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Genetic profile of dingoes (*Canis lupus dingo*) and free-roaming domestic dogs (*C. l. familiaris*) in the Tanami Desert, Australia

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Abstract

Context. Many rare and endangered species are threatened by the effects of hybridisation with their domesticated and often numerically dominant relatives. However, factors that influence interactions between hybridising species are poorly understood, thus limiting our ability to develop ameliorative strategies.

Aims. Here, we identify family groups and investigate patterns of gene flow between dingoes (*Canis lupus dingo*) and domestic dogs (*C. l. familiaris*) in the Tanami Desert of central Australia. We aimed to determine whether human-provided resources facilitate hybridisation or alter typical patterns of dingo breeding and social behaviour. We also ask whether remote townships are arenas for dingo–dog hybridisation.

Methods. Tissue samples and morphological details were collected from dingo-like animals around two mine sites where humans provide abundant supplementary food and water. Using molecular DNA analyses, we assigned animals to population clusters, determined kinship and the numbers of family groups. Rates of hybridisation were assessed around the mines and in two nearby townships.

Key results. Of 142 samples from mine sites, 'pure' dingoes were identified genetically in 89% of cases. This predominance of dingoes was supported by our observations on coat colour and body morphology. Only 2 of 86 domestic dogs sampled at the two townships showed evidence of dingo ancestry. Around the mine sites, there were two distinct population clusters, including a large family group of 55 individuals around a refuse facility.

Conclusions. Where superabundant and consistent food, and reliable water, was available, dingo packs were much larger and co-existed with others, contrary to expectations derived from previous research. Dingo sociality and pack structures can therefore be altered where human-provided food and water are constantly available, and this could facilitate accelerated rates of hybridisation.

Implications. The development of appropriate domestic-waste management strategies should be a high priority in remote areas to ensure only normal rates of population increase by dingoes, and other canids more broadly. It will also potentially impede hybridisation rates if typical canid social and behavioural traits remain intact. Additionally, areas surrounding remote human settlements are likely arenas for accentuated dingo–domestic dog interactions and should be a target for future studies.

Additional keywords: hybridisation, purity, relatedness, resource supplements, sociality.

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Introduction

A common consequence of the expansion of human industry and settlements is the increased potential for interaction between domestic and wild animals. Interactions such as predation and competition between these groups are relatively well known and can have dramatic effects on individuals and populations, especially at the interface between settled areas and natural habitats (e.g. Dickman 1996), whereas others such as interbreeding can have more subtle but, nonetheless, pervasive impacts (Mooney and Cleland 2001). Gene flow between

sympatric species may be beneficial from an evolutionary perspective if it shapes local adaptation, results in greater fitness or prompts speciation (Moore 1977; Barton and Hewitt 1985, 1989; Arnold 1992). However, from a conservation perspective, hybridisation can be detrimental if it disrupts adaptive gene complexes, erodes species boundaries or results in lost reproductive opportunities (Rhymer and Simberloff 1996; Allendorf *et al*. 2001).

Ultimately, hybridisation usually results in the loss of one taxon because of asymmetry in the respective population sizes of the species (Rhymer and Simberloff 1996). As a consequence, numerous rare and endangered species are threatened by interspecific hybridisation and genetic introgression (Rhymer and Simberloff 1996; Allendorf *et al*. 2001). Development of sound management strategies to minimise rates of hybridisation is therefore critical to ensure the long-term survival of 'at risk' vulnerable populations. However, despite increasing awareness and knowledge about hybridisation, and its recognition as a conservation problem (Bohling and Waits 2011), developing appropriate management strategies has proven to be a challenge because the factors that influence interactions between hybridising species remain poorly understood (Allendorf *et al*. 2001).

The dingo (*Canis lupus dingo*) is among the taxa that are currently under threat of extinction, with hybridisation with domestic dogs (*Canis lupus familiaris*) seen as a key threat (Corbett 2001*a*, 2001*b*; Daniels and Corbett 2003; Stephens 2011). The dingo was introduced to Australia most likely at points along the northern coastline at least 4000 years ago (Corbett 2001*a*; Savolainen *et al*. 2004). Indigenous Australians initially used dingoes for both practical and spiritual purposes (Meggitt 1965; Rose 1992; Tunbridge 1996), but the dingo became feral soon after its arrival (Savolainen *et al*. 2004). As a generalist predator with adaptable foraging tactics (Corbett 2001*a*; Fleming *et al*. 2001), the dingo was able to colonise most habitats, including arid and monsoon-arid environments. The dingo is now considered native to Australia and is expected to fulfill an important ecosystem role by moderating the densities of native herbivores (e.g. Pople *et al*. 2000) and introduced meso-carnivores (e.g. Johnson *et al*. 2007), but see Fleming *et al*. (2012) and Allen *et al*. (2013) for contrary discussion.

Many descriptions of dingo sociality implicitly suggest that these animals live in stable groups, comprising both sexes, within defined territories or home ranges (Corbett 1988, 2001*a*; Thomson 1992; Fleming *et al*. 2001). Further, it has been hypothesised that, when packs are fractured into smaller units, dingo numbers may increase exceptionally rapidly (Corbett 1988). Dingo-control programs that remove breeding individuals from a pack, and the onset of droughts, are mechanisms that have been proposed to cause such shifts in breeding behaviour (Corbett 1988, 2001*a*; Wallach and O'Neill 2009). Under these hypothetical circumstances, hybridisation rates could increase in the absence of physical barriers to movements and territorial and social limiters to domestic-dog introgression. Such a scenario would be difficult to quantify over large areas and has, consequently, not been tested. However, more recently it has been demonstrated that dingoes may not occupy exclusive home ranges if a surfeit of human-provided food and water resources (in excess of requirements for homeostasis) is locally available; there may be further effects on access to mates and social structuring (Newsome *et al*. 2013). It is therefore plausible that an unlimited food supply could remove social limitations on reproduction that are attributed to α-female breeding dominance and infanticide (Corbett 1988), and cause increases in pack fecundity and survival of pups. This is important to consider because humans provide supplementary food and water resources at focal locations throughout the ranges of dingoes and domestic dogs, potentially facilitating higher rates of hybridisation than would otherwise be expected.

