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Stable dingo population structure and purity over 11 years of lethal management

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ABSTRACT

Context. Interaction between predators and humans is a key driver of human–wildlife conflicts, and can underpin management of predator populations. Management of the impacts of dingoes on livestock and native species is a prime example of a persistent and contentious predator management issue with potential impacts on the integrity of dingo populations. To manage the potential impacts of dingoes and their control, it is imperative to understand the effects of control approaches on their populations in the short and long term. Hybridisation of dingoes with domestic dogs also threatens the genetic integrity of pure dingoes. It has been hypothesised that lethal control of dingoes can facilitate hybridisation through disrupting pack social structures leading to increased dingo–domestic dog interactions. **Aims.** We aimed to to investigate how dingo population structure and genetic purity have changed, assessing dingo purity, individual relatedness, population clustering and gene flow, particularly across land use types and barrier fences, in the context of ongoing lethal control within the Murchison Regional Vermin Cell area in Western Australia (WA). **Methods.** We tested dingo genetic samples from three distinct sampling periods (2009, 2014 and 2020) for changes in population summary statistics and dingo ancestry. Barriers and corridors to gene flow were also examined. **Key results.** We identified three genetically distinct populations in the study area, consistent with previous genetic studies in WA. We did not find any evidence of change in dingo purity or population characteristics; however, barrier fencing may be influencing recent gene flow. **Conclusions.** The metapopulation of dingoes in the southern rangelands of WA appears to be stable over the 11 years assessed. **Implications.** Because we were unable to demonstrate that lethal control has accelerated hybridisation between dingoes and domestic dogs in the study area over the last 11 years, we have no evidence that lethal control to reduce losses to livestock production and for conservation of native wildlife in the southern rangelands of WA is putting dingo purity at risk. Fencing appears to be an effective management tool because there is some evidence it is congruent with reduced gene flow in areas where the fences are well maintained.

Keywords: baiting, cell fencing, dingo, gene flow, hybridisation, lethal control, rangelands, wild dog.

Introduction

Management of predators is contested globally. Interactions between predators and humans, and between predators and human assets are key drivers of human–wildlife conflicts (Treves and Karanth 2003; Madden 2004). As a result of these conflicts, predators can be subject to both lethal and non-lethal control resulting in considerable population declines and local extirpation (Treves and Karanth 2003). The decline of predators is also heavily implicated in global biodiversity losses (Ripple *et al.* 2014), and there are significant evidence-based calls for the protection and in some cases reintroduction of predators for biodiversity benefits (Hayward *et al.* 2007; Baker *et al.* 2017). In this context it is imperative to understand the effects of control approaches on predator populations both in the short term, and over generations.

Management of dingo (*Canis familiaris*; Jackson *et al.* 2017) impacts on Australian landscapes is a persistent and contentious issue (Hayward and Marlow 2014;

Newsome *et al.* 2015). Dingoes are valued in Australian society (Archer-Lean *et al.* 2015), but as opportunistic predators, they can have negative impacts on livestock and native species (Fleming *et al.* 2014; Gentle *et al.* 2019; Augusteyn *et al.* 2021). Dingoes have also been demonstrated to regulate native and introduced herbivore populations (and hence grazing pressure; Choquenot and Forsyth 2013; Allen *et al.* 2021), and it has been proposed that they regulate other introduced eutherian predators, benefiting native species (Hayward and Marlow 2014; Newsome *et al.* 2017; but see Kreplins *et al.* 2021). It is important to note that dingoes, domestic dogs and their hybrids are all the same species, *C. familiaris*, and within this paper we are discussing genetics within a species (Jackson *et al.* 2017, 2019).

Hybridisation of dingoes with domestic dogs (*C. familiaris*) threatens the genetic integrity of pure dingoes (Elledge *et al.* 2006; Stephens *et al.* 2015). It has been hypothesised that lethal control of dingoes can fracture packs (Corbett 1988), leading to increased dingo–domestic dog hybridisation (Wallach *et al.* 2009). In turn, hybridisation may result in changes in predation behaviour (Elledge *et al.* 2006; Glen *et al.* 2007). Anecdotal comments from livestock producers report that predation of livestock varies in rate and type depending on the genetic make-up of the predator (i.e. dingoes attack fewer livestock individuals than hybrids; Claridge and Hunt 2008). Although there are currently no data to support these statements, these assertions are accompanied by calls for the reduction of lethal dingo control to preserve dingo genetic purity (Cairns *et al.* 2017, 2022).

In Western Australia (WA), baiting, trapping and shooting are common forms of dingo control (Kreplins *et al.* 2018, 2022). Investment in barrier and cell fencing, or cluster fencing (mesh fencing on the external boundary of several properties) to increase livestock production by preventing reinvasion after the eradication of dingoes within cells, is also increasing. One large cell fence has been completed and others are under construction. The completed cell, named the Murchison Regional Vermin Cell (MRVC) was completed in 2021 and is currently the largest cell fence in Australia. It links two pre-existing dingo-exclusion fences to create an approximately 1400-km fence that encompasses 61 pastoral stations and an area of 6 536 198 ha.

Understanding broad-scale movement and genetic structure of managed species can lead to more informed control efforts (Robertson and Gemmell 2004). If geographic barriers and distances between kin-groups are known, concerted effort can be made to control discrete populations that impact livestock production (Hampton *et al.* 2004). However, if populations are large, open and panmictic, control is more difficult. For example, camel populations in Australia are a single panmictic population, reducing control options (Spencer *et al.* 2012). The WA dingo population is characterised by a higher proportion (59%) of pure dingoes (≥90% dingo ancestry) than most other regions in Australia, with variation in purity correlative with proximity to human habitation (Stephens *et al.* 2015). WA dingoes comprise four genetically distinct populations that occupy different geographical areas of the state, three of which intersect in the area of the MRVC (Stephens 2011).

