillios & Taçon, 2016; Balme, O'Connor & Fallon, 2018; Zhang *et al.*, 2020). Since arriving on the continent, dingoes have been subject to natural selection and display many distinctive phenotypic traits (Crowther *et al.*, 2014; Smith *et al.*, 2019; Zhang *et al.*, 2020). However, dingoes can hybridize with domestic dogs, and since British colonization of Australia, there has been opportunity for dingoes to interbreed with dogs (Newsome & Corbett, 1985; Stephens *et al.*, 2015; Cairns *et al.*, 2019). This is particularly the case in eastern Australia where opportunities for mating between dingoes and dogs have been facilitated by higher densities of pet dogs and active suppression of dingo populations (Stephens *et al.*, 2015; Cairns *et al.*, 2019).

There has long been debate about the physical appearance of dingoes and influence of hybridization on coat colour variation and skull morphology (Corbett, 2001b; Crowther *et al.*, 2014; Fleming *et al.* 2001; Elledge *et al.*, 2006; Newsome & Corbett, 1985; Jones, 1921; Macintosh, 1975; Barker & Macintosh, 1979). Skull morphology was once widely used as a method of discriminating between dingoes and hybrids (Newsome, Corbett & Carpenter, 1980; Corbett, 2001a; Elledge *et al.*, 2008). However, a recent study has shown that skull morphology is highly conserved and may have limited utility in discrimination of pure dingoes (Parr *et al.*, 2016).

Historical reports from the 18th and 19th centuries commonly described observations of dingoes that were red, yellow, black, white, black and white, tan or tawny (Collins, 1798; Mitchell, 1839; Abbott, 2008). Whilst ginger (Fig. 1) is the most common pelage colouration observed in genetically or morphologically identified pure dingoes, other accepted colours include black & tan and white (Elledge *et al.*, 2006; Fleming *et al.* 2001; Corbett, 2001a; Corbett, 2001b; Newsome & Corbett, 1985; Crowther *et al.*, 2014; Smith, 2015; Newsome *et al.*, 2013). Many dingoes, regardless of colour, have white markings on their chest, feet, legs and tail tips, dark eyes and undercoat that is white, cream or grey (Table 1). Sable (Fig. 1) pelage has long been viewed as an indicator of dog gene introgression by some authors (Fleming *et al.* 2001; Corbett, 2001b), but because it has been recorded in dingo pelts from the early 1800s in remote regions it is likely to be another 'wild-type' dingo colouration (Crowther *et al.*, 2014). The observation of pure sable dingoes by Tatler *et al.* (2021) in remote South Australia provides further support that sable is an ancestral colour variation. Other colour patterns (Fig. 1) that have been attributed to be evidence of significant dog ancestry include brindle, patchy (or parti colour), merle and brown (Corbett, 2001b; Crowther *et al.*, 2014; Elledge *et al.*, 2006; Fleming *et al.* 2001; Newsome & Corbett, 1985; Smith, 2015).

In the field, wild dog and dingo trappers often rely upon coat colour to assess the likelihood of a dingo having domestic dog ancestry (Elledge *et al.*, 2008; Elledge *et al.*, 2006; Fleming *et al.* 2001; Fleming, Allen & Ballard, 2012). Some wildlife managers base field assessments on the strict definition of a dingo provided by Corbett (2001) which allows only animals with ginger coat colour to be pure dingoes. Elledge *et al.*

(2008) found that visual diagnosis of wild dingoes by trappers and wildlife managers based on their pelage characteristics was not consistent with diagnoses derived from genetic methods. Specifically, they found that their survey respondents only defined dingoes with ginger or black & tan coat colour as pure and that the ginger animals visually identified as pure were not the same individuals identified by skull morphology or genetic methods. This is concerning because it implies that visual assessment of ancestry by trappers and wildlife managers may not be accurate and that they may preferentially remove 'non-ginger' wild dingoes with unknown consequences for the genetic integrity of populations. Indeed, there is widespread appreciation that selective culling based on a specific phenotypic trait can influence the physical (and genetic) characteristics of wild populations in unknown ways (Harris, Wall & Allendorf 2002; Garel *et al.*, 2007).

Another consideration is that some coat colour patterns may have introgressed into the dingo population through hybridization but have been maintained as they are neutral or confer some selective advantage. In wolves (*Canis lupus*), the black coat colouration introgressed from domestic dogs approximately 1500–7200 years BP (Anderson *et al.*, 2009; Schweizer *et al.*, 2018). It is believed that once it entered the wolf gene pool, the associated genetic regions conferred some advantage, in the form of increased immunity, leading to its rapid spread throughout the North America wolf population (Schweizer *et al.*, 2018). It is important to note here that black wolves are still considered to be wolves not wolf-dog hybrids. This raises the question of whether coat colour is an effective and useful tool for field assessment of dingoes in Australia, particularly if coat colours might reflect historical introgression.