In the central-western portion of the Tanami Desert, dingoes were formerly considered to be naturally sparse (Breckwoldt 1988; Fleming *et al*. 2001). However, there are now relatively large populations of dingo-like dogs living in close proximity to pastoral and mining operations where human-provided food and water exist (Newsome 2011). Europeans have been intermittently active in the Tanami Desert since the early 1900s, and increasingly so since the mid-1960s (Gibson 1986; Baume 1994; Mahood 1996), so it is possible that some of these animals are hybrids. The few remote towns in the region also contain large numbers of free-ranging domestic dogs. However, because this region was not included in sampling by Newsome and Corbett (1985), the hybrid status of these populations is unknown. The Tanami region, therefore, offers a unique opportunity to investigate the effects of localised and recent European settlement on the genetic integrity of the dingo, both in areas where humans provide large quantities of supplementary resources at focal locations at waste facilities, and also at remote towns where domestic dogs occur at high densities.

In the present paper, we profile the genetics of free-living animals and free-roaming domestic dogs in the Tanami Desert in two contrasting areas. In the first area, we sampled animals near pastoral and mining operations where humans provided large quantities of food resources at focal waste-refuse facilities. In the second area, we focussed our sampling in and around two townships where there were large numbers of domestic dogs. Data were used to test two hypotheses. First, we investigated levels of hybridisation across the region using genetic and visual characteristics. Under the expectation that remote regions with little human settlement should support pure dingo populations (e.g. Newsome *et al*. 1980; Newsome and Corbett 1982, 1985), we predicted that most animals around the pastoral and mining operations, which are distant from major human and domestic dog presence, would be pure dingoes. Conversely, we predicted that there would be few pure dingoes in and around townships where large numbers of domestic dogs occur. Second, we investigated population clustering around mine sites where anthropogenic resources were abundant and contrasted this to areas away from the mines where food resources were not provided. Under the hypothesis that supplementary food changes dingo breeding behaviour, and because of their capacity to disperse (e.g. Thomson 1992; Robley *et al*. 2010), we predicted that family groups at mine sites would be large and there would be gene flow between neighbouring packs. We use the results to provide insight into how access to human-provided resources might alter patterns of dingo breeding and social behaviour.

Materials and methods

DNA collection sites

We focussed our animal sampling around two mine sites, The Granites and Dead Bullock Soak (DBS) (20°30′S, 130°18′E), and along an east to west gradient ~100 km either side of the mines where dog sign (footprints, urine and faecal deposits) was present (Fig. 1). This area is referred to collectively as the 'mine sites'. Waste facilities at The Granites and DBS consistently received large quantities of food scraps that were available to, and eaten by, dingoes (Newsome 2011). Dietary analysis indicated that dingoes living further from the mine areas hunted and ate natural prey (Newsome 2011), thus suggesting that these dingoes had access to vastly different food resources. Dingo–dog hybridisation, family size and relatedness were therefore compared across gradients at and away from the mines. To determine rates of hybridisation under an alternative scenario, we also sampled animals at two townships, Yuendumu and Mt Theo, where there are large numbers of free-roaming domestic dogs. Those two sites are referred to collectively as the 'township sites' (Fig. 1).

DNA collection – mine sites

We undertook field excursions on seven occasions, for up to 3 weeks at a time, in April, August and November in 2008 and 2009 and in April 2010. Up to 18 Victor #3 soft jaw steel traps (Oneida Victor Ltd, Euclid, OH, USA) were used to capture animals on each excursion, with the exception of November 2009 when no trapping was undertaken. Combinations of lures were used to attract animals; mostly, these comprised domestic dog urine and/or crushed dead house mice (*Mus musculus*). Sampling took place in seven general locations (Fig. 1).

On successful capture, a ketch-all pole (1.8-m-long pole with an adjustable noose at one end; Ketch-all Company, San Luis Obispo, CA, USA) was used to restrain the animal. It was then placed on a holding board, with straps fitted around the waist, shoulder and neck. To identify individuals from a distance, we placed a button tag (Allflex, Capalaba, Qld, Australia) in one ear of each captured animal. To minimise distress and ensure good-quality tissue, we used a 4-mm biopsy punch to take a small piece of tissue from the ear, and the tag was placed through the resulting hole. Tissue samples were stored in lysis buffer at room temperature until DNA extraction. If a dead animal was encountered in the field, tissue samples were collected. A hand-held GPS receiver was used to record locations of collected DNA samples.

All trapped and recently dead study animals were weighed and sexed. Full-body photographs were taken to provide a record of coat colour and visual characteristics. Twenty-one ear-tissue samples collected at The Granites in 2006 by the Northern Territory Government Parks and Wildlife Service were also incorporated into the analysis. The coat colour of each animal from which an ear sample was collected, was also recorded.