In the context of ongoing lethal control in WA, increasing investment in cell fences and the completion of the MRVC, we aim to investigate how dingo population structure and genetic purity have changed. The MRVC has been the site for collection of dingo samples at three separate periods: ~2009, 2014 and ~2020, allowing population changes to be traced over time and across the landscape. Here, using samples from the MRVC and a surrounding 200-km buffer we aim to: (1) establish the purity of dingoes in the broader MRVC area (MRVC + 200 km) over the entire study period; (2) compare genetic diversity indices, dingo ancestry, and mean relatedness among the 2009, 2014 and 2020 cohorts, to establish whether there have been any significant shifts in dingo demographics during ongoing lethal control; (3) assess population structure in the MRVC and surrounding region to identify any discontinuities in gene flow and the spatial extent of multi-generational dingo movement; and (4) identify any barriers and corridors to gene flow and assess geographic distances between closely related individuals within and around the MRVC.

Methods

Site description

This study was conducted in the Murchison region of the southern rangelands of WA. The southern rangelands are typified by an arid environment with annual rainfall of 239 mm and mean maximum temperatures in January of 38.2°C (Mount Magnet Station, 007057; Bureau of Meteorology 2020). The vegetation is composed of *Acacia* spp. woodlands. Properties within and surrounding the MRVC generally have a history of sheep farming; however, sheep are now largely absent from the MRVC, with cattle and unmanaged goats the main stock on livestock production properties. Dingo control using sodium fluoroacetate (1080) baiting (biannual), trapping (by landholders and licensed pest management technicians) and *ad hoc* shooting have occurred at varying intensities within most of the properties of the MRVC for over 40 years (Gooding and Freeth 1964).

Sample collection

Tissue samples were collected from three time periods: 2007–2009 (hereafter '2009'), 2014 and 2019–2021 (hereafter '2020'). 1207 dingo tissue samples were selected for analysis. Microsatellite data for the 2009 cohort were selected from the broader sampling of Stephens *et al.* (2015), which used the same loci processed on the same fragment analysis equipment, to cover the area of interest. Initially all 2009

samples within 200 km of the MRVC boundary were identified. Because 97% of the samples south of the MRVC were collected by two professional dog control officers, some of these were removed to reduce bias from family groups potentially being collected, and additionally, to improve the evenness of the data spread. Data from dingoes south of the MRVC collected by these individuals (n = 233) were randomly assigned a number (using the RAND function in Microsoft Excel), sorted by that number, and the first 123 individuals were removed, leaving 110 remaining in the final data set. The 2014 cohort included all available samples from a State Government bounty trial conducted that year, and 2020 samples were taken from ongoing control work. Because tissue was submitted by third parties, no live animals were handled in this study. Tissue samples were included if they were within or up to 200 km from the MRVC, and ≥14 microsatellite markers from the 23-marker dingo ancestry test panel (described below) were successfully amplified. Individuals with fewer than 14 loci successfully genotyped were removed as recommended by Alan Wilton, who selected the markers for the original likelihood-based DNA testing (pers. comm.) and for consistency with previous studies (Stephens *et al.* 2015). The location of the samples, the MRVC and fences are shown in Fig. 1.

Due to the differing analysis types in this study, four different data sets were used (Fig. 2.). Initially a data set containing all specimens within the MRVC and surrounding 200 km was assessed for dingo and domestic dog ancestry. For the remaining analyses, specimens with <60% dingo ancestry were excluded from the data set because samples with high levels of domestic dog ancestry do not contain a strong signal of recent geographic history in their genome. A cut-off of 60% was chosen to limit the study to animals with a majority dingo ancestry (>50%) plus up to 10% error as estimated for the dingo ancestry testing in Stephens *et al.* (2015). After this restriction, sample sizes were 769, 87, and 346 for the 2009, 2014 and 2020 cohorts respectively. For comparison among the cohorts, samples were limited to the MRVC area only, because there was a bias towards the eastern side of the wider study area in the 2009 sample. Confining the sampling area resulted in a more even geographic distribution of the specimens.

DNA extraction, amplification, and dingo ancestry testing

Typically, samples consisted of approximately 1 cm^2 of ear tissue. Tissue samples were stored in Longmire buffer (Longmire *et al.* 1997) until DNA extraction. Extraction was performed using Qiagen DNeasy blood and tissue kit (Qiagen Inc., Valencia, CA, USA) using the recommended protocol, with 100 μL final elution. DNA was amplified at 34 microsatellite markers in seven multiplexed PCRs; five

