



# Phenotypic variation and promiscuity in a wild population of pure dingoes (*Canis dingo*)

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## Abstract

Phenotypic diversity occurs in natural populations as a result of the interaction between an individual's genotype and the environment. Nevertheless, individual variation in phenotypic traits such as coat colour and body size is routinely used to differentiate between “pure” dingoes *Canis dingo* and dingo-dog hybrids. Extensive anthropogenic impacts and widespread hybridization with domestic dogs has hindered our ability to study intact dingo populations and, therefore, most of our basic understanding of dingo biology (e.g., phenotypic variation, mating systems, genetic diversity) stems from observational studies on perturbed populations. We sampled a relatively undisturbed population of dingoes, from arid Australia, to determine their purity and genetic diversity. We explored their mating strategy using a pedigree built from genetic data and examined how phenotypic variation was influenced by age, sex, heterozygosity, and relatedness. Coat colour was our measure of phenotype and our population displayed four types (sandy, black & tan, white, and sable). All dingoes ( $n = 83$ ) possessed a high level of dingo ancestry (mean purity > 90%) and were closely related to each other; with all but one individual related as full-sibling or parent-offspring. Our pedigree shows both monogamous and promiscuous mating strategies exist within an undisturbed population. Variation in coat colour or body size cannot be used to infer a dingo's level of purity because the phenotype of pure dingoes is intrinsically variable. The breeding system of dingoes was long thought to be monogamous, but we provide genetic evidence for numerous mating strategies including both long-term monogamy and extreme promiscuity.

## KEYWORDS

hybridization, monogamy, phenotypic variation, promiscuity, relatedness

## 1 | INTRODUCTION

Phenotypic diversity occurs in all sexually reproducing natural populations, and is one of the basic tenets of evolution by natural selection (Fisher, 1958). Intraspecific variation in phenotypic traits

such as pelage and body size is a result of the interaction between genotype and environment and is therefore predicted to vary within and between populations throughout time and space. Phenotypic differences within a population are considered important for generating variation in individual attributes such as habitat preference,

competitive ability, anti-predator defense, parasite load, and diet (Bolnick et al., 2003; Hayes & Jenkins, 1997; Lankau & Strauss, 2007). Although strong ecological effects of phenotypic variation have been identified, few broad commonalities have emerged (Bolnick et al., 2011).

Admixture between wild and domestic animals is largely viewed as a detrimental process because it threatens the long-term persistence of wild species, and can contribute to population and species extinction (Levin, Francisco-Ortega, & Jansen, 1996; Rhymer & Simberloff, 1996). In addition to genetic assimilation, hybridization can result in a different set of phenotypes that alter the functional role of a species (Stronen et al., 2012). In north-eastern North America, the larger body size of coyotes (*Canis latrans* Say 1823) is a product of their historical hybridization with eastern wolves (*Canis lupus lycaon* Schreber, 1775), enabling them to hunt larger prey species than their western counterparts and occupy a different ecological niche (Benson & Patterson, 2013). There are a number of examples of human-facilitated hybridization around the world, with domestic dogs *Canis familiaris* Linnaeus, 1758 the primary threat to wild canids (e.g., Gottelli et al., 1994; Randi & Lucchini, 2002). Australia's only wild canid, the dingo *Canis dingo* Meyer, 1793, arrived from Asia c. 4,000 years ago and was once distributed across the entire continent (Balme, O'Connor, & Fallon, 2018; Fillios & Taçon, 2016). Since European arrival, however, rapid and widespread hybridization with domestic dogs has resulted in only the most remote parts of central Australia containing pure dingo populations (Stephens, Wilton, Fleming, & Berry, 2015).

Dingoes are medium-sized generalist predators and one of Australia's most provocative species. They hold considerable cultural significance to indigenous Australians, represented in their Dreaming narratives and prehistoric art (Cahir & Clark, 2013). More recently, European colonization introduced extensive pastoralism, which relegated dingoes to a pest species (Fleming, Corbett, Harden, & Thomson, 2001). Nevertheless, dingoes are an apex predator and maintain a functional role in a variety of ecosystems (e.g., Johnson & VanDerWal, 2009; Letnic & Koch, 2010). Dingoes are the closest extant relative of gray wolves *Canis lupus* and an ancient, phylogenetically distinct breed of domestic dog (Crowther, Fillios, Colman, & Letnic, 2014; Savolainen, Leitner, Wilton, Matisoo-Smith, & Lundeberg, 2004). However, their genetic and phenotypic similarity to domestic dogs perpetuates their uncertain taxonomic position, which in turn promotes discordance around their conservation status and management in Australia.

Introduced to northern Australia by Australasian seafarers, dingoes spread rapidly throughout the continent and soon occupied a broad variety of ecosystems from alpine habitat to tropical rainforests and arid deserts (Fleming et al., 2001). Environmental gradients across their distribution are reflected by their phenotypic variation, with substantial intra and inter-population differences in body size (mean weight varies from 13 to 19 kg; Allen & Leung, 2014), coat colour (e.g., sandy, white, black and tan; Fleming et al., 2001), social

behavior (e.g., pack sizes from 2 to 23; Thomson, 1992b), and breeding systems (e.g., monogamy; Thomson, 1992a). Indeed it is this natural individual variation that can be mistaken for hybridization and promotes the stereotypical view that pure dingoes display a certain set of phenotypic traits (i.e., sandy coat with white tips to tail and feet), despite several studies reporting otherwise (Corbett, 1995; Newsome & Corbett, 1985; Newsome, Stephens, Ballard, Dickman, & Fleming, 2013). Inability to distinguish dingoes and their hybrids based on phenotype alone has created the need for genetic approaches to test purity (Banks, Horsup, Wilton, & Taylor, 2003; Stephens, 2011).