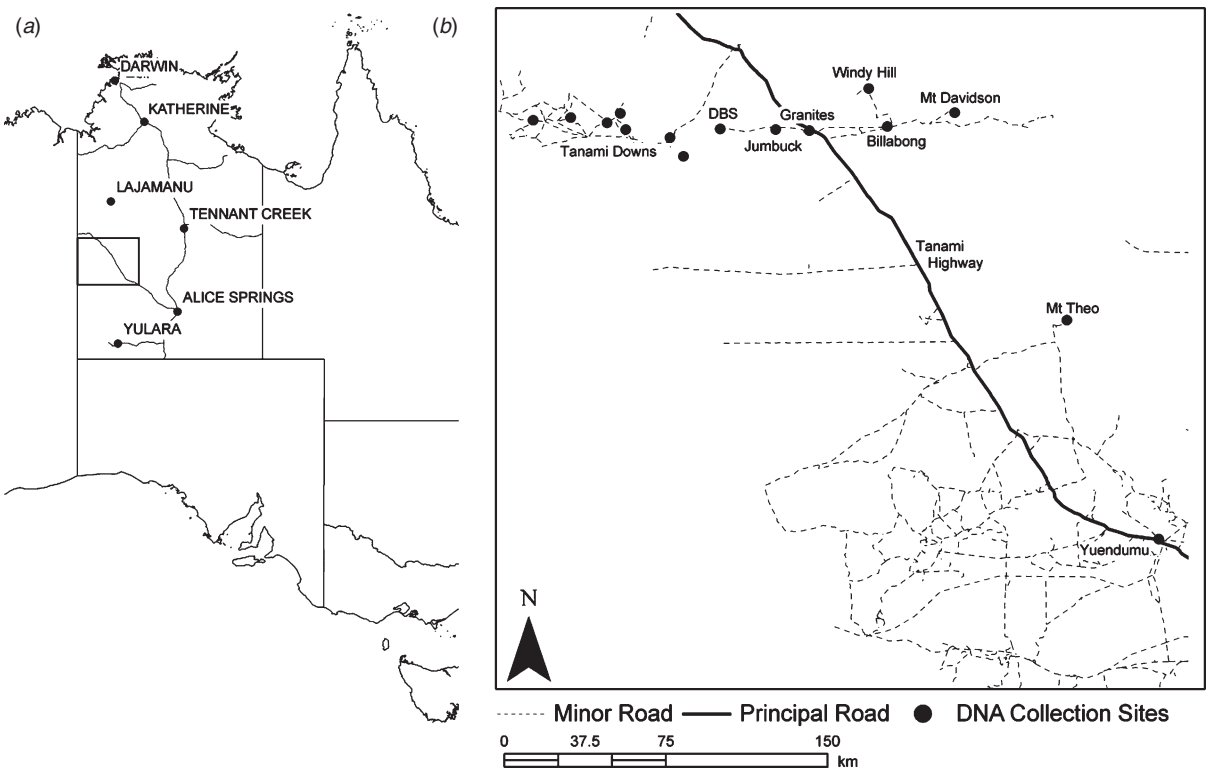

Fig. 1. (*a*) Location of the study region (box) in relation to the major towns and roads in the Northern Territory and (*b*) location of areas where DNA samples were collected from free-living animals (Tanami Downs, DBS, Jumbuck, The Granites, Windy Hill, Billabong and Mt Davidson – mine sites) and from free-roaming domestic animals at two human settlements (Mt Theo and Yuendumu – township sites).

DNA collection – township sites

Field excursions were undertaken in August 2009 and April 2010 for 2 weeks, to sample animals at the township sites. Because these sites were over 100 km from the mine sites, little or no gene flow was expected to or from the mine sites because dingo home ranges (95% MCP) around the mines are between 2 and 2000 km^2 (Newsome *et al*. 2013). However, the township sites have the highest known concentration of domestic dogs in the Tanami Desert and, thus, represent possible locations where dingoes and domestic dogs could encounter each other and interbreed. The exact origin of the domestic dogs was unknown; however, of those sampled, none was reported to have been taken from wild populations. However, dogs were known to frequently foray outside the towns, sometimes for days at a time. Taking and rearing of dingo pups by Aboriginal people in the area was not a common practice during the time of the study.

Study animals were captured by hand, manually restrained, and an endocervical pap-smear brush (Surgipath Medical Industries Inc., Richmond, IL, USA) was used to collect buccal epithelial cells from inside the mouth (Richards *et al*. 1993; Handel *et al*. 2006; Broquet *et al*. 2007). This method was chosen because the alternate approach of taking tissue samples by biopsy from animals captured and restrained with foothold traps was not preferred by community members. Each brush was stored in lysis buffer at room temperature until DNA extraction. Opportunistically, skin-tissue samples were also collected while veterinarians were undertaking surgical sterilisation procedures in April 2010. Photographs were taken as a record of coat colour and identifiable morphological features were noted to ensure that the same individual was not sampled twice. All sampled township animals were also sexed.

DNA extraction and amplification – all samples

DNA was extracted from each sample by Helix Molecular Solutions Pty Ltd (Perth, WA, Australia), by using the glass-fibre method described in Ivanova *et al*. (2006). Twenty-one microsatellite loci were amplified (Table 1) using 5 µL of Qiagen Multiplex polymerase chain reaction (PCR) solution (Qiagen Inc., Hidden, Germany), 1 µL of Qiagen Q-Solution, 1 µL of DNA and 0.2 µM of each primer, and then adjusting up to 10-µL reactions with DNAase/RNAase-free water. PCR cycling conditions were as follows: 15 min at 95°C; 35 cycles of 30 s at 94°C; 90 s at 60°C; 60 s at 72°C; plus a 30-min final extension at 60°C. Fragments were run on an ABI 3730 capillary sequencer and results were analysed using GeneMarker software (SoftGenetics, LLC, State College, PA, USA). Multiplexes 2 and 3, and 4 and 5 (Table 1), were combined for capillary sequencing analysis.

Hybridisation – all samples

There has been debate about the best methods to identify dingoes (Daniels and Corbett 2003; Elledge *et al*. 2006, 2008), with new analyses revealing genotypic differentiation among Australian free-roaming dogs (Wilton *et al*. 1999; Wilton 2001). To determine whether there were any hybrids in the study region (north and south), we therefore employed genetic analysis following the methods of Wilton (2001), as further described in Elledge *et al*. (2008). This analysis is based on comparison with reference genotypes of putative dingoes from both remote areas and captive populations (Wilton 2001), which display allele frequencies that are distinct from those of domestic dogs (Wilton 2001; Stephens 2011). The test sample genotypes were then compared with dingo and domestic-dog alleles as well as simulated hybrids to establish the probability that an animal was a pure dingo rather than being 75% dingo, scaled to the number of loci tested (the '3Q' score; Elledge *et al*. 2008). The final assignment to one of seven purity categories also included the presence or absence of any alleles found only in domestic dogs (Table 2). To strengthen the analyses, we used the descriptions in Table 2 of Elledge *et al*. (2008), to determine whether there were any features indicating hybridisation. Because there were no broad-scale population-reduction campaigns during the study and, except for 16 animals found dead, the sampled animals were either companion dogs or subjects of a broader ecological study, analysis of skull morphology (Newsome *et al*. 1980; Newsome and Corbett 1982, 1985) was impossible.

Table 1. Microsatellite loci used in the study

Locus	Multiplex	Reference
AHT103	1	Holmes *et al*. 1995
FH2247	1	Mellersh *et al*. 1997
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CXX434	1	Ostrander *et al*. 1993
CXX460	1	Ostrander *et al*. 1995
FH2199	1	Francisco *et al*. 1996
AHT109	2	Holmes *et al*. 1995
FH2313	2	Mellersh *et al*. 1997
CXX30	2	Ostrander *et al*. 1993
CXX109	3	Ostrander *et al*. 1993
FH2079	3	Francisco *et al*. 1996
CXX410	3	Ostrander *et al*. 1995
CXX402	3	Ostrander *et al*. 1993
CPH2	4	Fredholm and Winterø 1995
AHT125	4	Holmes *et al*. 1995
CXX406	4	Ostrander *et al*. 1993
LEI008	4	Mellersh *et al*. 1997
FH2346	5	Mellersh *et al*. 1997
FH2293	5	Mellersh *et al*. 1997
VIAS-D10	5	Primmer and Matthews 1993
FH2138	5	Francisco *et al*. 1996