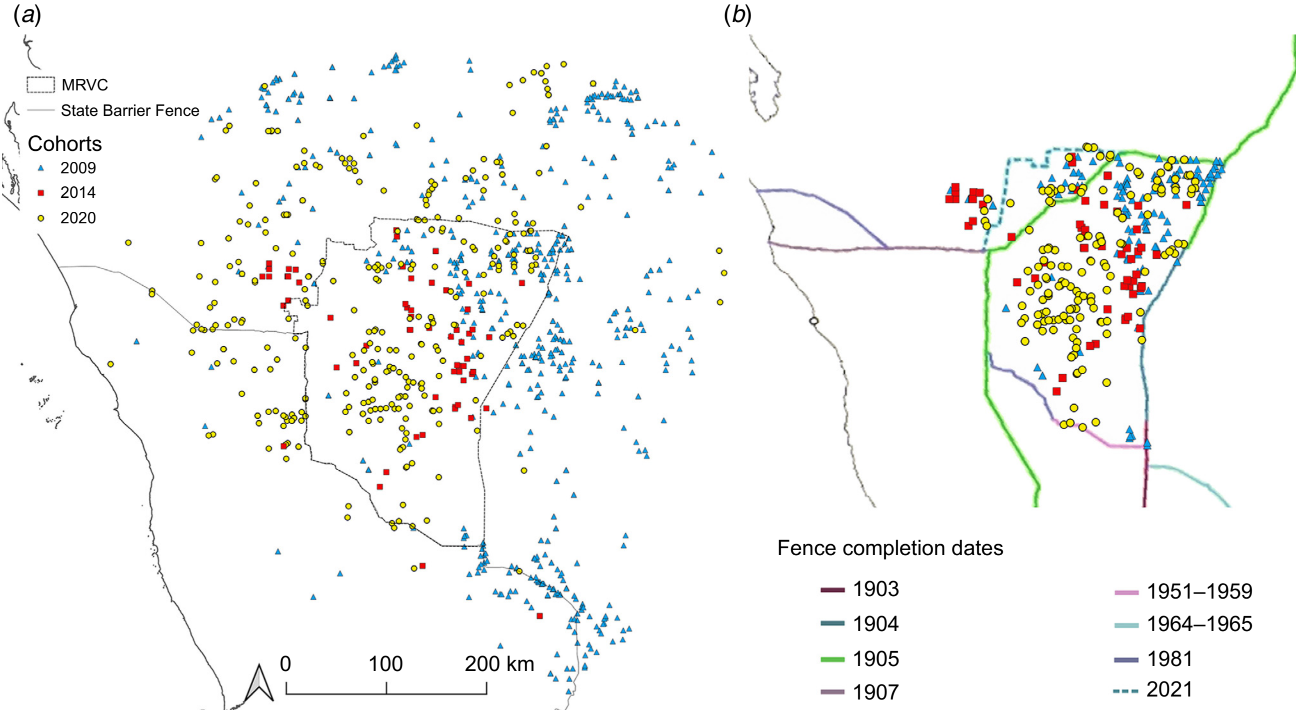

Fig. 1. Specimens used in this study, (*a*) categorised by collection cohort (2009, 2014 and 2020), and (*b*) limited to specimens within the MRVC for comparison among cohorts (the sampling was extended to the northwest corner slightly to include extra 2014 samples, because this was the cohort with the fewest specimens), and the year of fence construction for the State Barrier Fence (SBF) and MRVC.

multiplexes were as described in Stephens et al. (2015) and two additional multiplexes as described in Stephens (2011) and Tatler et al. (2021). PCRs were performed in 10 μL reactions, containing 5 μL Qiagen Multiplex PCR solution (Qiagen Inc.), 1 μL Qiagen Q-Solution, and 1 μL DNA, 0.2 μM of each primer and DNAase/RNAase-free water. PCRs were executed with 15 min at 95°C, followed by 35 cycles of 30 s at 94°C, 90 s at 55°C (for the initial five multiplexes), or 58°C (additional multiplexes) and 60 s at 72°C, then 30 min final extension at 60°C. The initial five multiplexes (23 loci) were used for dingo ancestry testing because they are optimised for this purpose, and all 34 loci were used for all other analyses.

Hybridisation analyses were conducted using the program Structure v2.3.4 (Pritchard et al. 2000) to evaluate the contribution of dingo and domestic dog ancestry to each individual. Briefly, 23 loci selected for consistent differences in allele frequencies between dingoes and modern domestic dogs by Wilton et al. (1999) were analysed in Structure, along with 322 reference dingoes and 109 domestic dogs (Stephens et al. 2015). The sample was run for 300 000 iterations and 30 000 burn-in iterations were discarded, for 10 replicates, and the results combined in CLUMPP v1.1.2 (Jakobsson and Rosenberg 2007). The proportion of each individual's genotype assigned to the same population as the reference dingoes was then reported as a percentage estimate of dingo ancestry. Interpretation of results included a conservative error of ±10%.

Summary statistics on cohorts

Cohorts within the MRVC were analysed in two ways: divided into the three cohorts (2009, 2014 and 2020); and using only the first and last cohorts. For the three-cohort analyses the size of each cohort was restricted to the size of the smallest cohort (2014; 83 specimens) by random removal of individuals from the larger cohorts. In the analyses with only 2009 and 2020 cohorts, the sample sizes were similar so were not altered (199/174 specimens; Fig. 2). Summary statistics were calculated using GenAlEx v6.51b2 (Peakall and Smouse 2006, 2012) (Number of alleles (N_a), Number of effective alleles (n), Shannon's diversity index (I), number of private alleles (P_A), and expected heterozygosity (H_e)) or the R package diveRsity v1.9.90 (Keenan et al. 2013) (Inbreeding coefficient (F_{IS}) and allelic richness (A_r)). The percentage of dingo ancestry was also compared between the cohorts. Both cohort groups showed skewness in the distribution of dingo ancestry, so were assessed using a Wilcoxon rank sum test with continuity correction (cohorts = 2) or a Kruskal–Wallis rank sum test (for cohorts = 3). Both tests were calculated using the R package dplyr v1.0.4 (Wickham et al. 2021).

Mean relatedness for each cohort was calculated using the Lynch and Ritland pairwise relatedness estimators (LREs; Lynch and Ritland 1999) in GenAlEx, using 999 bootstraps and permutations to assess significant difference from the average relatedness and standard error, respectively.

Population structure

To examine population clustering, the broader MRVC sample was analysed using both spatially naive and spatially explicit clustering methods. Initially, the sample was tested for significant isolation by distance (Supplementary material S1). Analysis without spatial information was then performed using Structure v2.3.4 (Pritchard et al. 2000), for 500 000 iterations with 50 000 burn-in iterations for 10 replicates each of 1–10 assumed populations (K). The sample was run with alpha allowed to vary among populations, initialising at 0.3, using the admixture model and both correlated and uncorrelated allele frequencies. Structure output was then assessed for optimal K by the Delta K method of Evanno et al. (2005) using Structure Harvester v0.6.94 (Earl and vonHoldt 2012), and by inspection of the mean of the estimated ln probability for each K ($L(K)$) for the point where increases in probability become less pronounced. Replicate runs of the optimal K were combined in CLUMPP (Jakobsson and Rosenberg 2007) using the Greedy algorithm and 10 000 replicates.