Here we present coat colour and DNA purity assessment of 1325 wild canids from New South Wales and Victoria. We use these data to examine the utility and accuracy of coat colour in field-based ancestry assessments of dingoes, particularly in southeastern Australia. These data also provide further knowledge about the genetic and physical identity of dingoes in Australia.

Materials and methods

Dingo samples

We obtained tissue samples from wild canids killed or trapped through routine 'wild dog' management activities in New South Wales, The Australian Capital Territory and Victoria. DNA of these individuals was sampled through either blood, ear clips or buccal swabs. These samples were collected on public and private lands between 1998 and 2014 and were sent to UNSW (Alan N. Wilton and KMC) for a long-term research programme on the ancestry of wild canids in Australia. Upon arrival at UNSW, DNA was extracted using Qia-gen DNeasy kits (Qiagen Sciences, Germantown, MD, USA) and samples were genotyped using a widely used DNA test for estimating admixture in dingoes (Wilton, Steward & Zafiris, 1999; Wilton, 2001; Elledge *et al.*, 2008; Stephens *et al.*, 2015; Cairns *et al.*, 2019). The 23 microsatellites genotyped are distributed across the genome (Fig. 2). The data



FIGURE 1 A selection of photographs of wild dingoes from Kosciuszko National Park in southeastern Australia. Examples of sable (a), ginger (b), black & tan (c), brindle (d) and patchy (e) coat colour patterns are evident. See Table 1 for a detailed description of coat colour patterns. Photographs courtesy of Michele J Photography, Cooma NSW.

used in this study come from a large database of ancestry estimates and biological data from over 4000 wild and captive dingoes across Australia.

For the purpose of this study, we identified wild samples which had coat colour information recorded, this resulted in 1325 samples with raw genotype data from more than 14 microsatellites (out of the total 23) and coat colour information (Table S1). We restricted the samples to southeastern Australia as this is where a majority of the dingo samples came from and we did not wish to introduce geographic bias which may be present between southeastern and northwestern dingo populations (Cairns & Wilton, 2016; Cairns *et al.*, 2017; Cairns *et al.*, 2018).

Ancestry analysis

We carried out ancestry estimation using the STRUCTURE method as per Cairns *et al.* (2019). Briefly, simulations were run in STRUCTURE v2.3.4 (Pritchard, Stephens & Donnelly,

2000; Falush, Stephens & Pritchard, 2003) using the 1325 wild canids and a set of pre-defined reference populations. We used the extended reference population with 50 dingoes and 66 dogs to allow for geographic variation in ancestry estimates from Cairns *et al.* (2019). The dog reference population contains mixed breed dogs to provide a genetically diverse domestic dog population compared to dingoes, with the knowledge that dingoes form a distinct evolutionary lineage compared to domestic dogs (Cairns *et al.*, 2018).

Analyses were run in STRUCTURE (Pritchard, Stephens & Donnelly, 2000; Falush, Stephens & Pritchard, 2003) with the admixture and correlated allele frequency models, default settings for alpha were used. As $K = 2$ was identified as the most appropriate K for these data (Stephens *et al.*, 2015; Cairns *et al.*, 2019), we ran simulations for only $K = 2$ for 200 000 iterations with a 20 000 iteration burn-in period, and 10 replicates were performed. All simulations were run with the USE-POPFLAG on. CLUMPAK was used to average individual q values across the 10 replicates (Kopelman *et al.*, 2015). We

TABLE 1 Description of commonly observed dingo (*Canis dingo*) coat colour patterns

Coat Colour Pattern	Description
Ginger	A solid red coat varying in shade from deep red to sandy yellow to warm cream. Occasional interspersed black hairs present on muzzle which may be dark in juvenile and pale out to grey by puberty; and sometimes appear on sides of neck and shoulder region or top of tail. Often present are white markings particularly on the chest, feet, legs and tail tip. Often, the colouration is lighter on the underbelly. Undercoat where present varies from white to grey. The tail may exhibit cream and/ or agouti undercoat. Eyes dark.
White	A solid whitish or pale cream coat with no black pigment throughout. Can also exhibit white spotting on chest, neck, digits and extremities. Eye rims remain pigmented. Nose can pale to liver colour in winter. Undercoat when present is white. Iris pigment remains dark.
Black & tan	A solid black coat with tan points, brow pips, muzzle, cheek spots, chest, belly, feet and legs. Lighter underbelly. The markings may vary from deep tan to cream, also with white spotting at extremities. The undercoat, if present, is pale cream or grey. The tail may show both cream and grey undercoat. Eyes dark brown.
Black	A solid black coat. May be white markings particularly on the chest, feet, legs and tail tip. The undercoat when present is dark grey. Eyes dark.
Sable	A ginger to cream base coat with dark juvenile muzzle, greying to adult form. Black tipped hairs spreading from the midline and interspersing down shoulder area and along upper line of tail. White extremities, tail tip and chest markings. feet, etc. In some cases, the coat colour may appear almost dark grey or there may be a distinct saddle pattern along the back. Underbelly lighter in colour. Undercoat may be white, cream or greyish. Eyes dark brown.
Brindle	A coat pattern with ginger background and irregular dark banding across midline spreading down sides of body and legs. May also exhibit white extremities and chest markings. Undercoat where present may be white or cream. Eyes dark.
Patchy (parti colour)	A basic ginger or sandy or black and tan base coat pattern broken with extensive white markings, forming patches. The white markings may run together and be so extensive as to leave only small areas of ginger or black ie on the body or head, or form a white-collar pattern. White extremities and tail tip. Undercoat where present is white. Eyes dark brown.