Table 2. Scoring system used to assign dingo, hybrid or dog status to animals on the basis of analyses of genetic variation (modified after Elledge *et al*. 2008)

Score	Status	Average 3Q score	No. of alleles 'diagnostic of dog' ancestry
1	Dingo	>0.1	0
2	Likely dingo	0.05–0.1	0
3	Hybrid (>75% dingo genes)	0–0.05	≥1
4	Hybrid (<75% dingo genes)	–0.1–0	≥1
5	Hybrid (<65% dingo genes)	–0.25 to –0.1	≥1
6	Hybrid (<50% dingo genes)	–0.5 to –0.25	≥1
7	Domestic dog	<–0.5	≥1

Population assignment – mine sites

The program STRUCTURE (Pritchard *et al*. 2000) was used to determine whether there were distinct population clusters in the mine sites. The analysis was compared with and without spatial data incorporated into the model; the addition of location data can increase the sensitivity of the clustering method by using the sampling site of each individual to inform the prior distribution of the model (Hubisz *et al*. 2009). Sampling sites were used as an approximation of the location of each individual because the STRUCTURE input does not accept coordinates. For this analysis, Jumbuck and The Granites were entered as a single site, as were Windy Hill, Billabong and Mt Davidson (Fig. 1).

For all STRUCTURE analyses, the admixture model was used with correlated allele frequencies, a 20 000 chain burn-in and 200 000 replicates, which was sufficient to reach convergence. To determine the most likely number of clusters (K), the 'ΔK' method (described in Evanno *et al*. 2005) was used. Each value of K from 1 to 10 was run for 10 replicates. Once the optimum K-value was selected, each individual population assignment ('Q-value') was averaged across the 10 replicates using the program CLUMPP (Jakobsson and Rosenberg 2007). Samples with a Q-value assignment above 0.9 to a cluster were considered to belong fully to that cluster; samples with Q-values below 0.9 were considered 'admixed', having ancestry from more than one cluster.

For further comparative analyses among STRUCTURE clusters, each individual was assigned wholly to the cluster with the highest ancestry (Q) score. Genetic-diversity statistics (number of alleles, observed and expected heterozygosity, and fixation index) were determined using Genalex v6.41 (Peakall and Smouse 2006), and subdivision between genetic clusters was estimated using both D_{EST} (Jost 2008) in the program SMOGD v1.2.5 (Crawford 2010), and F_{ST} (Weir and Cockerham 1984) using Genepop v.4 (Raymond and Rousset 1995; Rousset 2008).

Analysis of kin relationships – mine sites

The program Kingroup v2 (Konovalov *et al*. 2004) was used to test for first-order (parent–offspring or full sibling) relationships of dingoes at the mine sites. To do this, a full sibship reconstruction was run using the descending ratio algorithm. The primary hypothesis was that pairs were full siblings or parent–offspring, and the complex null hypothesis was that pairs were half-siblings or unrelated.

Ethics and work permits

This research was undertaken under the Animal Care and Ethics Authority O06/009 from Orange Animal Ethics Committee, clearance Number A05020 from Charles Darwin University Animal Ethics Committee and permit Number 33607 from Northern Territory Parks and Wildlife. The Central Land Council provided permit Number CD004 for conducting research on Aboriginal Land.

Results

DNA collection – mine sites

In total, 152 DNA samples were collected at the mine sites. These included 21 samples collected in 2006 (which was before our study), 16 samples from dead animals, and 115 from live-trapped individuals. Most (65%) samples were obtained from The Granites, where density was highest. More males than females were sampled at the mine sites (63 females, 86 males, 3 unknown).

DNA collection – township sites

In total, 86 DNA samples were collected from animals at the two settlements at the township sites. The majority (95%) of those sampled was from Yuendumu. Similar numbers of males and females were sampled (41 females and 45 males). All dogs seen at Mt Theo were sampled and approximately one-quarter of those seen at Yuendumu were sampled.

Field observations of coat colour and morphology – mine sites

The animals seen and sampled at the mine sites were dingo-like (*sensu* Newsome and Corbett 1985; Corbett 2001*a*): most (95%) had ginger-coloured coats and most had white tips on their feet and tails (Table 3). The remaining animals were black-and-tan, including six from The Granites, one from Billabong and one from Tanami Downs. One additional black-and-tan individual was sighted at Tanami Downs and another at Billabong. There were two other sightings of untagged black-and-tan individuals at The Granites; all others were ginger.

No distinguishing morphological features were identified in any of the animals sampled at the mine sites that would suggest, on the basis of the criteria in Elledge *et al*. (2008), that they were hybrids (Table 3). However, there were some minor differences observed across the study region. For example, muzzle colour varied, with combinations of ginger, white and/or black being noted.

Table 3. Visual appearance (predominant coat colour) and status of hybridisation of animals sampled at the mine sites and township sites, as determined by genetic analysis (modified after Elledge *et al.* 2008)

Parameter	Mine site		Township site							
	Ginger	Black-and-tan	Ginger	Black-and-tan	Black	Sable	Brindle	Patchy	White	Black-and-white
n	144	8	21	12	7	7	11	13	3	12
Genetic analysis										
Dingo	119	7	0	0	0	0	0	0	0	0
Hybrid	15	1	1	0	0	0	0	1	0	0
Dog	0	0	20	12	7	7	11	12	3	12
Unknown	10	0	0	0	0	0	0	0	0	0
% pure	89.5	87.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

Field observations of coat colour and morphology – township sites

No dominant morphological or coat-colour characteristics were observed in animals sampled at the township sites. Coat colours included ginger, black-and-tan, black-and-white, black, brindle, sable, patchy and/or mottled, white, and different combinations of these (Table 3). Seven individuals had visual characteristics similar to those of a 'typical' central Australian dingo, i.e. ginger coat colour with white tips to the feet and tail, and a body with similar size and shape to that of a dingo (Newsome and Corbett 1985). These were suspected potentially to have some level of dingo ancestry, but the genetic analysis did not support this (see below).