The social behavior of dingoes differs from other canids in that it is driven by the availability of resources, and therefore can be highly variable between populations (Corbett & Newsome, 1987; Thomson, 1992b). When there is a surplus of food (e.g., anthropogenic resource subsidies) dingoes can form large social groups of related individuals (Newsome et al., 2013; Thomson, 1992b), or when only smaller sized prey are available their group size decreases (Newsome, Catling, & Corbett, 1983; Robertshaw & Harden, 1985). Interactions between conspecifics are also influenced by relatedness, with several studies reporting a hierarchical social system dominated by a breeding pair, not unlike wolves and coyotes (Moehlman, 1989; Thomson, 1992b; Thomson, Rose, & Kok, 1992). Although the mating system of wild dingoes is not well understood, ecological inference from observational studies indicates that they are cooperative breeders, where a monogamous breeding pair is supported by related individuals, which are often their young (Asa & Valdespino, 1998; Thomson, 1992a). However, a number of studies on captive and wild dingoes suggest subordinate dingoes can also produce offspring and therefore their mating system may not be strictly monogamous (Catling, Corbett, & Newsome, 1992; Corbett, 1988; Newsome et al., 2013).

Pervasive human impacts and widespread hybridization have created few, if any, regions in Australia where populations of pure dingoes persist without disturbance. Despite advances in our understanding of dingo ecology and genetics, there is little information on free-ranging dingoes beyond the influence of anthropogenic disturbance (i.e., lethal control, pastoralism, resource subsidies). Here, we sampled a relatively undisturbed population of dingoes from arid central Australia to determine their purity and genetic diversity. We used genetic data to build pedigrees in order to explore their mating strategy, and examined phenotypic variation from direct observations. Given the history of low anthropogenic disturbance in remote central Australia, and apparent lack of feral dogs in the study area, we predicted that the population of dingoes would display a high level of purity. We expected coat color to be variable and unrelated to purity. We were also interested in whether genetic diversity explained differences in coat color. We expected our genetic pedigree to reveal a high level of monogamy given the population was likely to exhibit a stable social structure. This study presents an exceptional opportunity to investigate the biology of a remote, unperturbed population of dingoes.

## 2 | MATERIALS AND METHODS

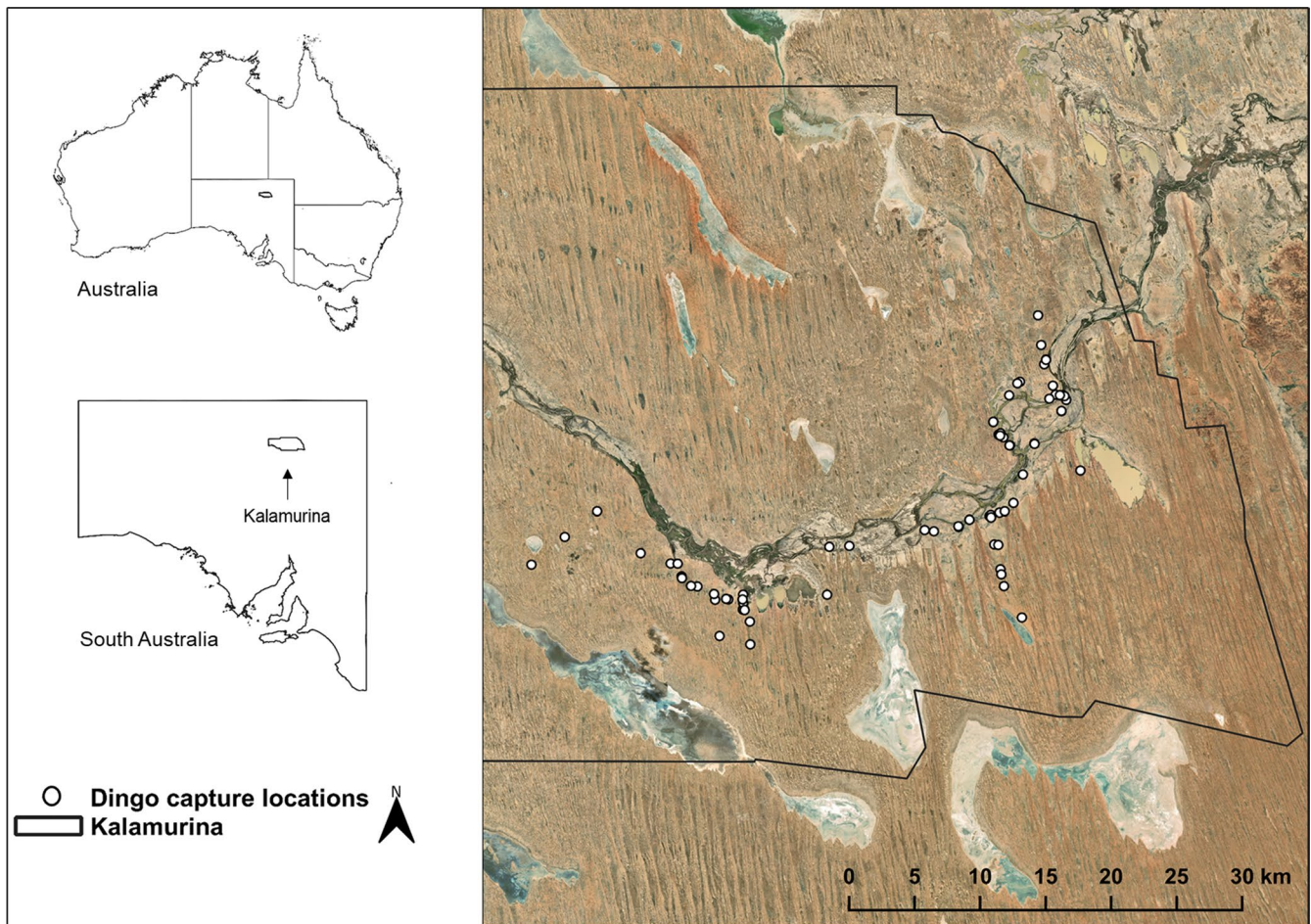
DNA from 84 samples was amplified at 23 microsatellite markers to obtain a unique DNA fingerprint, which was then examined for the likelihood that it had come from a dingo or a domestic dog ancestor using the computer program STRUCTURE v2.3.4 (Pritchard, Stephens, & Donnelly, 2000). For relatedness testing, we amplified our DNA samples at an additional 11 microsatellite markers ( $n = 34$ ).