Spatially explicit analysis of population structure was performed using the R package TESS3 v1.1.0 (Caye et al. 2016). Analysis was performed for K = 1–10 for 20 replicates per K, with the remaining parameters left at defaults. The optimal number of populations was inferred by inspection of the cross-validation score.

The methods implemented in Structure rely on assumptions about the life history of the taxon under study, specifically that the populations are in Hardy–Weinberg equilibrium and linkage equilibrium – assumptions that may not hold for continuously distributed, vagile taxa such as canids. An assumption-free method – spatial analysis of principal components (sPCA) – was also implemented in this study for comparison with the previous analyses. sPCA was run from the R package adegenet (Jombart 2008; Jombart et al. 2008; R Core Team 2020). Individual geographic coordinates were first converted to a projected coordinate system using the package PBSmapping v2.73.0 (Schnute et al. 2004). Spatial PCA analysis was performed using 'Neighbourhood by distance' connection (type 5), with minimum distance between neighbours = 0 and the maximum distance set between 20 and 100, with distance = 50 used in the final analysis (changing this variable had minimal effect on the results). For interpolation and display of the results, a small amount of noise was added to the coordinates so that there were no identical coordinates in the analysis, using the 'jitter' function in the R base package (R Core Team 2020). A contoured map of lagged principal scores was then generated using the package akima v0.6–2.1 (Akima et al. 2016).

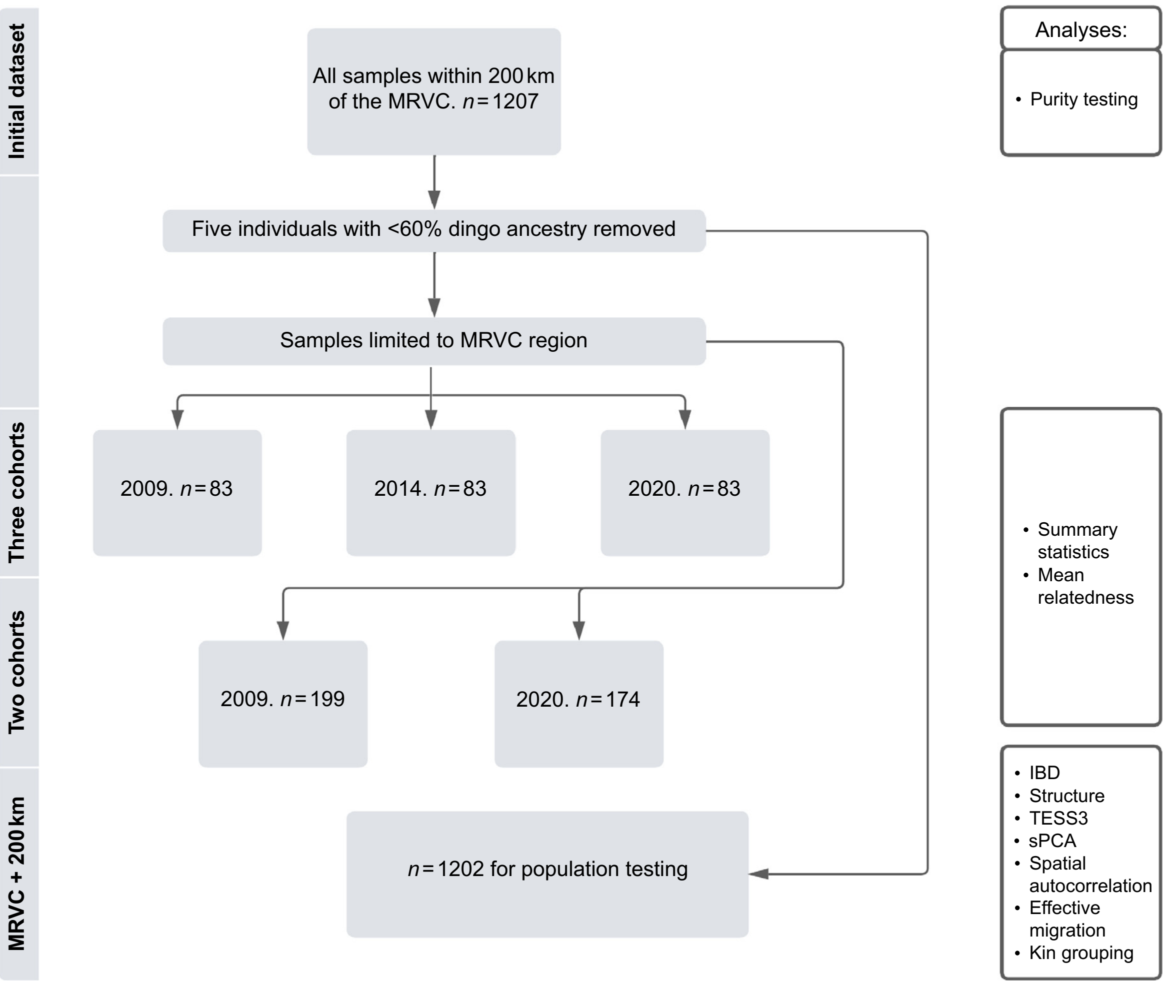

Fig. 2. Data sets used for the three analysis types in this study.

Analyses of gene flow

Typical movement patterns of dingoes within the study area were assessed using an estimated effective migration surface (EEMS; Petkova *et al.* 2016). This method generates an interpolated surface that highlights areas that deviate from isolation by distance across the study area, which can indicate barriers and corridors to gene flow. EEMS analysis was performed for 700 demes (vertices of each triangular division of the study area) for three replicates with different starting seeds and run for 2 million Markov chain Monte Carlo (MCMC) iterations with 1 million burn-in and thinning every 9999 iterations. Parameters affecting acceptance proportions for proposal types were adjusted until the acceptance values were within the range 10–40%, as recommended in the program documentation. The three replicate analyses were then combined onto a single plot using the rEEMSplots v0.0.0.9 package in R (Petkova *et al.* 2016).