Distribution of dingoes and hybrids – mine sites

A successful genotype (≥14 microsatellite loci amplified, as in Elledge *et al*. 2008) was obtained from 142 of the 152 tissue samples collected at the mine sites. Overall, 89% of samples screened were identified as dingoes belonging to 3*Q*-score Categories 1 or 2 (Table 2). Sixteen hybrids (11.1% – score Categories 3 or 4 in Table 2) were identified from the collected samples (Fig. 2). Only one hybrid was found away from the mine sites (The Granites and DBS). Fourteen hybrids were identified at The Granites (including four directly around the waste facility), one at the DBS mine and one on the eastern edge of Tanami Downs (Fig. 2). Hybrids in The Granites mine area represented 15% of the total dingoes sampled at that site. No individuals in 3*Q*-score Categories 5–7 (<65% dingo genes) were found. A one-tailed Fisher's exact test for difference in the number of hybrids at the mine sites (Granites and DBS; 15 hybrids, $n = 109$) and the remaining sites (1 hybrid, $n = 33$) was not significant ($P = 0.073$). Similarly, a one-sided Student's *t*-test showed no significant difference in the mean 3*Q*-score between the mine sites and the other sites ($P = 0.17$). There were no obvious trends associated with the distribution of hybrids and coat colours (Table 3).

Distribution of dingoes and hybrids – township sites

Of the 86 study animals sampled at Yuendumu and Mt Theo, most were classified as domestic dog, with little or no evidence of dingo ancestry (score Category 7 in Table 2). Two individuals were placed into score Category 6 (<50% dingo genes), providing evidence of some gene flow between those dogs and hybrids or dingoes. One of these latter individuals had morphological characteristics similar to those of a dingo. The other had stunted legs, floppy ears and was ginger, with large white spots on the body.

Population assignment – mine sites

From the STRUCTURE (Bayesian clustering) analysis, the 'ΔK' values and the consistency of results among replicate runs indicated that the most likely number of clusters was $K = 2$ (Fig. 3). These clusters both contained an excess of homozygotes (Table 4), which could be due to the high prevalence of sibs and parent–offspring pairs present (see below).

Comparison between STRUCTURE analyses with and without the spatial priors showed a consistent pattern and few differences in the *Q*-values of individuals (mean difference = 0.043 ± 0.057 s.d.). Fifteen individuals were placed in a different group between the methods, because of the *Q*-assignment changing above or below the 0.90 threshold for assignment to one of the populations or the admixed group. The spatial model is shown in Fig. 4*a* to incorporate the most data in the model. No geographically discrete population clusters were apparent, but one cluster constituted most of the animals sampled around The Granites mine site, and was not found in the outlying areas. Admixed individuals were found at all sites except for Tanami Downs (Fig. 4*a*). F_{ST} between the two STRUCTURE clusters was 0.106 and D_{EST} was 0.062, further

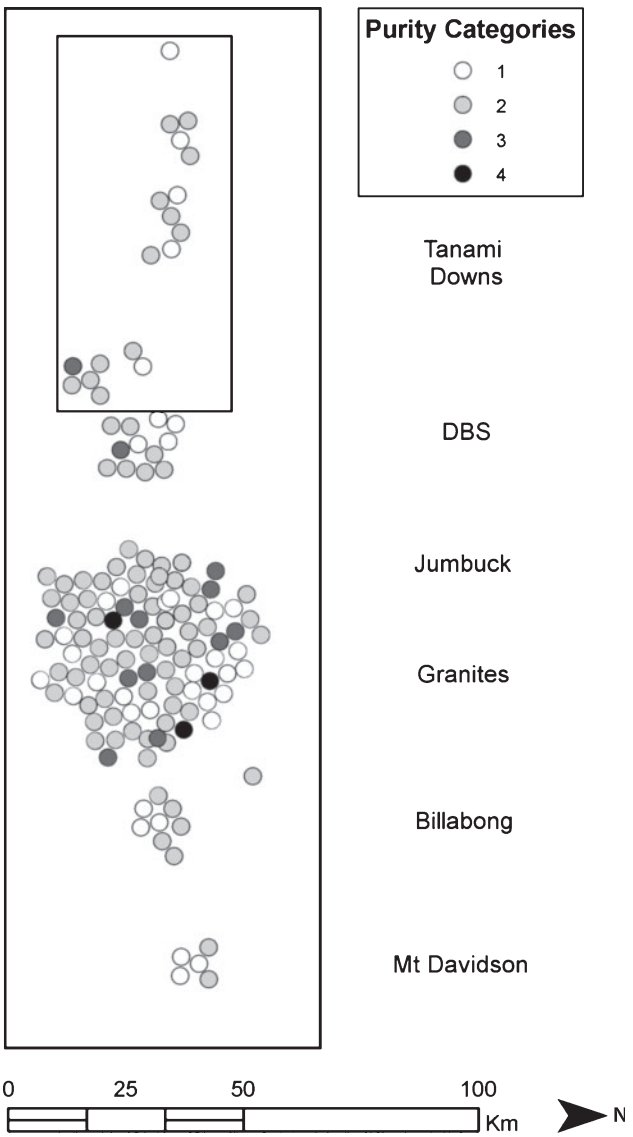

Fig. 2. Proportion of dingoes and hybrids across the mine-site study region as indicated using the methods of Wilton (2001). Samples have been randomly dispersed around a central point when multiple individuals were collected at the same location, to display all individuals. See Table 2 for details of purity Categories 1–4 (where the lower the number, the purer the dingo). No individuals from Categories 5–7 were found. See Fig. 1 for location of the study sites.

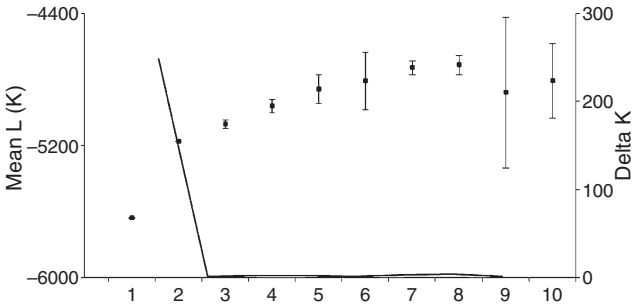

Fig. 3. Estimators of the 'true' number of populations (K) sampled at the mine sites. Mean $L(K)$ (solid squares) shows the mean estimate of the log probability of each K as described in Pritchard *et al*. (2000). Vertical bars show s.d. The most likely K is at the point where gains in likelihood begin to diminish ($K = 2$). Delta K (solid line) shows a peak at the probable value of K (Evanno *et al*. 2005). $K = 1$ cannot be evaluated by this method because the calculations require the difference in the rate of change from the previous value.