### 2.1 | Study area

The study was conducted between April 2016 and May 2018 at Kalamurina, a 6,670 km<sup>2</sup> wildlife sanctuary situated between the north shore of Kati Thanda-Lake Eyre and the southern boundary of the Simpson Desert Regional Reserve, South Australia (27°48'S, 137°40'E; Figure 1). Kalamurina lies at the intersection of three of Australia's central deserts: the Simpson, Tirari, and Sturts Stony Desert. The site adjoins protected areas to the north and south to create a 64,064 km<sup>2</sup> contiguous area that is managed for conservation. The site has a short history of low grazing

pressure and sporadic dingo control, which ceased in 2007 when it was purchased by the Australian Wildlife Conservancy (AWC). Destocking and regular control of introduced species (e.g., camels, feral cats) by AWC, coupled with the re-establishment of natural hydrological processes, has restored much of the landscape. Neighboring properties to the east and west operated as cattle stations during the study.

The region's climate is arid, characterized by very hot summers and mild winters; mean temperatures ranging from 23.1° to 37.9°C in the hottest month (January) and 5.9° to 19.7°C in the coldest month (July; BOM, 2017). Kalamurina is one of the driest areas in the country with a median annual rainfall of 133.5 mm (BOM, 2017). It is located in the Simpson-Strzelecki Dunes Bioregion and the dominant landform is sand dunes (<18 m), with scattered dryland river floodplains, claypans, and salt lakes. The dune crests and flanks are dominated by Sandhill Canegrass (*Zygochloa paradoxa*) with an overstorey of scattered shrubs including species of *Acacia* and *Hakea*. The dune swales are characterized by Chenopod shrubland where the main vegetation are species of *Acacia*, *Eremophila*, and *Atriplex*. Extensive coolabah (*Eucalyptus coolabah*) woodlands exist along the banks and floodplains of the larger watercourses.



**FIGURE 1** Location of study site in central Australia and where dingoes were sampled during this study, from 2016–2018 ( $n = 84$ ). White dots indicate the locations where dingoes were caught throughout the study and the black outline indicates the boundary of Kalamurina

## 2.2 | Trapping and handling of animals

Dingoes were captured using Victor Soft Catch® #3 leg-hold traps modified with Paws-I-Trip pans and a Jake Chain Rig (Professional Trapp Supplies, Molendinar, Queensland). These traps and modifications are designed to reduce the impact on the trapped limb (Meek, Jenkins, Morris, Ardler, & Hawksby, 1995). The majority of the study site is inaccessible and as such, all traps were set within close proximity (<20 m) to traversable tracks and checked twice daily within three hours of sunrise and sunset. Initially, captured dingoes were controlled using a ketch-all pole and then restrained on a holding board by straps across their waste, shoulders, and neck. Once secured, the ketch-all pole was released and the trap removed. We recorded capture location, weight (to the nearest 0.25 kg), age class, sex, coat color, identifying marks, and body condition. The age of each individual was approximated by examining their body size, tooth wear, and presence/ extent of gray fur. Dingoes were then categorized into four distinct age classes: sub-adult, young adult, adult, and older adult. Coat color was defined broadly as sandy (light yellow to orange), white, black and tan (combination of black, tan, and white), and sable (sandy with a dorsal strip of black-tipped hairs). Despite a positive correlation with weight, body condition provides a valuable assessment of general health (e.g., disease, parasite load, injuries). We scored dingoes between 1 and 5, with 1 indicating poor condition and 5 representing excellent. A small hair sample (<20 hairs with follicles attached) was taken for DNA analysis and kept refrigerated below 4°C. All methodology employed as part of this study were ethically reviewed and approved (University of Adelaide Animal Ethics Committee S-2015-177A).

## 2.3 | Genetic analyses

All laboratory analyses were performed by Helix Molecular Solutions (Perth, Western Australia). As per Stephens et al. (2015) analyses were run with a set of predefined reference samples incorporating 322 pure dingoes and 102 domestic dogs. Modelling was run with 200,000 iterations (20,000 burn in) and 10 replicates for  $K = 2$ . Modelling by Stephens et al. (2015) indicates that there is only moderate geographic structure within dingo populations based on these markers, although work on mitochondrial, Y-chromosome and SNPs suggest that there is strong geographic divergence between dingoes found in south-eastern Australia versus north-western Australia (Cairns, Brown, Sacks, & Ballard, 2017; Cairns, Shannon, Koler-Matznick, Ballard, & Boyko, 2018; Cairns & Wilton, 2016). This is not surprising, as the 23 ancestry markers were chosen to be variable between domestic dogs and dingoes, rather than variable between dingoes (Wilton, 2001). An overall percentage of dingo ancestry present in the sample is obtained from the mean of the 10 replicate STRUCTURE analyses for  $K = 2$ , with pure dingoes scoring > 90% and 80%–90% representing “probable” pure dingoes (Stephens et al., 2015). Purity scoring and STRUCTURE analyses were carried out by Zoological Genetics (Adelaide, South

Australia) to ensure that microsatellite genotyping was performed consistently and could be compared to the existing Stephens et al. (2015) dingo and dog reference populations.