then assigned individuals to categories based on their average *q* value representing dingo ancestry (Cairns *et al.*, 2019).

Pelage variation in wild canids

Coat colour descriptions provided by sample collectors on submission were categorized into the following fields: ginger, white, sable, black & tan (or white) points, brindle, patchy and black. Analysis was carried out in SPSS v26 (IBM, Armonk, NY) and R v3.6.2 (R Development Core Team, 2010) with packages ‘*graphics*’ and ‘*corrplot*’ using the dataset of 1325 animals with records for coat colour and genetic ancestry estimates. For statistical analyses, we categorized the animals as follows: dingoes with only dingo ancestry, that is pure dingoes (*q* value > 0.8); dingoes with greater than 75% ancestry (*q* value between 0.7 and 0.79) and dingoes with 75–50% ancestry (*q* value between 0.5–0.69) based on Cairns *et al.* (2019) and Stephens *et al.* (2015). First, we summarized observed coat colour between the three categories of dingoes in SPSS v26. Then, in R v3.6.2, we performed Pearson’s chi-squared tests of independence to compare coat colours between dingoes and dingoes with varying degrees of dog ancestry. We calculated adjusted standardized residuals (ASR’s) from the contingency table to investigate where differences in coat colour

were observed. ASR’s of greater than 2 or less than –2 indicate departure from the null hypothesis.

Results

Ancestry analysis

According to the STRUCTURE simulations using extended Wilton dingo and dog reference populations, 27.4 % of the 1325 samples were classified as having only dingo ancestry or were likely to only have dingo ancestry (*q* value > 0.8). 40.3 % of samples were admixed dingoes with greater than 75% dingo ancestry (*q* value 0.7–0.79) and 32.3 % of samples were dingoes with between 50 and 75% dingo ancestry (Fig. 3, Figure S1, Table S1). There were only 5 feral domestic dogs (0.4%) and 15 feral domestic dog hybrids with less than 50% dingo ancestry (1.1%) out of 1325 wild dingo samples; they were removed from subsequent analyses due to the small sample size (Fig. 3, Figure S1, Table S1).

Pelage variation in wild canids

Dingoes in our sample set displayed a variety of coat colours (Table 2, Table S1). Across our 1305 dingo samples, we