Fine-scale movement was tracked by assessing distances between kin. First-order relationships (parent–offspring or full siblings) within the full data set were identified using Kingroup v2 (Konovalov *et al.* 2004) using the descending ratio algorithm and a primary hypothesis that individuals were full siblings or parent–offspring, and the null hypothesis that individuals were unrelated. This analysis assumes simple Mendelian inheritance in a diploid organism, with non-overlapping generations and without significant inbreeding. Dingoes often violate the latter two assumptions of the Kingroup analysis, which likely affects the accuracy of the results. For this reason, the LREs calculated in GenAlEx were compared with Kingroup pairs to assess agreement between the two methods.

Results

Dingo ancestry

The overall proportion of dingo ancestry across all 1207 samples tested is high, with only 2% classified as hybrid. A summary of the results is presented in Table 1. Five

individuals were removed from the subsequent data set due to low dingo ancestry (2–44%).

Summary statistics of cohorts

No significant difference was detected between the mean percentage of dingo ancestry in the three cohorts (Kruskal–Wallis chi-squared, $P = 0.116$) and the two cohorts (Wilcoxon test, $P = 0.286$). All the values calculated in GenAlEx are within the standard error of the other cohorts (Table 2). The mean relatedness values (Fig. 3) are all within the 95% confidence interval of the other cohorts, indicating no statistically significant difference between the groups.

Population structure

Although isolation by distance appears to be the dominant cause of genetic distance across the study area (Fig. S1), we conducted tests for population structure to determine whether there are discontinuities in sub-regions of the study site that were masked by the large area and number of samples tested. Both the Structure and TESS3 analyses found distinct population clusters in the sample (Fig. 4). The Delta K and $L(K)$ approaches (Fig. S2*a*, *b*) to estimating the number of Structure populations both indicated that the most likely number of populations was three. Uncorrelated allele frequencies also showed $K = 3$ using the Delta K approach and 98% agreement in population assignment with the correlated allele frequencies, so only the correlated model is shown here. The cross-validation plot for the TESS analysis showed smaller decreases in the cross-validation score after $K = 3–4$ (Fig. S2*c*) The populations showed agreement between the two clustering methods, displaying a more distinct population in the southeast of the study area ('South') and two overlapping populations in the north of the study area ('North' and 'East'; Fig. 4*a, c*). Structure results (Fig. 4*b*) shows less admixture between the South and East population than between the East and North populations.

Spatial PCA analysis showed significant clustering in the data (Fig. S3) based on global structuring. The interpolated plot of the individual scores (Fig. 4*d*, PC1) agreed with the separation of the South population found in the Structure and TESS analyses. The second principal component showed the weaker discontinuity between the east and north populations (Fig. 4*d*, PC2).

Table 1. Results of dingo ancestry testing in the broader MRVC region ($n = 1207$).

Dingo ancestry categories	No. of individuals	% of sample
Dingo (≥90%)	830	69
Possible dingo (80–89%)	351	29
Hybrid (11–79%)	25	2
Domestic dog (≤10%)	1	0

Gene flow and fine scale movement

Parameters for the effective migration surfaces were adjusted until the proposal variances were between 20 and 38%. Parameter adjustments from the default values were as follows: Proposal qSeedsProposalS2 = 0.02; mEffctProposalS2 = 0.9; and qEffctProposalS2 = 0.005. Inspection of the posterior trace plot showed reasonably constant MCMC sampling, which was consistent with the chains having converged. The EEMS surfaces (Fig. 5) indicate heterogeneity of gene flow within the study area. The barrier to gene flow in the south of the study area identified in Fig. 4 is again apparent in this analysis. The EEMS surface was overlaid on road and water data (Fig. 5*c*) and land use data (Fig. 5*d*) because there were similarities in the locations of these features; roads largely overlapped areas of average to

Table 2. Summary statistics measuring differences in genetic parameters between the three-cohort and two-cohort data sets.

	Three cohorts			Two cohorts	
	2009	2014	2020	2009	2020
N_a	6.44 (0.74)	6.53 (0.73)	6.06 (0.70)	7.53 (0.87)	7.12 (0.75)
n	3.07 (0.39)	3.03 (0.37)	2.98 (0.40)	3.12 (0.39)	3.06 (0.41)
I	1.05 (0.13)	1.06 (0.13)	1.02 (0.13)	1.08 (0.13)	1.05 (0.13)
P_A	0.62 (0.18)	0.62 (0.13)	0.41 (0.11)	1.24 (0.32)	0.82 (0.17)
H_e	0.48 (0.05)	0.48 (0.05)	0.47 (0.05)	0.49 (0.05)	0.47 (0.05)
F_{IS}	0.10 (0.07–0.14)	0.13 (0.08–0.19)	0.13 (0.09–0.16)	0.11 (0.09–0.14)	0.13 (0.11–0.16)
A_r	5.91	6.02	5.66	6.92	6.61
Dingo	91.30	91.30	93.20	91.30	93.20

Values inside parentheses are standard errors when single numbers, and 95% confidence intervals where a range is given.
N_a, number of different alleles; n, number of effective alleles; I, Shannon's diversity index; P_A, number of private alleles (alleles found only in that population); H_e, expected heterozygosity; F_{IS}, inbreeding coefficient; A_r, allelic richness; Dingo, mean percentage of dingo ancestry.