Pairwise relatedness ( $r$ ) and corresponding p-values were calculated using the symmetrical Queller–Goodnight estimator (Queller & Goodnight, 1989) implemented in Kingroup version 2 (Konovalov, Manning, & Henshaw, 2004) for each pair of individuals. Expected relatedness for first-order relatives (parent–offspring or full siblings) is c. 0.5, but in practice may vary between 0.3 and 0.8 (e.g., Kaiser et al., 2019). Full-sibling reconstruction was performed using the descending ratio algorithm and samples were sorted into putative groups of first-order relatives (kin groups; Table 2). Parentage reconstruction was carried out using a likelihood-based parentage analysis in the software program Cervus 3.0.7 (Kalinowski, Taper, & Marshall, 2007). We used each individual's age at capture and capture date to differentiate the cohort into approximate generations before we defined our set of candidate parents and offspring. For example, older adult dingoes trapped in session 1 (April 2016) could only be considered as candidate parents and not offspring, whereas sub-adult dingoes trapped in session 5 (May 2018) could only be offspring and never a candidate parent. The simulated parameters were 10,000 simulated offspring, 38 candidate mothers, 46 candidate fathers, 80% of the candidate parents sampled, and allowing for genotyping error rate of 1%. We only report parentage assignments where Cervus identified confidence of 95% (Kalinowski et al., 2007; Marshall, Slate, Kruunk, & Pemberton, 2003); however, the presence of close relatives in the pool of candidate parents or inbreeding may have an influence on the confidence of parentage assignment (Jones & Ardern, 2003; Marshall et al., 2003). The outcome of pedigree analyses may differ based on the specific parameters employed, and we attempted to reduce any uncertainty by combining our observations of the population with the results from a methodological study conducted by Harrison, Saenz-Agudelo, Planes, Jones, and Berumen (2013).

## 2.4 | Statistical analyses

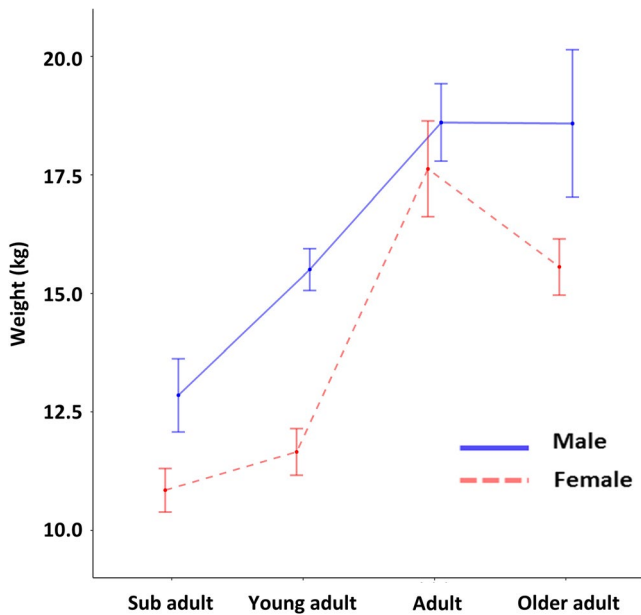
All statistical analyses were conducted in the R software environment for statistical and graphical computing (version 3.5.1; R Core Team, 2017). We tested the effect of age and sex on the weight of dingoes using a generalized linear model (GLM) with a Gaussian error distribution. We also analyzed the effect of age, coat color, sex and purity on the body condition score using a GLM with a Poisson error distribution. Finally, we used quasi-binomial GLMs to explore: (a) the effect of coat color, age, and sex on the purity (proportion of dingo ancestry) of dingoes, and (b) the relationship between coat color and genetic diversity ( $H_E$ ).

## 3 | RESULTS

Eighty-four individual dingoes (38 females and 46 males) were captured (one recapture) and released from five sampling sessions (c.

**TABLE 1** Number of dingoes sampled at Kalamurina displaying different coat colors. Mean weights (kg) and standard errors are presented for each age class and sex. Females and males and presented in brackets, respectively

	Sandy	Black & Tan	Sable	White	n	Mean Weight $\pm$ SE	
						Female	Male
Sub-adult	17 (11, 6)	3 (1, 2)	3 (1, 2)	0 (0, 0)	23 (13, 10)	11.0 $\pm$ 0.4	13.0 $\pm$ 0.6
Young adult	18 (5, 13)	4 (1, 3)	4 (2, 2)	0 (0, 0)	26 (8, 18)	11.5 $\pm$ 0.5	15.5 $\pm$ 0.5
Adult	14 (6, 8)	2 (1, 1)	0 (0, 0)	4 (1, 3)	20 (8, 12)	17.5 $\pm$ 1.0	18.5 $\pm$ 0.8
Older adult	12 (7, 5)	2 (1, 0)	2 (1, 1)	0 (0, 0)	15 (9, 6)	15.5 $\pm$ 0.6	18.5 $\pm$ 1.5



**FIGURE 2** Mean weights ( $\pm$ SE) of dingoes in each age class, separated by sex. Sample size = sub-adult male (10) and female (13), young adult male (18) and female (8), adult male (12) and female (8), and older adult male (6) and female (9)

700 traps nights) at Kalamurina, with one capture related mortality of an older adult incurred in our last session (Table S1). One other mortality was recorded three weeks after capture. There was a minor age bias with fewer older dingoes captured, though the sex ratio was mostly even (Table 1). Age had the biggest effect on the weight of dingoes with sub- and young adults weighing significantly less than adults (Figure 2). Young adult males weighed significantly more than young adult females (mean  $\pm$  se; males = 15.5  $\pm$  0.44 kg, females = 11.66  $\pm$  0.5 kg,  $p < .05$ ) and males weighed more than females in general, though it was not significant ( $\beta = 0.98$ ,  $p = .35$ ). Dingoes were in average condition (3.3  $\pm$  0.12) with the lowest scores consistently recorded by sub-adults. However, there was no significant relationship between body condition and age, sex, or coat color (Table S2). Some evidence for an age bias in coat color was evident with white coats only recorded in adults, whereas the sable coloration was never observed in adults. Dingoes with sandy coats were the most common regardless of age (73.5% of all individuals).