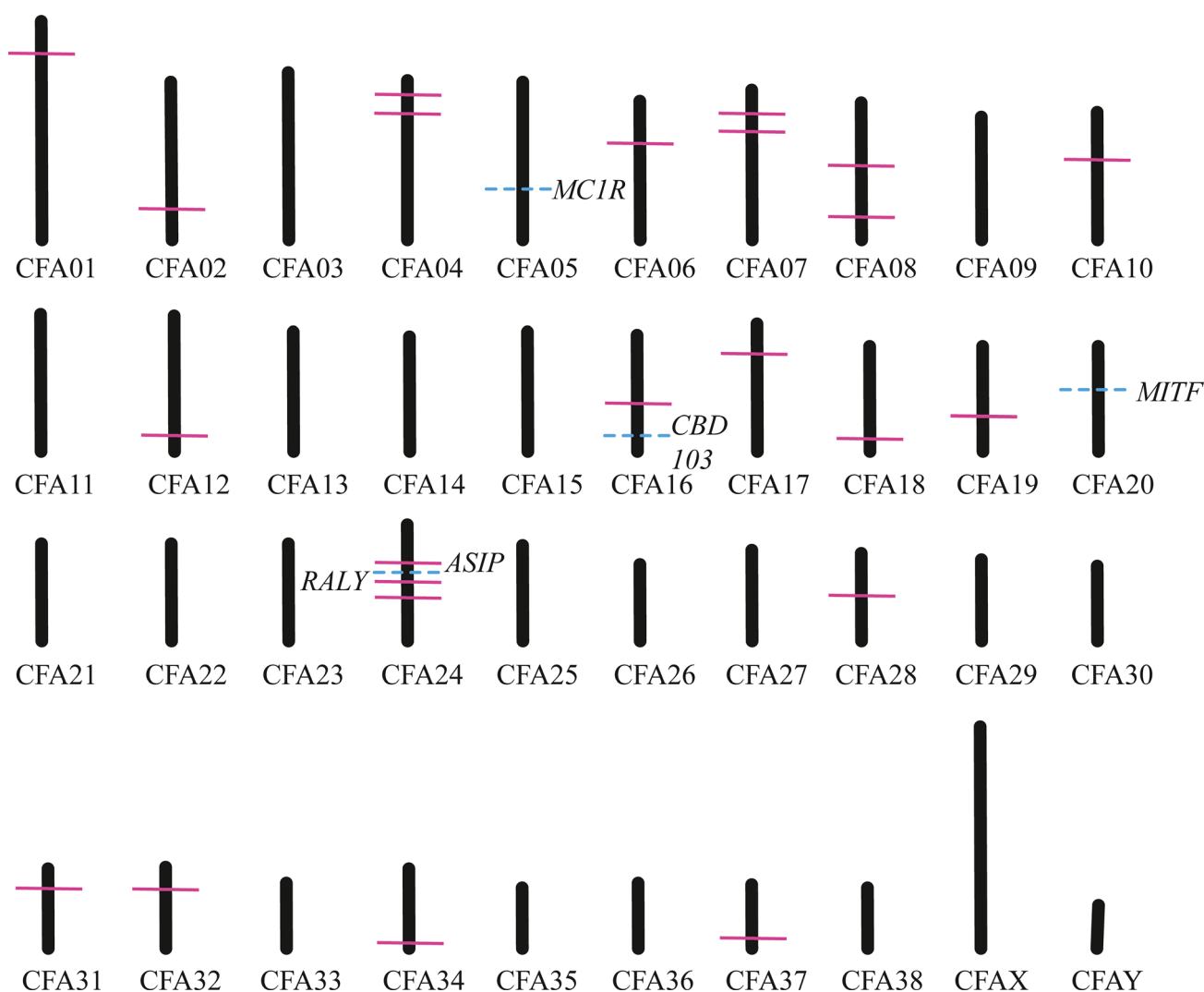


FIGURE 2 Chromosome and relative position of the 23 microsatellite markers used in dingo DNA ancestry testing and the coat colour genes *ASIP*, *RALY*, *MITF*, *MC1R* and *CBD103* which are responsible for coat colour variation in canines

observed the following coat colours: 53.5% ginger, 10.7% black & tan, 5.5% black, 1.4% white, 13.9% brindle, 8.9% sable and 6.2% patchy (Table 2). All of the coat colours were observed in dingoes and dingoes with varying degrees of dog ancestry (Fig. 4). Comparing the proportion of colours observed in dingoes (q value > 0.8), dingoes with greater than 75% dingo ancestry (q value 0.7 – 0.79) and dingoes with between 50 and 75% dingo ancestry (q value 0.5 – 0.69), we observe that ginger is the most common colour of all dingoes (Fig. 4). We observed feral dogs with ginger, black & tan and sable coat colours (Table 3).

There are significant associations between coat colours and their genetic ancestry ($\chi^2 = 58.052$, d.f. = 12, P -value < 0.001). We used ASR's to identify where the differences in coat colour between dingo categories occurred (Table 4, Fig. 5). There was a strong positive association

between pure dingoes and the colour brindle (ASR = 3.31) and a strong negative association between pure dingoes and the colour black (ASR = -2.42). There was a weakly negative association between pure dingoes and the colour black & tan (ASR = -1.96). There was a strong positive association between 50 and 75% dingoes and the coat colours black (ASR = 2.24) or black & tan (ASR = 2.56), but a very strong negative association with the coat colours brindle (ASR = -3.19 ; Fig. 5). There was a weak negative association between 50–75% dingoes and the colours patchy (ASR = -1.98) and White (ASR = -1.99). The strongest differences between dingo categories were based on the colours brindle, black and black & tan (Fig. 5). Dingoes with $> 75\%$ ancestry had no positive or negative associations with any of the pelage colours, indicating that they were not more or less likely to carry any of the coat colourations.

■ } Dingoes (Pure dingoes + >50%)
■ } Feral dogs (Dogs + <50% dingo)

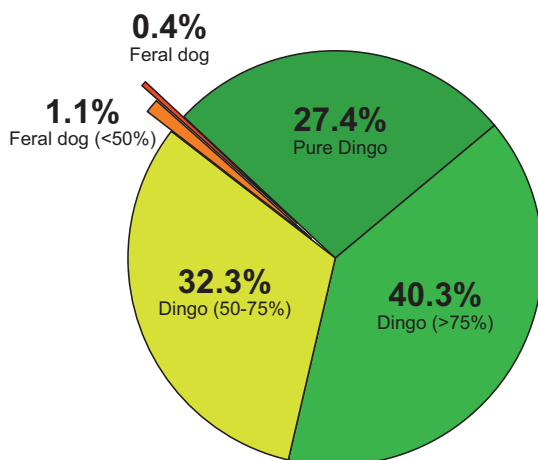


FIGURE 3 Pie chart depicting proportion of pure dingoes, dingoes with >75% ancestry, dingoes with 50-75% ancestry and feral dogs based on STRUCTURE analysis of 23 microsatellites.