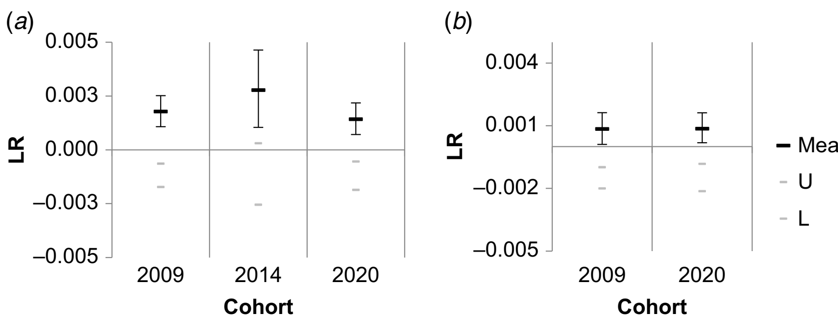

Fig. 3. Mean relatedness of cohorts, displayed as Lynch and Ritland (1999) relatedness (LR), averaged over individuals in each cohort. Grey bars indicate the 95% confidence limits for the null hypothesis of no difference from average relatedness. Black bars are the 95% confidence interval around the mean. (*a*) three cohorts, all restricted to 83 individuals by random removal of genotypes from the larger 2009 and 2020 cohorts. (*b*) two cohorts only, with 199 individuals in the 2009 cohort and 174 in the 2020 cohort.

Fig. 4. Population structure in the MRVC and surrounding 200 km. (*a*) Map of the Structure populations with three populations assumed, with each individual presented as a pie chart indicating the proportion of their ancestry assigned to each cluster. (*b*) Barplot of each individual's assignment to populations, with each vertical line representing a single individual. Individuals are sorted approximately from northwest (left) to southeast (right). The *y*-axis shows the percentage of the individual's genotype assigned to each population. (*c*) Assignment of individuals to populations using the spatially explicit analysis in TESS3. Lighter colours on this plot indicate more admixed individuals, darker colours indicate more individuals assigned fully to one population. (*d*) Interpolated 2D kernel estimation plot of spatial PCA, which shows agreement in the differentiation between the South population and the remainder of the sample found by Structure and TESS3 in the first principal component (PC1) and between the east and north populations in PC2.

high gene flow, and both lakes and land use boundaries overlapped the main gene flow barrier found above the South population. Within the MRVC there is only one, central area of significantly reduced effective migration, overlapping with the town of Mount Magnet, but dingoes seem to move and breed freely around the perimeter of the MRVC.

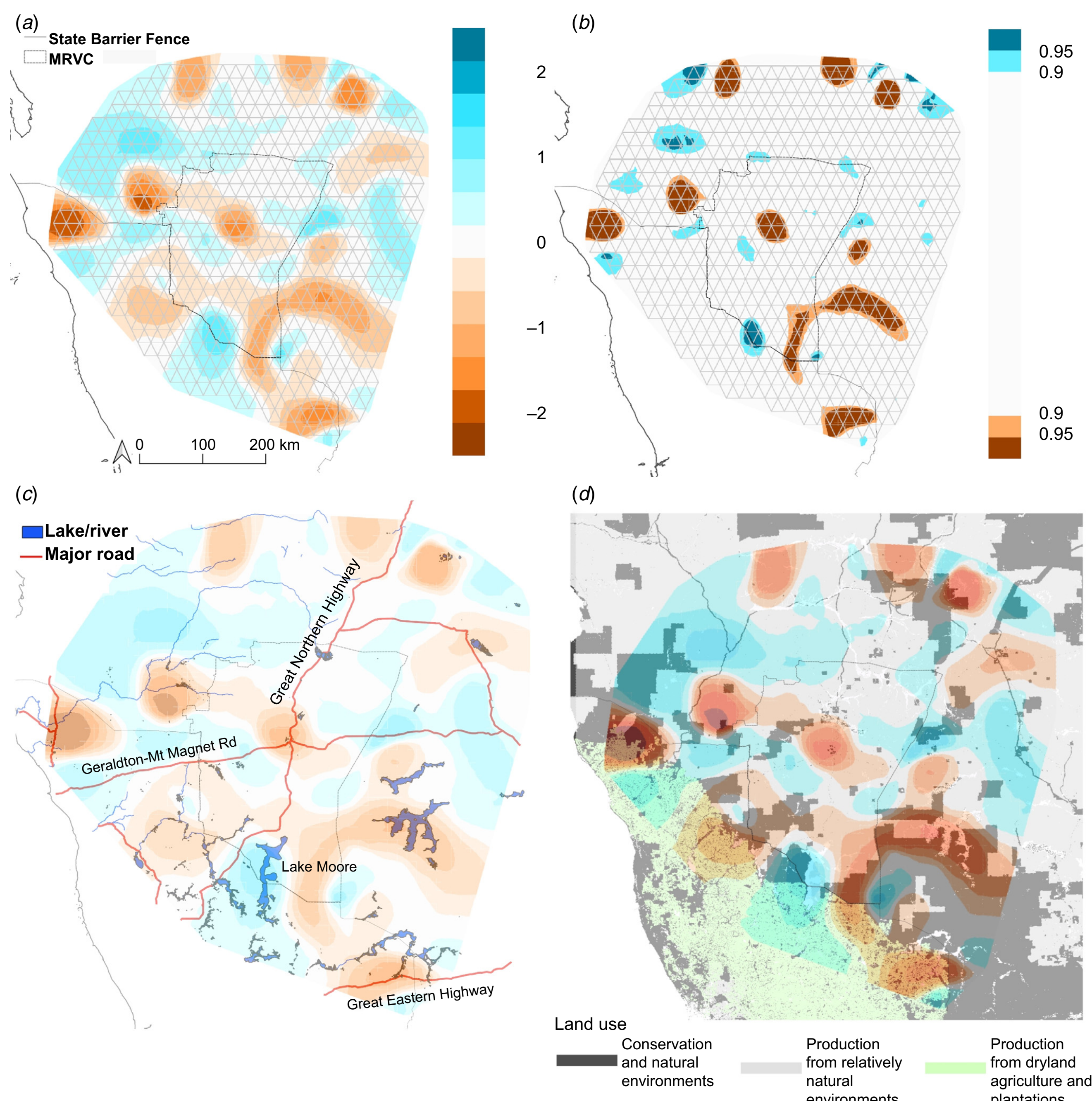

Fig. 5. Estimated effective migration surfaces for the broader MRVC. (*a*) The interpolated EEMS surface on the log10 scale. Blue indicates higher than expected relative gene flow and brown indicates lower than expected gene flow. White areas are as expected for the decay of genetic similarity with distance only (no barriers or corridors). (*b*) As in (*a*), but only areas where the posterior probability exceeds 90%. (*c*) Migration surface as in part (*a*), overlaid on major roads, rivers and lakes to show association between EEMS results and roads (red lines) and water courses (blue lines and shapes) in the study area. Road/water data © OpenStreetMap contributors and used under Open Database licence (openstreetmap.org). (*d*) EEMS results overlaid on primary land use categories (categories are from ABARES 2016).