### 3.1 | Purity and relatedness

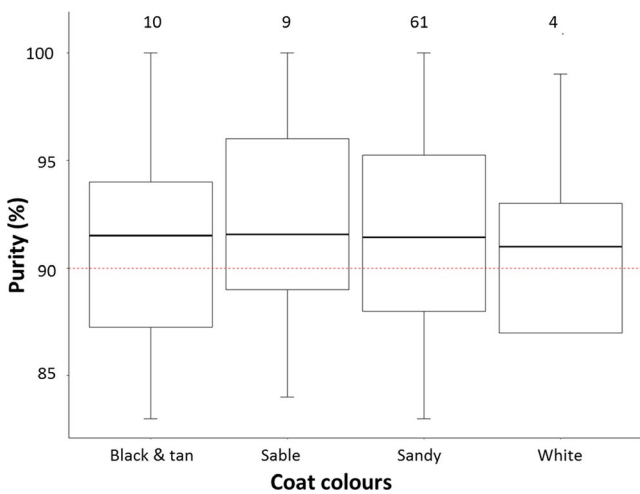
We obtained purity scores for 84 dingoes based on STRUCTURE analyses (Figure 3), one sample gave a spurious result (unlikely purity score) and was removed from subsequent analyses (leaving  $n = 83$ ). The mean purity of dingoes at Kalamurina was high (91.4%  $\pm$  0.5%; Figure 4) and it did not change based on the dingo's coat color (i.e., there was no relationship between purity and phenotypic variation; Figure 4). We also found no effect of sex, age, or weight on purity (Table S3). All 83 dingoes were closely related to at least one other, with only one individual yielding an  $r$  score  $< 0.2$  (i.e., it was a cousin or uncle, rather than a parent, offspring, or sibling; Table S4). We found 18 kin groups, the largest consisted of nine individuals and represented all age classes and both sexes (Table 2). Twenty-one individuals were not assigned to any kinship group. The maximum capture distance between first-order relatives was 32 km (mean = 12.3 km).

### 3.2 | Dingo pedigree and genetic diversity

Of the 74 successfully sequenced offspring both parents were identified with high confidence in 20 cases, and one parent for a further 23. This resulted in  $>70\%$  of our samples being placed in a predicted pedigree (Figure S1). We observed that six dams and three sires dominated our pedigree, identified as likely parents to 73% of all offspring with identified parents. We observed from our pedigree that the mating system for dingoes at Kalamurina was commonly promiscuous, with only one monogamous pair (JT320 & JT53) confidently identified. This monogamous pair produced offspring over at least three generations (Figure 5a), and all of their offspring were trapped within c. 4 km from each other. Conversely, many of the other breeding dingoes were identified as having mated with more than one individual across years. For example, one male (JT08, 25 kg) was identified as the parent of offspring from three different females in one breeding season, all of which were trapped within c. 6.5 km of each other six and 12 months later (Figure 5b). Although the inbreeding coefficient for our population was low at 0.012, three offspring had inbreeding coefficients of 0.25 (JT106, JT212, and JT206), which were identified to be the result of incestuous breeding between sire and grandam (sire's dam).



**FIGURE 3** STRUCTURE plot of average population coefficients ( $q$ -value) for 83 dingo samples from Kalamurina compared to 102 dog and 322 dingo reference samples from Stephens et al. (2015). Dotted lines represent thresholds for pure dingoes (>0.9) and likely pure dingoes (>0.8) based on Stephens et al., 2015 and Cairns, Nesbitt, Laffan, Letnic, & Crowther, 2019



**FIGURE 4** The purity scores for different phenotypes (coat colors) from 83 dingoes sampled at Kalamurina between 2016 and 2018. Each boxplot shows the range of purity scores within each coat color category. The solid line represents the mean, lower and upper hinges correspond to the first and third quartiles, and the whiskers extent to the minimum and maximum scores. Numbers above each boxplot indicate the sample size, and the horizontal dashed-line shows the percentage purity above which individuals are classified as pure dingoes. Between 80% and 90% indicates a probable dingo (i.e., likely no domestic dog-like alleles present)

All inbred offspring were male with black and tan coats. There was a further observation of a possible familial mating between JT08 and JT52, with offspring JT110. Indeed, JT52 is closely related to JT06, the mother of JT08, with  $r = 0.4819$ , equivalent to a parental or full-sibling relationship.

### 3.3 | Genetic diversity

Overall genetic diversity was low (mean  $H_E = 0.51$ ; Table 3). Dingoes with the phenotype for a black and tan coat exhibited the lowest mean  $H_E$  (0.47), but we found no significant relationship between coat color and  $H_E$ .