Table 4. Estimates of genetic variation between populations at the mine sites identified by STRUCTURE

Calculated values are averaged across loci, s.e. for each value is reported in parentheses. n, number of specimens per population; N_a, number of alleles; H_o observed heterozygosity; H_e, expected heterozygosity; F_{IT}, fixation index

Population	n	N_a	H_o	H_e	F_{IT}
1	95	5.29 (0.88)	0.40 (0.06)	0.43 (0.07)	0.08 (0.03)
2	47	5.62 (0.85)	0.43 (0.06)	0.48 (0.07)	0.07 (0.03)

indicating low-to-moderate genetic subdivision between the two populations.

Kinship analysis revealed 14 family groups (Fig. 4*b*), defined as cases where two or more animals were related at the full-sibling or parent–offspring level (Fig. 4*b*), the largest containing 55 individuals (mean = 9.34 ± 14 s.d.). The individuals from the largest group were all assigned to the same STRUCTURE cluster (the 'black' group in Fig. 4*a*, plus two admixed individuals), although the cluster also contained 23 additional individuals. Four family groups found at Tanami Downs were all discrete and contained within that area, whereas three further groups were found at The Granites and nearby Jumbuck. All other sites contained kin that were also found at other sites, demonstrating that recent and recurrent gene flow has occurred in the area between DBS and Mt Davidson (Fig. 4*b*).

Discussion

The results provided support for both our initial hypotheses. Most (89%) animals sampled at the mine sites were classified as dingo, on the basis of genetic analysis (3Q-score 1 or 2 in Table 2). If new tests are developed using different reference populations or older reference material, the genetic classification of these dingoes could change. However, our concurrent observations of coat colours and body morphology supported the findings of the genetic analysis, with no obvious hybrids being identified. This result was not unexpected because of the genetic dominance of dingo-type coat colorations (Corbett

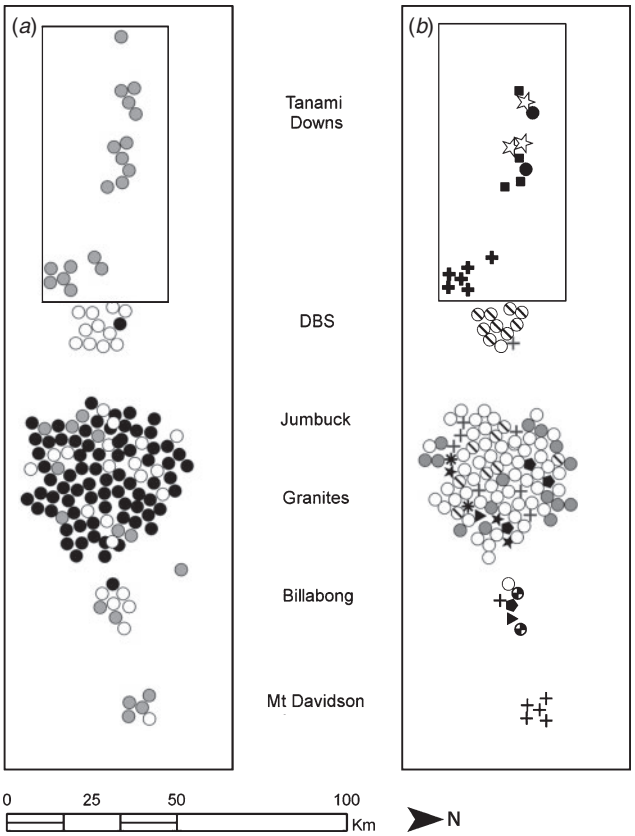

Fig. 4. Genetic segregation of dingoes at the mine-site study region by (*a*) population clusters and (*b*) family groups. Samples have been randomly dispersed around a central point at which multiple individuals were collected at the same location, to display all individuals. (*a*) Results of STRUCTURE analysis for $K = 2$. Black and grey circles represent each of the two clusters found, white circles are admixed individuals (Q-value < 0.9). (*b*) Family groups as determined by full sibship reconstruction. Individuals that were not assigned to a family group are not shown. Each symbol represents a unique family group. See Fig. 1 for location of the study sites.

2001*a*), meaning that hybrid status in some cases might be obscured by coat colour. The overall proportion of 'pure' dingoes identified at the mine sites was lower than that reported by Newsome and Corbett (1985) for inland central Australia (97.5%), which could be indicative of an increase in domestic-dog genes since the 1970s; however, these two studies are not directly comparable because skull morphology and genetic analysis do not always yield the same results (Elledge *et al*. 2006).

Of the few hybrids identified, most were located at The Granites mine site. In time, this site could therefore be a source of hybrids that diffuse into the surrounding region. There have been various stages of European occupancy dating back to the 1900s at The Granites. For example, Baume (1994) stated that both dogs and dingoes were kept as pets at The Granites during the early years of exploration (i.e. pre-1940s). More recently, however, domestic dogs are likely to have been brought to the outstation near The Granites where there is frequent human occupation. Therefore, if conservation of 'pure' dingoes is a management objective in the Tanami

Desert, the region should be kept free of domestic dogs or attempts should be made to de-sex extant domestic animals. Other management options include removing obvious hybrids from the population. However, on the basis of the sampling undertaken for the present study, hybrids could not be reliably identified solely on the basis of coat colour and body morphology. The only variation in the population was the occurrence of black-and-tan individuals; all but one was classified as dingo (3*Q*-score 1 or 2 in Table 2). Additionally, the percentage of black-and-tan animals sampled in the present study was the same that Corbett (1985) reported for the northern desert areas and for Thai dingoes. The coat colour of dingoes is also known to encompass ginger, black-and-tan and white and this is supported by cross-breeding experiments (Newsome and Corbett 1982; Corbett 2001*a*; Elledge *et al*. 2006). Therefore, there were no morphological characteristics identified that could be used to distinguish hybrids in the current population.

Other factors indicating hybridisation include changes in breeding cycles. Dingoes have one breeding cycle per year and domestic dogs of similar size can potentially breed twice per year (Newsome and Corbett 1982). Jones and Stevens (1988) observed that the breeding season of hybrid dogs in the Victorian highlands was extended in comparison with central Australian dingoes and that two oestrus cycles sometimes occurred, but that only one litter was ever raised by a female in a year. After 3 years of observations in the mine sites, we saw no evidence of any shift in breeding cycles, despite hybrids being identified by genetic analysis. Females were observed on heat around April each year but not at other times over the 3 years; aggressive encounters were also observed among males in April (Newsome 2011). Pups were observed in August, with none out of the single, typical season previously reported (Corbett 2001*a*; Fleming *et al*. 2001). If there is a management imperative to preserve this seasonality, it is therefore critical to prevent any further introgression by domestic dogs.