Discussion

Coat colour is highly variable in wild dingoes across southeastern Australia (Newsome & Corbett, 1985; Corbett, 2001b) and our data show it is not a reliable measure of domestic dog introgression. We observed pure dingoes with coat colour patterns such as brindle and patchy (Fig. 4), colours often asserted as being observed only in dingo-dog hybrids or dogs (Corbett, 2001b; Elledge *et al.*, 2006; Fleming *et al.* 2001; Smith, 2015). There were differences in the proportion of coat colour patterns between pure dingoes, dingoes with low levels of dog ancestry and dingoes with moderate dog ancestry (Fig. 4). However, there was no coat colour that could be used to distinguish between pure dingoes and those with dog introgression (Fig. 4). Therefore, we caution wildlife managers and conservation organizations against using coat colour to assess dog introgression in dingo populations.

Our findings indicate there are some differences in the frequency of coat colours between pure dingoes and those carrying dog ancestry (Figs. 4 and 5, Table 4). For example, whilst white coat colour was observed in pure dingoes and those with >75% dingo ancestry, it was very rare in dingoes with 50-75% dingo ancestry. Surprisingly, patchy coat colour was most commonly observed in pure or high ancestry dingoes (Fig. 4),

TABLE 2 Ancestry estimates of 1325 wild canids (*Canis dingo* or *Canis familiaris*) in southeastern Australia from STRUCTURE modelling of 23 microsatellites

Ancestry	Structure q value range	Number of individuals (n)	Percentage
Dingo	0.8–1.0	358	27.4
Dingo with >75% dingo ancestry	0.7–0.79	526	40.3
Dingo with 50-75% dingo ancestry	0.5–0.69	421	32.3
Feral dog with < 50% dingo ancestry	0.25–0.49	15	1.1
Feral dog with no dingo ancestry	–0.24	5	0.4