## 4 | DISCUSSION

The strong signal of dingo ancestry present in each of the sampled dingoes indicates a pure population. Individuals displayed considerable differences in their coat color yet this phenotypic variation was not related to their purity nor genetic diversity. Our data effectively demonstrate that a pure dingo population in arid Australia may feature a range of coat colors including white, sandy, sable, and black & tan. This implies that pure dingoes can exhibit considerable variation in their appearance within a single population, and consequently it is unlikely that there is an archetypal dingo phenotype. Describing the relationship between genetics and coloration in mammals is complex, with more than 150 genetic loci involved in pigmentation (Hubbard, Uy, Hauber, Hoekstra, & Safran, 2010). Moreover, mutations at these loci may produce color variations similar to that of hybridization (Randi, 2011).

The population of dingoes in this study has been free from pervasive human impacts, such as lethal control and pastoralism, for a decade. In addition, the study site was distinct from most of the continent in that it has only ever experienced very low levels of (post-Indigenous) anthropogenic disturbance. The remoteness of a dingo population was found by Stephens et al. (2015) to reflect the level of hybridization, with the most widespread examples of dingo-dog hybridization occurring in populated coastal areas near human settlement. In 2019, Cairns, Nesbitt, Laffan, Letnic, & Crowther reported that whilst approximately 20% of the dingoes in south-eastern Australia were pure, the occurrence of dog ancestry was a widespread in the population, plausibly due to long-term lethal control in the region. They also observed that some geographic “hotspots” maintained high dingo ancestry. Corbett (1995) theorized that social stability (destabilized by human actions) might be negatively correlated with hybridization between dingoes and dogs, which has also been suggested for other canids such as wolves (Rutledge et al., 2010) and foxes (Sacks, Moore, Statham, & Wittmer, 2011). Indeed, lethal persecution of coyotes, red wolves and gray wolves is believed to increase the risk of hybridization with sympatric wild canids or domestic dogs because of low mate availability (due to low population density following lethal control) and disruption of social structures (Bohling & Waits, 2015; Moura et al., 2014). Although

**TABLE 2** The number of dingoes with different coat colors in each kin group (first-order relatives). Capture distance represents the maximum distance between individuals in each kin group, regardless of the session they were captured in. Although dingoes that were not assigned to a kin group were related, they were not first-order relatives

Kin group	Dingo ID	Sandy	Black & Tan	Sable	White	Max. capture distance (km)
1	JT100, JT101	–	2	–	–	1.50
2	JT02, JT103	1	–	–	1	15.0
3	JT201, JT202	2	–	–	–	3.50
4	JT05, JT203, JT204, JT207, JT210, JT211	4	–	2	–	5.00
5	JT217, JT222	2	–	–	–	4.50
6	JT04, JT224	1	1	–	–	25.0
7	JT205, JT231	2	–	–	–	18.5
8	JT220, JT228, JT32, JT33	4	–	–	–	5.50
9	JT221, JT35, JT36	3	–	–	–	1.50
10	JT34, JT39	1	1	–	–	1.00
11	JT06, JT08, JT106, JT110, JT212, JT214, JT52	3	3	1	–	9.50
12	JT03, JT107, JT111, JT206, JT307	4	1	–	–	18.5
13	JT38, JT308	2	–	–	–	30.0
14	JT229, JT51, JT55, JT309, JT312	4	–	–	1	32.0
15	JT09, JT209, JT54, JT306, JT317	3	–	1	1	4.50
16	JT31, JT318	2	–	–	–	25.0
17	JT10, JT319	2	–	–	–	14.5
18	JT208, JT050, JT053, JT301, JT302, JT303, JT311, JT314, JT320	3	–	6	–	7.00
Not assigned	JT01, JT07, JT104, JT108, JT109, JT213, JT215, JT218, JT219, JT223, JT225, JT226, JT227, JT230, JT37, JT304, JT305, JT310, JT313, JT315, JT316	15	2	3	1	–

social behavior was not explicitly explored in this study, low levels of human interference suggest the population could have maintained a stable social structure and thus another buffer to hybridization. Moreover, this dingo population persists in one of Australia's hottest and driest regions where free water is largely restricted to the Warburton Creek (a single source of bore water also lies adjacent to the Warburton Creek). The shortage of free water and harsh climatic conditions are likely to present an environmental barrier to movement and thus further reduce chances of introgression from roaming domestic dogs, which can have poor survivorship in the wild (Geffen et al., 2011; Stephens et al., 2015). These factors are likely to have worked synergistically to mitigate hybridization and preserve the purity of the dingo population.

Species with complex social structures often possess innate behaviors that mitigate introgression and inbreeding (Bohling & Waits, 2015; Sacks et al., 2011). Many canids express kin recognition and evade inbreeding through strict social hierarchies that permit only one pair in a social group to breed in a given season (Geffen et al., 2011). Moreover, maturing offspring will often be forced to disperse into new areas by dominant individuals in order to reduce kin encounter rate. In canids, dispersal is often solitary and sex biased, and dispersal distance can be highly variable (Moehlman, 1989). In dingoes, dispersal is prompted by locally limited resources and the

vacancy of adjacent areas (Thomson et al., 1992). The primary limiting resource for dingoes at Kalamurina is access to water and this is likely to impede their ability to disperse, possibly explaining the high levels of relatedness that was observed between individuals. Inbreeding has been observed in dingo populations across Australia (Stephens, 2011), though the observed levels of inbreeding were lower in our population than might be expected given the number of kin groups and their close spatial association with one another (Table 2; Geffen et al., 2011). Surprisingly our pedigree analysis did identify a mother–son mating as well as another close familial mating (Figure 5), suggesting that occasional familial breeding may occur naturally in dingo populations. In red wolves, Sparkman, Adams, Steury, Waits, and Murray (2012) observed that 8% of mating's were parent–offspring or sibling. They posited that that parent–offspring mating's represent occasions when an offspring replaces a resident parent in the social grouping. Low levels of inbreeding despite exposure to related individuals is consistent with cooperative breeding in canids, where their social behavior and dispersal generally impedes breeding between related individuals (e.g., Jamieson, Taylor, Tracy, Kokko, & Armstrong, 2009; Koenig, Stanback, & Haydock, 1999).