Where there are many free-roaming domestic dogs in and around towns in central Australia, there is a higher risk of hybridisation with dingoes (Newsome and Corbett 1985). The present study sampled domestic dogs at two towns and there was little evidence of possible introgression associated with the settlements; only two animals had dingo genes. Although this provided possible evidence of gene flow between domestic dogs and dingoes, the proportion of animals with dingo genes could have been biased down by the procedural limitations that were imposed on capture and restraint. Only those animals that could be manually restrained were sampled and there was no sampling in areas surrounding the towns. Free-roaming domestic dogs in urban and rural environments often go on forays and can have large home ranges (Meek 1999). Newsome and Corbett (1985) recovered an obvious domestic dog 4 km from a township and we sighted domestic dogs ~10 km outside the boundary of Yuendumu. It is possible that areas surrounding the settlements are potential arenas for hybridisation. Sampling in areas surrounding settlements should therefore be a priority to assess levels of hybridisation. This is particularly important in circumstances where food for resident domestic animals is only irregularly provided (thus increasing their need to forage and scavenge more widely) and where there is no control of animal movements through fencing or leashing.

The collected DNA allowed us to investigate the purity of dingo populations at the mine sites and, in conjunction with other field observations, determine whether access to human-provided food at the mines altered 'typical' dingo breeding and social behaviour. For example, we investigated whether there were stable groupings and defined territories or home ranges as observed elsewhere (Thomson 1992; Corbett 1988, 2001*a*; Fleming *et al*. 2001)? Although there was no measure to determine which dingoes belonged to particular packs, the genetic analyses at the mine sites revealed several important trends. First, the kinship analyses identified 14 family groups (i.e. full siblings or parent–offspring). Samples from Tanami Downs were independent from (or at least not directly related to) those sampled elsewhere at the mine sites (Fig. 4*b*). There was spatial separation of family groups within Tanami Downs, with one family group identified on the eastern edge of the station, some 10 km from the other groups (Fig. 4*b*). This suggests a level of territoriality on Tanami Downs, in contrast to the other mine-site areas, although further sampling would be needed to quantify and confirm that possibility. However, there were no recaptures or sightings of any dingoes caught from another site on Tanami Downs, or *vice versa*. In addition, none of the 13 dingoes fitted with GPS collars in the surrounding region during the study period visited Tanami Downs (Newsome *et al*. 2013). The STRUCTURE analysis also supported the separation of the Tanami Downs animals, with the presence of admixed individuals (white dots in Fig. 4*a*) being found in all areas except Tanami Downs.

Corbett (1988) suggested that fracturing of dingo packs into smaller groups can lead to very high rates of overall population increase because every female would have the opportunity to breed, which is in contrast to the dominance-hierarchy breeding limitation model. In the present study, the analysis identified a large family group of 55 individuals at The Granites (white dots in Fig. 4*b*). This may represent a rapidly breeding family, an inbred group or a very large pack. Corbett (1988) and Wallach and O'Neill (2009) suggested that lethal control programs might cause packs to fracture. A one-off control program, implemented at The Granites 2 years before the present study, may have caused fracturing of local social groups. The large numbers of members of one group could indicate successful breeding by multiple related females, as in the model by Corbett (1988).

However, the more likely explanation is that the high density dingo population at The Granites during our study resulted from the large quantities of human-provided resources that were available to dingoes at the waste facilities (Newsome 2011). This surfeit of continuously available food could result in greater survival of pups, reduced mortality or increased production of pups, which would also account for the observed high densities, regardless of potential fracturing of packs. Hence, rather than pack fracturing, the large number of family groups using the refuse tip at The Granites, each with a large number of individual members, indicates amalgamation of kin groups into a larger single pack. The high number of individuals using the resource is indicative of a rich resource base and possibly greater reproductive success and population growth. Thus, we suggest that the social limitations on dingoes (i.e. infanticide of the pups of subordinate kin females by dominant females, decreasing potential competition for

resources from their offspring; Corbett 1988) are likely to be removed or greatly reduced at The Granites and similar sites because of the excess food supply for the animals. More females could breed successfully if social population-regulatory pressures were reduced, and the abundant and constant food supply would likely also increase pup survival to independence. It is also possible that the removal of social constraints and the surplus resources act in concert to increase population density. It is possible that aggressive interactions among dingoes are more risky to individual animals when densities are high which, along with generally less aggression, would reduce agonistic encounters that enforce dominance among females.

Although Thomson (1992) and Robley *et al*. (2010) showed that dingoes and other wild dogs can disperse prodigious distances, our findings suggested that *in situ* reproduction has a great effect on increases in the numbers of wild canids and that this can occur without substantial immigration from uncontrolled neighbouring areas. This is useful information for planning among pastoralists who implement lethal control, through accounting for local reproduction first and immigration second. Relatedness testing similar to ours could be used on dingo populations elsewhere, to further resolve this issue for other ecosystems. For example, our STRUCTURE analysis identified a population cluster at The Granites and a second one either side (Fig. 4*a*). This indicated either dispersal of the second population from one side of the mine to the other or that the population at The Granites grew in the middle, dividing an original population. The kin analysis did not identify dingoes in the same family group from Tanami Downs and any other area, so the latter is more likely — that is, a different group of dingoes bred prolifically around the mine site because of the abundance of resources. The mine cluster may have begun as only a few migrants from elsewhere or may be differentiated because of founder effect (i.e. population founding by a small number of individuals) (Mayr 1954).

Alternatively, prey-related variables have been cited as a potential mechanism for population subdivision between specialists on a particular prey, and generalists (e.g. grey wolves, *Canis lupus*; Carmichael *et al*. 2001). Although the size of our study area around the mine site is small, there were clear changes in dietary preferences between animals around the mine sites and those away from them (Newsome 2011). For example, there was far greater switching of prey in relation to prey availability by dingoes at sites away from the mine, in contrast to those nearby where human-provided food was continuously available and reliance on natural prey was not necessary to meet daily energetic requirements (Newsome 2011). Clearly, much more work is needed to elucidate this trend, although it does demonstrate that genetic subdivision as well as distance should be considered when attempting to determine the spatial extent at which anthropogenic activities will affect populations of wild canids.