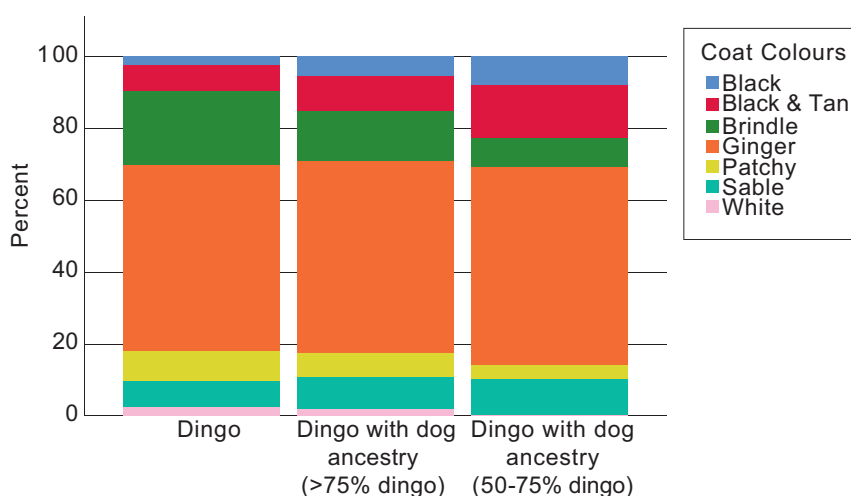


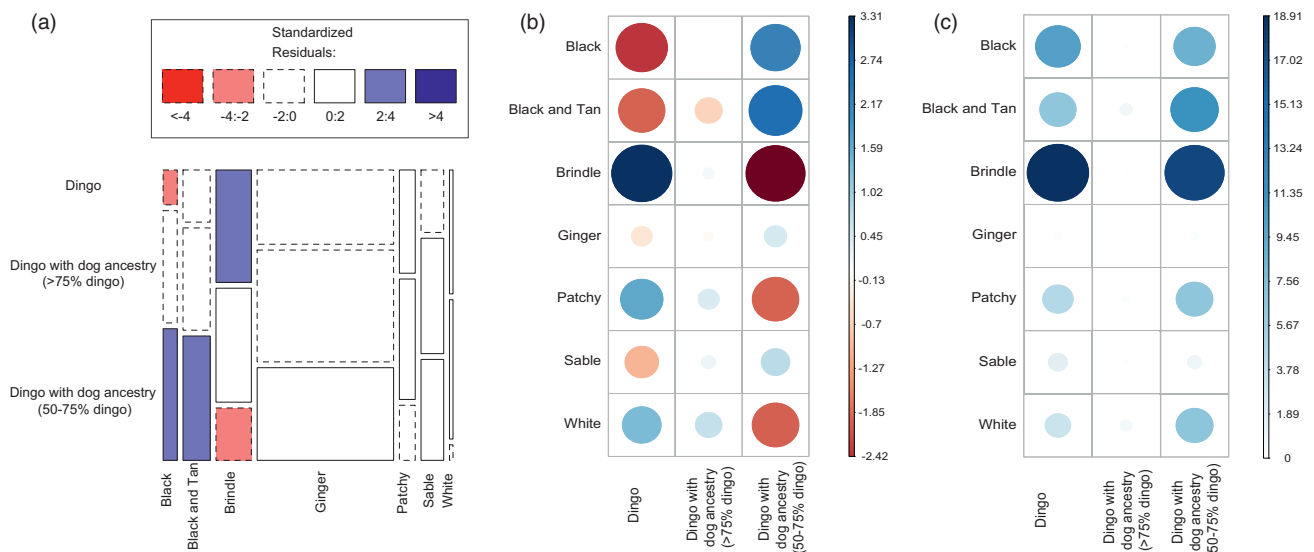
FIGURE 4 Observed coat colour patterns in 1305 dingoes, dingoes with >75% ancestry and dingoes with 50-75% ancestry.

TABLE 3 Observed coat colours of feral dogs (*Canis familiaris*) in southeastern Australia across different categories of ancestry and total observed proportion of coat colours across dataset

	Feral dog hybrid (n)	Feral dog (n)	All feral dog categories (%)
Black	0	1	5.3
Black & tan	3	0	15.8
Brindle	0	0	0.0
Ginger	10	2	63.2
Patchy	0	0	0.0
Sable	1	2	15.8
White	0	0	0.0

TABLE 4 Observed coat colours of dingoes (*Canis dingo*) in southeastern Australia across different categories of ancestry and total observed proportion of coat colours across dataset

	Dingo (n)	Dingo >75% (n)	Dingo 50–75% (n)	All dingo categories (%)
Black	9	29	34	5.5
Black & tan	26	51	62	10.7
Brindle	73	74	34	13.9
Ginger	186	280	232	53.5
Patchy	30	35	16	6.2
Sable	26	48	42	8.9
White	8	9	1	1.4

**FIGURE 5** Adjusted standardized residual (ASR's) analyses of coat colour variation between dingoes, dingoes with > 75% ancestry and dingoes with 50–75% ancestry. (a) Mosaic plot of ASR results, values of greater than 2 or less than –2 indicate departure from the null hypothesis. The size of tiles reflects the sample size (n) within each category. (b) ASR correlation plot to investigate positive and negative associations between rows and columns in the contingency analysis with positive values as blue circles and negative values as red circles. (c) ASR contribution plot indicating the relative contribution of each cell to the contingency table analysis.

contradicting the widespread belief that animals with patchy coats are likely to be hybrids (Corbett, 2001b; Elledge *et al.*, 2006, Fleming *et al.* 2001; Newsome & Corbett, 1985).

Brindle, a coat colour, commonly cited to be a result of dog hybridization (Corbett, 2001b; Elledge *et al.*, 2006; Fleming *et al.* 2001), was strongly associated with pure dingoes and

negatively associated with dingoes carrying 25–50% dog ancestry (Fig. 5). This suggests that brindle colouration is not informative for distinguishing dingoes with or without dog introgression. Whilst black or black & tan colours were positively associated with lower ancestry dingoes (20–25% dog ancestry, Fig. 5), the black & tan colour pattern is well established as being an ancestral dingo colour, limiting the utility of this result for wildlife managers. Sable was observed relatively evenly between pure dingoes and those carrying dog ancestry, suggesting limited association with hybridization (Fig. 4). These data are consistent with observation of sable colouration in contemporary pure dingo populations (Tatler *et al.*, 2021) as well as historical pelt collections (Crowther *et al.*, 2014), suggesting that sable colouration be considered an ancestral colour variation and challenging its use as an indicator of domestic dog introgression. The findings of this study challenge the widespread understanding that coat colour can be used to identify hybrids (Corbett, 2001b; Elledge *et al.*, 2006; Fleming *et al.* 2001, Newsome & Corbett, 1985). Indeed, some coat colours commonly believed to be ‘hybrid’ colours were more commonly observed in pure or high ancestry dingoes.