Within the Kalamurina population, many of the dingoes were closely related, with some evidence of occasional familial mating but overall low inbreeding (Figure 5, Figure S1). It is possible that

**TABLE 3** Genetic diversity of the 34 microsatellite loci used to measure purity and relatedness. We used a total of 84 samples.  $k$  = number of alleles at the locus,  $N$  = number of individuals typed at the locus,  $H_O$  = observed heterozygosity,  $H_E$  = expected heterozygosity

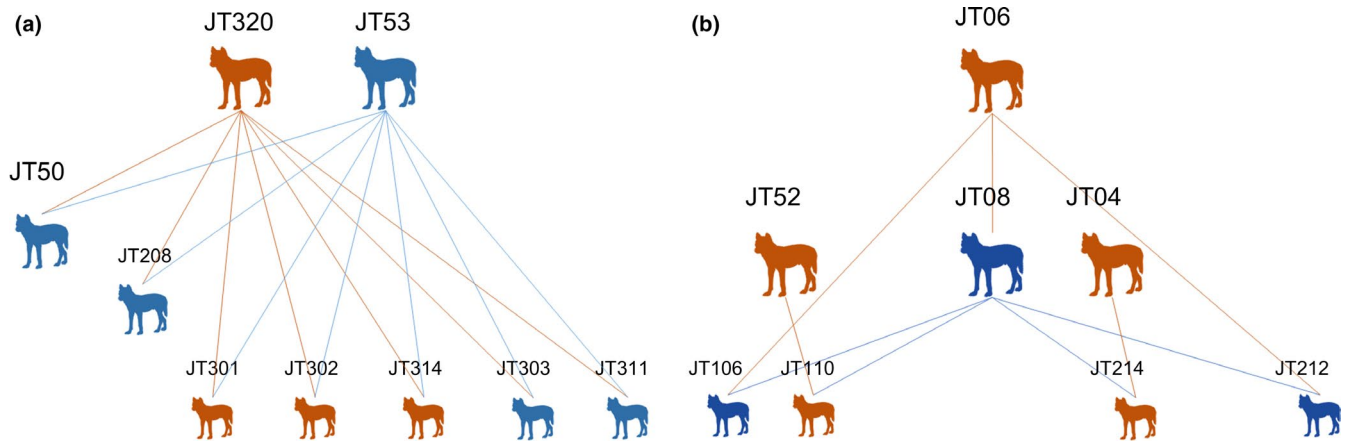
Locus	$k$	$N$	$H_O$	$H_E$
AHT103	6	83	0.627	0.691
FH2247	11	84	0.821	0.839
m13c19	2	81	0.049	0.048
FH2257	5	83	0.711	0.649
CXX434	3	83	0.193	0.176
CXX460	5	83	0.253	0.328
FH2199	19	82	0.841	0.891
AHT109	8	84	0.714	0.729
CXX109	4	84	0.238	0.239
FH2079	3	82	0.244	0.287
CXX410	3	83	0.036	0.036
m13tt	2	82	0.329	0.323
CXX402	2	84	0.143	0.173
FH2313	6	84	0.738	0.769
CXX30	5	84	0.357	0.417
CPH2	3	83	0.024	0.024
FH2346	14	83	0.843	0.865
AHT125	6	83	0.651	0.717
CXX406	5	84	0.250	0.230
FH2293	13	83	0.807	0.885
VIASD10	4	84	0.452	0.410
LEI008	3	83	0.277	0.278
FH2138	15	82	0.744	0.827
ladeC213	4	13	0.308	0.403
FH2168	14	83	0.783	0.819
FH3591	5	84	0.083	0.082
WanV142	4	84	0.560	0.667
FH3295	6	84	0.726	0.676
FH3413	14	80	0.813	0.852
Ren195	4	83	0.289	0.261
FH2537	8	78	0.769	0.798
FH3278	5	84	0.690	0.721
Ren47D	6	84	0.524	0.55
Ren229	7	84	0.738	0.787
Overall	6.59	80.94	0.489	0.513

parentage analyses included siblings or close relatives within the pool of candidate parents, potentially overestimating confidence in parentage assignment (Jones & Arden, 2003; Marshall et al., 2003). Future researchers should consider applying panels of single nucleotide polymorphisms (SNPs) or multiple marker types rather than just microsatellites to provide more confident discrimination of parentage and inbreeding (Fernandez et al., 2013; Kraus et al., 2015). This is particularly true in species where genetic diversity may be low, such as dingoes (Ardalan et al., 2012). Although higher numbers of SNP

markers are required technology improvements mean that these are now cost-effective to genotype and provides data other detailed population genetics analyses (Cairns, Wilton, & Ballard, 2011; Fernandez et al., 2013).