Relatedness between individuals

Distances between first-order relatives were 0–360 km. The histogram of distances between kin (Fig. 6) highlights a strong bias to kin within 50 km and occasional longer dispersal events. Only one pair of kin with LRE > 0.35 was identified with individuals on different sides of the SBF, and no individuals from the South population were identified as having kin in the northern populations.

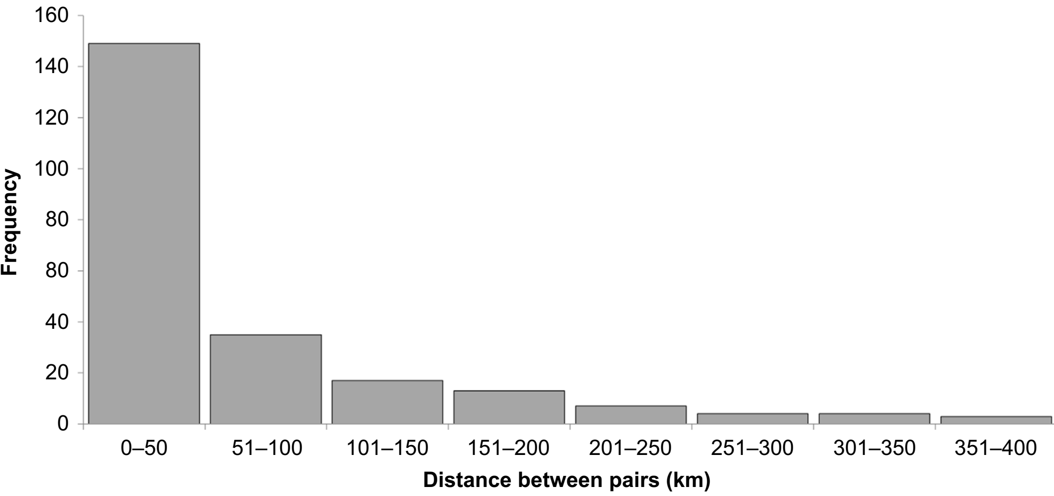

Fig. 6. Histogram of the distribution of distances between kin.

Discussion

We examined the population structure and genetic purity of dingoes across an area approximately 352 000 km^2 using three sampling periods over 11 years. The genetically distinct populations in this area are consistent with the work of Stephens (2011), but we did not find any evidence of change in dingo purity nor any detectable expansion, contraction, or increase in inbreeding/outbreeding. There is little evidence that ongoing lethal control affected dingo purity or population structure over the study period; however, barrier fencing may be influencing gene flow.

Dingo ancestry and population summary statistics

Genetic purity of dingoes remained high, with 98% of the individuals tested having ≥80% dingo ancestry and 69% having ≥90% dingo ancestry. Each of the population parameters examined remained stable between cohorts, which may represent up to six generations of dingoes (18–24 months to first breeding). The limited change in population demographics over the three sampling periods occurred during a period of ongoing dingo control. This does not support the hypothesis that lethal control increases hybridisation (Wallach *et al.* 2009). We note that baiting may not have been as effective as intended in reducing dingo populations over the study period (Kennedy *et al.* 2021), but effective trapping and shooting were ongoing, including a pilot bounty trial in 2014. The continually low hybridisation in this area is likely to be influenced by a lack of opportunities for domestic dogs and dingoes to interact. Stephens *et al.* (2015) demonstrated that hotspots for hybridisation co-occur with areas of human habitation. WA rangelands are characterised by extensive tracts of native vegetation and pastoral properties with few towns and low human densities, providing limited opportunities for interactions between dingoes and domestic dogs.

Population structure

We identify evidence for a genetic discontinuity in the southeast of the MRVC area, between the South and North/East populations. The boundary of this population sits at the southern corner of the MRVC area, and indicates that dingoes are less likely to be migrating between north and south regions than among other areas. The curve of this boundary closely matched the intersection between vacant crown land, Mount Manning Range Nature Reserve, and pastoral land. The north and west of the curve is also the boundary between the Goldfields and Wheatbelt regions and salt lakes. The gap in sampling in the southern MRVC area cannot be discounted as a potential cause for the discontinuity; however, a slightly smaller gap (~100 km across) is present within the North population, to the immediate north of the MRVC boundary, which shows no such population structuring. The main barrier to the south is also apparent on the lateral edges, which do have sparse but continuous sampling. Regardless of the cause, for management considerations the South population can still be treated as a mostly independent unit without regular gene flow to the north.

The discontinuity found between the North and East populations appears to be more consistent with a pattern of isolation by distance. There is reduced gene flow between these areas, but many admixed individuals occur in the transitional area between the two populations. There may be weak or recent separation between these areas, or gene flow may be being maintained by occasional long-distance forays (as documented by Thomson *et al.* (1992) and Robley *et al.* (2010)), which is preventing complete separation of the two populations and the resulting genetic differentiation.

Bayesian analysis methods, including using Structure, have also been shown to produce spurious clusters in the presence of isolation by distance, which may not represent a localised discontinuity, but instead the inevitable decrease in genetic similarity with increasing distance between individuals (Frantz *et al.* 2009; Perez *et al.* 2018). Given the finding of a dominant pattern of isolation by distance and the weak geographic demarcation between these 'populations', we do not believe the Structure and TESS results for the north of the study area likely to be driving noticeable or ongoing separation between the groups, and it is not likely to be relevant for management.