The most common colour for both dingoes and dingo hybrids in our sample was ginger (ranging from cream to sandy and red), consistent with observations of dingoes across Australia (Newsome *et al.*, 2013; Tatler *et al.*, 2021; Newsome & Corbett, 1985; Fleming *et al.* 2001; Corbett, 2001b). Approximately 53% of the population exhibited this colouration, irrespective of ancestry (Table 2, Figure 4). This finding is consistent with observational studies of the frequency of pelage colouration in southeastern Australia. However, in northern, western and central Australia 70–90% of the population have ginger colouration (Newsome & Corbett, 1985; Corbett, 2001b). Previous authors have commented that the greater range of phenotypic variation in dingoes from southeastern Australia was a result of higher levels of domestic dog hybridization (Corbett, 2001b; Fleming *et al.* 2001; Newsome & Corbett, 1985). However, recent genomic studies have demonstrated that there are multiple evolutionary lineages of dingo which are geographically subdivided (Cairns & Wilton, 2016; Cairns *et al.*, 2017). Thus, it is possible that the south-eastern and northwestern lineages have different phenotypic appearances unrelated to hybridization.

It is plausible that some coat colour patterns such as brindle and patchy have originated from dingo-dog hybridization, and that subsequent backcrossing has spread these colours into the dingo population with little remnant dog ancestry remaining. It is also possible that coat colour variation in dingoes has some adaptive potential. For example, introgression from Black-tailed jackrabbits (*Lepus californicus*) into Snowshoe hares (*Lepus americanus*) has led to adaptive variation in winter-moult colours in areas with low snow cover (Jones *et al.*, 2018). Black coat colour in North American wolves is the result of introgression from early American dogs approximately 1500–7200 years ago (Anderson *et al.*, 2009; Schweizer *et al.*, 2018). Schweizer *et al.* (2018) found that the melanistic coat colour spread widely through the wolf population in a selective sweep, because surrounding genomic regions conferred enhanced immunity. Strikingly, the same gene (*CBD103*) is

responsible for solid black and brindle colouration (Kerns *et al.*, 2007; Dreger *et al.*, 2019), plausibly the appearance of brindle coat colour in dingoes may have some adaptive benefit which warrants further investigation with genome-wide data.

Whilst it is possible that ‘non-typical’ colours such as brindle, patchy and sable are the result of introgression from dogs into the dingo population, it is also possible that these colours are ancestral to dingoes but were poorly described by early European explorers. There are few historical records describing dingo colours and those that exist, use only basic descriptors such as ‘yellow-dog’ (Abbott, 2008), ‘red with some white about it’ (Collins, 1798) or ‘black native dog’ (Mitchell, 1839). A synthesis of museum records and historical accounts of coat colour in dingoes suggest that at the time of European arrival, dingoes were predominately ginger, sable, black and tan, white or black (Jones, 1921; Macintosh, 1956; Macintosh, 1975; Elledge *et al.*, 2006; Abbott, 2008; Crowther *et al.*, 2014); however, this cannot exclude the possibility that other colours were present.

The antiquity of other pelage colourations such as patchy and brindle is unclear. Macintosh recorded coat colour variation across much of Australia and observed that it was highly variable with some regional differences (Macintosh, 1956; Barker & Macintosh, 1979). There have been no verified reports of brindle or patchy coat colour dingoes by early explorers, implying these may not be ancestral (Troughton, 1958; Barker & Macintosh, 1979; Newsome & Corbett, 1985; Crowther *et al.*, 2014). More detailed genetic data such as whole genome sequencing or interrogation of archaeological remains will be needed to identify the antiquity these pelage patterns in dingoes. Nevertheless, Newsome & Corbett (1985) reported that $\pm 9\%$ of their morphologically identified pure dingo samples from southeastern Australia were brindle, suggesting that its occurrence in wild dingoes has been relatively stable over the last 60 years and its prevalence is unlikely to be the result of contemporary dingo-dog introgression. The origin of patchy coat colour may be more complicated. Dingoes are often characterized as having white points such as white feet, socks, toes and/or tail tips (Corbett, 2001b; Elledge *et al.*, 2006; Fleming *et al.* 2001) and genomically these markings are controlled by the *MITF* gene (Schmutz, Berryere & Dreger, 2009). According to Chew *et al.* (2019), some dingoes may carry a *MITF* genotype predictive of extreme white or piebald markings. Intriguingly, Macintosh (1956) observed that patchy coat colour (ginger with white patches and/or collars; Fig. 6) arose after multiple generations of inbreeding in a captive bred colony. It is possible that the extent of white markings in dingoes is controlled by *MITF*, a co-dominant inheritance pattern and an unknown modifier gene (Karlsson *et al.*, 2007; Baranowska Körberg *et al.*, 2014; Chew *et al.*, 2019), manifesting in dingoes carrying a range of phenotypes between solid ginger with white points and patchy (Figs. 1 and 6). This might explain the appearance of excessive white markings in some dingoes without the presence of dog introgression. Future research should aim to use whole genome or genome-wide SNP data to investigate the timing, genomic mechanisms and possible origin of patchy and brindle coat colours in dingoes.