Observational accounts of sociality and mating system in dingoes suggest they are similar to gray wolves in that they follow a hierarchy and are cooperative breeders (Corbett, 1988; Newsome et al., 2013). Thomson (1992b) tracked 34 dingoes across 3 years in arid Australia and reported five main packs that consisted of a dominant breeding





**FIGURE 5** Pedigree analysis revealing two different breeding strategies from a population of pure dingoes at Kalamurina. (a) Shows a monogamous pair that have produced three generations of offspring (i.e. three breeding seasons), and (b) is an example of male promiscuity in our population where one male (central) sired offspring to three females in the same breeding season. Generations are represented by different levels and sexes are blue (male) and orange (female). Lines indicate parentage. Individual ID shown above each dingo

pair and their offspring of various years. Although not well understood, observational studies suggest the dingo mating system is monogamous (Corbett, 1988), and we did find some evidence to support this. However, unexpectedly promiscuity appeared to be a common mating strategy for the dingoes at Kalamurina (Figure 5b). The lack of genetic-based pedigrees for dingo populations may be shadowing the frequency of extra-pair copulations akin to what has been reported in other “monogamous” species such as humans *Homo sapiens* (Small, 1992), saddle-back tamarins *Saguinus fuscicollis* (Terborgh & Goldizen, 1985), and aardwolves *Proteles cristatus* (Richardson, 1987). Further, recent genetic-based investigations have revealed that other members of the canid family may not be genetically monogamous as previously thought, but possess a flexible mating structure similar to that of socially monogamous birds (Baker, Funk, Bruford, & Harris, 2004; Hughes, 1998; Kitchen, Gese, Waits, Karki, & Schauster, 2006; Moehlan, 1989). In addition, the dingoes in this study persist under extremely harsh environmental conditions and therefore it is entirely possible that high levels of mate mortality would foster a promiscuous mating strategy. Further exploration of the mating strategies of dingoes across Australia would be interesting and may help identify if dingoes seek monogamous or promiscuous mating usually or only where mate mortality is high (i.e., in regions experiencing lethal control or harsh climate). This could have important management and conservation considerations for dingoes and other canids.

It has often been proposed that promiscuous breeding is a strategy to avoid inbreeding (e.g., Brooker, Rowley, Adams, & Baverstock, 1990; Sillero-Zubiri, Gottelli, & Macdonald, 1996; Tregenza & Wedell, 2000), and empirical studies have shown it can provide genetic benefits to females (reviewed in Kempnaers, 2007). The baseline level of genetic diversity for dingoes in Australia is low, presumably due to a small number of founder animals (Cairns et al., 2017; Savolainen et al., 2004; Stephens, 2011), which is consistent with our findings. Low genetic variation is predicted to lower

individual fitness and population adaptability (Lande, 1988), which may warrant concern for the future conservation of dingoes; particularly those that are geographically constrained. Paetkau et al. (1998) identified a gradient of genetic diversity in brown bears *Ursos arctos* that was much lower on the fringes of their range and in populations with limited connectivity. Connectivity between dingo populations is limited in some parts of Australia due to human settlement and human-wildlife conflict. In the most remote parts of their range, the flow of genes between populations may be restricted due to harsh climatic conditions, physical barriers such as cluster fencing and the widespread use of lethal control measures including aerial baiting. However, this reduction in connectivity between populations may be unexpectedly beneficial if it limits the spread of dog genes into remote dingo populations, as long as the genetic diversity of dingoes does not result in inbreeding depression (see Tatler, 2019a for spatial data on tracked dingoes at Kalamurina).

Phenotypic variation is well documented among and between dingo populations. Coat color is often used to distinguish pure dingoes from dingo-dog hybrids (Corbett, 2001; Fleming et al., 2001). Although recent genetic testing has shown pure dingoes may exhibit a number of coat colors and patterns (Elledge, Allen, Carlsson, & Leung, 2008). Newsome et al. (2013) used genetic analyses to show two different coat colors (ginger, and black and tan) were present in pure dingoes, while eight different coat colors (including ginger, and black and tan) were observed in sympatric dogs. Sable coloration and white ticking are often reported to only occur in dogs and dingo hybrids, however, we provide evidence that pure dingoes may also carry this phenotype. This is consistent with Crowther et al. (2014) who observed sable coloration in pre-19th century museum specimen. Body weight of adult dingoes can be highly variable depending on geographic location and available resources (see Allen & Leung, 2014), and we reported some of the heaviest weights for a dingo population (Table 1). The primary prey item of dingoes in this study was European rabbits (c. 1.6 kg; Tatler, Prowse, Roshier, Allen, & Cassey, 2019b), which indicates that

it is not the size of the prey items that dictate the body size of dingoes. Akin to wolves, intact populations of dingoes are likely to be intrinsically regulated and therefore we might expect a male sex bias (Phung, Wayne, Wilson, & Lohmueller, 2018; Wolff, 1997). However, the similar sex ratio observed in our study is consistent with other studies on dingoes (e.g., Newsome et al., 2013; Robley, Gormley, Forsyth, Wilton, & Stephens, 2010; Thomson, 1992b) as well as coyotes *C. latrans*, a medium-sized canid with many traits comparable to dingoes (Moehlman, 1989).

## 5 | CONCLUSIONS

Variation in coat color or body size cannot be used to infer a dingo's level of purity because the phenotype of pure dingoes is intrinsically variable. Remoteness, environmental barriers, and social stability are likely to act synergistically and additively as barriers to hybridization. The breeding system of dingoes was long thought to be monogamous but we provide genetic evidence for a flexible mating strategy within a population that ranges from long-term monogamy to promiscuity, which is consistent with emerging research on other "monogamous" species.

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## DATA AVAILABILITY STATEMENT

Microsatellite data from our study will be made freely available online at FigShare <https://doi.org/10.25909/5c75cabc58024>

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

**Figure S1.** Pedigree analysis revealing parentage of 60 dingoes at Kalamurina.

**Table S1.** Capture details for dingoes trapped at Kalamurina from 2016–2018.

**Table S2.** Model summary for the effect of age class, coat color, and sex on body condition of dingoes at Kalamurina.

**Table S3.** Model summary for the effect of coat color, sex, age class, and weight on body the purity (amount of dingo ancestry) of dingoes at Kalamurina.

**Table S4.** Relatedness scores for 84 dingoes captured at Kalamurina.

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