Movement barriers and corridors

The effect of landscape features, both natural and anthropogenic, on animal movement is valuable information. Roads, water, fencing and land use are the most notable landscape features in the region. The impact of roads has been studied in many species, with fragmentation of populations the most common outcome, but results vary depending on the age, size, and usage frequency of the road, plus the size and behavioural characteristics of the species under study (reviewed in Holderegger and Di Giulio 2010). In central-west WA, roads have low frequency of traffic, and roadways are typically not fenced, allowing space for travel along the side of the road. Dingoes have been observed to preferentially travel along roads, trails or other cleared land (Gabriele-Rivet *et al.* 2020; Duncan *et al.* 2022), as have their congenerics wolves (*Canis lupus*; Zimmermann *et al.* 2014; Newton *et al.* 2017) and coyotes (*Canis latrans*; Hinton *et al.* 2015), which is consistent with the gene flow pattern in this study. At all but two points there is no intersection between significant barriers to gene flow and the roads; furthermore, in the north and west of the study area, the roads closely border patches of reduced gene flow, or perhaps divide them.

One of the intersections between reduced gene flow and a major road is in the south of the study area (Great Eastern Highway), which also coincides with several lakes. The other area of significantly reduced gene flow overlaps the intersection of Geraldton–Mt Magnet–Sandstone Rd and the Great Northern Highway, where the town of Mount Magnet is located. This townsite may be acting as a sink or patch of optimal habitat that retains dingoes once they travel into it via the roadways. The remaining areas of roadway mostly show gene flow consistent with or greater than isolation by distance expectations, although this effect is strongest at the intersections of fences and roads. The roads may therefore be providing a transit point through fences, and the roadways that do not cross fences (e.g. the intersection in Mt Magnet and the Great Eastern Highway) could be having a different effect on gene flow.

There is some indication that the SBF is having an impact on the movement of dingoes, despite the fence being of inconsistent age and permeability until its upgrade. The SBF was maintained at a dingo-proof standard for the duration of the study, and coincided with a weak barrier to gene flow in EEMS analysis. The only exception to this was at Lake Moore, which has been a known dingo 'hot spot' from the early 1990s, and until an upgrade in 2011 would have allowed gene flow across this section of the SBF. Only one kin pair with LRE > 0.35 was collected on opposite sides of the SBF, further indicating minimal crossing of the fence in the recent past. Given the historic permeability of the fence, it is unsurprising its impact is only apparent in the most fine-scale analyses, but ongoing monitoring around this and other fences may provide more detailed insights into the effectiveness and genetic impacts of anthropogenic barriers to movement on dingoes.

The division of populations by barriers can create new subpopulations and increase genetic heterogeneity across the landscape. Although fragmenting populations can sometimes spur conservation concerns associated with low genetic diversity (Blanchet *et al.* 2010), we believe this is unlikely to be a concern for dingoes in this instance; their large movement capabilities and rapid expansion across the continent since their relatively recent introduction from a small founder population indicates persistence and adaptability, despite relatively low genetic variation (Wilton *et al.* 1999; Zhang *et al.* 2020). In addition, populations of dingoes with documented isolation and decreased genetic diversity, such as those on K'gari/Fraser Island (Conroy *et al.* 2021) and in western Victoria (Stephens *et al.* 2022), currently persist without noticeable negative effects.

Kin grouping

In addition to facilitating hybridisation between dingoes and domestic dogs, lethal control has been hypothesised to affect dingo dispersal (Allen 2015) and genetic integrity of packs (Wallach *et al.* 2009; O'Neill *et al.* 2017). Here we demonstrate a pattern of spatial distribution of kinship heavily skewed to related individuals occurring in proximity. Most related individuals were captured within 25 km of one another. Although this value may be biased downward by collection of whole litters of pups at once, and by recording animals collected across a property as a single set of coordinates, it does show a pattern consistent with high site fidelity and occasional long-distance dispersal (Thomson *et al.* 1992).

Limitations

Our sampling methodology was related to dingo control and research effort within and surrounding the MRVC at the time, therefore the study site was not sampled uniformly. It is possible that if these areas were sampled uniformly the final analyses of dingo ancestry and population structure may be altered. We are encouraged that this is not the case

given the lack of variation between cohorts in every population parameter we assessed. Lower sampling effort in the southeast of the study site limits our ability to understand gene flow between the south and other dingo populations, and the sharpness of this discontinuity. The lack of pre-lethal control data or a control site is also a hindrance to the interpretations of the data.

Conclusions

The ecological role of dingoes continues to be highly contested (Castle *et al*. 2021), as does the use of lethal control to mitigate their impacts on agriculture and biodiversity (Allen *et al*. 2017; Smith *et al*. 2021). Arguments that lethal control leads to a decline in dingo purity are not supported by this study, because dingo ancestry was and remained high after more than a decade of lethal control. If the 'fractured pack' hypothesis relating to hybridisation applies in any context, proximity to higher densities of domestic dogs than were present in our study area is likely to be a necessary condition. We were unable to demonstrate that lethal control has accelerated hybridisation between dingoes and domestic dogs, therefore there is no evidence that lethal control to reduce losses to livestock production and the conservation of native wildlife in the southern rangelands of Western Australia is putting dingo purity at risk. We have also indicated landscape features – roads, barrier fences and land-use types – may influence gene flow in dingoes, which could be further explored in future studies (Westekemper *et al*. 2021).

Supplementary material

Supplementary material is available online.

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Data availability. Microsatellite alleles, geographical coordinates, dingo ancestry and cohort information are available on Dryad, https://datadryad.org/stash/dataset/doi:10.5061%2Fdryad.2547d7wsx.

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