FIGURE 6 A photograph of NWG Macintosh with a patchy dingo from his breeding colony at University of Sydney. This individual was an offspring after multiple generations of inbreeding from the original wild ginger parents. Photo courtesy of Shellshear Museum, University of Sydney.

There has been ongoing debate about the genetic identity of dingoes and management of hybridization. In the wild, DNA testing demonstrates that most dingoes are pure or backcrosses with high levels of dingo ancestry and less than 1.1% of the population were estimated to be less than 50% dingo ancestry (Stephens *et al.*, 2015; Cairns *et al.*, 2019). Our data here depict a population where 27.4% are pure dingoes, 40.3% were >75% dingo and 32.3% were 50–75% dingo (Fig. 3, Table S1). We observed 15 feral dog hybrids with less than 50% dingo ancestry and only 5 feral domestic dogs within our dataset. Allen *et al.* (2017) suggest that a dingo should be considered pure if it is assessed as more than 93% dingo ancestry. Others suggest that strict genetic thresholds are not useful, particularly if mixed ancestry dingoes are morphologically and ecologically indistinguishable from pure dingoes (van Eeden *et al.*, 2018; Cairns *et al.*, 2019). Indeed, tolerance of dingoes with a small portion of dog genes (ie <25% dog ancestry) and maintenance of stable dingo packs may limit future dingo-dog hybridization, but this would require cessation of landscape level aerial and ground baiting programmes (Miller, Adams & Waits, 2003; Elledge *et al.*, 2008; Cairns *et al.*, 2019).

Genetic monitoring is useful for wildlife managers to observe patterns of introgression across the landscape and time, but as genetic estimates are not real-time DNA testing currently has limited utility to individual culling decisions. It is also important for end-users of DNA testing to consider the

accuracy and reliability of ancestry estimates, for example microsatellite testing may only be able to identify dog hybridization within 4 generations (Cairns, Wilton & Ballard 2011). Data presented here indicate that coat colour also has limited utility in field assessment of wild dingoes and may lead wildlife managers to cull high ancestry dingoes. Indeed, wildlife managers may be more likely to cull brindle dingoes rather than ginger dingoes (Fleming *et al.* 2001, Fleming, Allen & Ballard, 2012), but our data suggest that brindle colouration is more actually common in pure dingoes than hybrids (Figs. 4 and 5). Coat colour may appear to be an innocuous trait, but it could have adaptive potential in dingoes, as has been observed in wolves and other species (Hamilton & Miller, 2016; Schweizer *et al.*, 2018; Jones *et al.*, 2018).

As our knowledge about the occurrence of interspecific introgression and the adaptive potential of introgression increases, so too does debate about how introgression is managed in wild populations (Hamilton & Miller, 2016; Supple & Shapiro, 2018; vonHoldt *et al.*, 2018; Mable, 2019; vonHoldt & Aardema, 2020). In North America and Europe, there is ongoing discussion of how to manage and conserve canids despite the occurrence of admixture between wolves, red wolves (*Canis rufus*), coyotes (*Canis latrans*) and dogs (vonHoldt & Aardema, 2020, vonHoldt *et al.*, 2018, vonHoldt *et al.*, 2016, Donfrancesco *et al.* 2019, Hendricks *et al.*, 2019). There is an important balance in promoting the preservation of species genomic integrity, by limiting future introgression but this may not include ‘reversing’ introgression or removing introgressed individuals from a population (Toro, Villanueva & Fernández, 2014; vonHoldt & Aardema, 2020). In canids, ongoing research into recovery programmes has identified that introgression is facilitated by the disruption of social structures and low availability of conspecific mates (Bohling & Waits, 2015; Bohling *et al.*, 2016). This is why many scientists are now arguing against intensive suppression of dingo populations (Wallach *et al.*, 2009; van Eeden *et al.*, 2018; Cairns *et al.*, 2019), which likely increases the risk of dingo-dog matings. We now add that wildlife managers, conservation organizations and the public should not rely upon coat colour to assess the ancestry of dingoes or other wild canids.

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Conflict of interest

KMC is a scientific advisor to the Australian Dingo Foundation, New Guinea Highland Wild Dog Foundation and New Guinea Singing Dog Conservation Society. KDN is a volunteer at the Australian Dingo Foundation. No other interests declared.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Fig S1. Ancestry coefficient estimates of 1325 wild dingoes collected across southeastern Australia according to STRUCTURE analysis of 23 microsatellites. The dingo reference population (Dingo ref) contains 50 animals and the dog reference population (Dog ref) includes 66 animals.

Table S1. Table of 1325 wild canid samples with coat colour and STRUCTURE modelling ancestry estimate.