Developing sound-management strategies to minimise hybridisation between dingoes and domestic dogs requires an understanding of other influencing factors such as human-caused mortality (Rutledge *et al*. 2010), resource availability (Darimont *et al*. 2008) and environmental heterogeneity (Seehausen *et al*. 2008). As a start, however, if dingoes are to be preserved as a separate genotype, populations of domestic dogs and dingoes must be reproductively isolated. This is not a simple issue because of the complex relationships between indigenous Australians living in remote towns and both their companion animals and dingoes (Smith and Litchfield 2009). These relationships will influence the strategies that are available for managing dingoes on their lands. For example, dog owners are often reluctant to permit euthanasia of community dogs and/or dingoes because these often have special (e.g. cultural and familial) standing in the community (Hardaker 2012). That said, numbers of domestic dogs in remote settlement areas can be reduced over time by de-sexing and limiting immigration (Hardaker 2012). However, agreements with community members over strategies for reducing dog populations will take time, consultation and patience.

Removing hybrids from populations in the wild will also be more difficult because it is impossible to reliably identify hybrids in the field. Nonetheless, the importance of central Australian dingoes to the conservation of the dingo lineage as a whole and the rapidity with which hybridisation is progressing in other areas make management of these populations an urgent concern (Stephens 2011). However, if the management objective is to retain a lower rate of increase of the dingo populations in human-modified landscapes, it is important to reduce dingo access to domestic and commercial waste. Studies on foxes (*Vulpes vulpes*; Bino *et al*. 2010) and coyotes (*Canis latrans*; Fedriani *et al*. 2001) have demonstrated similarly that anthropogenic food sources support higher densities of wild canids than do nearby unmodified landscapes. In terms of managing the issue, Bino *et al*. (2010) demonstrated that fox abundance and use of human settlements could be reduced by effectively managing food waste. Therefore, at a minimum, a shift from *laissez faire* dumping to one in which waste is centralised, contained, safely stored and treated, or removed, is required to retain normal rates of increase by dingoes, and other free-ranging canids, in human-modified landscapes.

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References

Allen, B. L., Fleming, P. J. S., Allen, L. R., Engeman, R. M., Ballard, G., and Leung, L. K. P. (2013). As clear as mud: a critical review of evidence for the ecological roles of Australian dingoes. *Biological Conservation* **159**, 158–174. doi:10.1016/j.biocon.2012.12.004

Allendorf, F. W., Leary, R. F., Spruell, P., and Wenburg, J. K. (2001). The problems with hybrids: setting conservation guidelines. *Trends in Ecology & Evolution* **16**, 613–622. doi:10.1016/S0169-5347(01)02290-X

Arnold, M. L. (1992). Natural hybridization as an evolutionary process. *Annual Review of Ecology and Systematics* **23**, 237–261. doi:10.1146/annurev.es.23.110192.001321

Barton, N. H., and Hewitt, G. M. (1985). Analysis of hybrid zones. *Annual Review of Ecology and Systematics* **16**, 113–148. doi:10.1146/annurev.es.16.110185.000553

Barton, N. H., and Hewitt, G. M. (1989). Adaptation, speciation and hybrid zones. *Nature* **341**, 497–503. doi:10.1038/341497a0

Baume, F. (1994). 'Tragedy Track: the Story of The Granites.' (North Flinders Mines Ltd and Hesperian Press: Perth.)

Bino, G., Dolev, A., Yosha, D., Guter, A., King, R., Saltz, D., and Kark, S. (2010). Abrupt spatial and numerical responses of overabundant foxes to a reduction in anthropogenic resources. *Journal of Applied Ecology* **47**, 1262–1271. doi:10.1111/j.1365-2664.2010.01882.x

Bohling, J. H., and Waits, L. P. (2011). Assessing the prevalence of hybridization between sympatric *Canis* species surrounding the red wolf (*Canis rufus*) recovery area in North Carolina. *Molecular Ecology* **20**, 2142–2156. doi:10.1111/j.1365-294X.2011.05084.x

Breckwoldt, R. (1988). 'The Dingo: a Very Elegant Animal.'(Angus and Robertson Publishers: Sydney.)

Broquet, T., Berset-Braendli, L., Emaresi, G., and Fumagalli, L. (2007). Buccal swabs allow efficient and reliable microsatellite genotyping in amphibians. *Conservation Genetics* **8**, 509–511. doi:10.1007/s10592-006-9180-3

Carmichael, L. E., Nagy, J. A., Larter, N. C., and Strobeck, C. (2001). Prey specialization may influence patterns of gene flow in wolves of the Canadian Northwest. *Molecular Ecology* **10**, 2787–2798.

Corbett, L. K. (1985). Morphological comparisons of Australian and Thai dingoes: a reappraisal of dingo status, distribution and ancestry. *Proceedings of the Ecological Society of Australia* **13**, 277–291.

Corbett, L. K. (1988). Social dynamics of a captive dingo pack: population regulation by dominant female infanticide. *Ethology* **78**, 177–198. doi:10.1111/j.1439-0310.1988.tb00229.x

Corbett, L. K. (2001a). 'The Dingo in Australia and Asia.' (JB Books: Adelaide.)

Corbett, L. K. (2001b). The conservation status of the dingo *Canis lupus dingo* in Australia, with particular reference to New South Wales: threats to pure dingoes and potential solutions. In 'A Symposium on the Dingo'. (Eds C. R. Dickman and D. Lunney.) pp. 10–19. (Royal Zoological Society of New South Wales: Sydney.)

Crawford, N. G. (2010). SMOGD: software for the measurement of genetic diversity. *Molecular Ecology Resources* **10**, 556–557. doi:10.1111/j.1755-0998.2009.02801.x

Daniels, M. J., and Corbett, L. K. (2003). Redefining introgressed protected mammals: when is a wildcat a wild cat and a dingo a wild dog? *Wildlife Research* **30**, 213–218. doi:10.1071/WR02045

Darimont, C. T., Paquet, P. C., and Reimchen, T. E. (2008). Spawning salmon disrupt trophic coupling between wolves and ungulate prey in coastal British Columbia. *BMC Ecology* **8**, 14. doi:10.1186/1472-6785-8-14

Dickman, C. R. (1996). Impact of exotic generalist predators on the native fauna of Australia. *Wildlife Biology* **2**, 185–195.

Elledge, A. E., Leung, L. K. P., Allen, L. R., Firestone, K., and Wilton, A. N. (2006). Assessing the taxonomic status of dingoes *Canis familiaris dingo* for conservation. *Mammal Review* **36**, 142–156. doi:10.1111/j.1365-2907.2006.00086.x

Elledge, A. E., Allen, L. R., Carlsson, B. L., Wilton, A. N., and Leung, L. K. P. (2008). An evaluation of genetic analyses, skull morphology and visual appearance for assessing dingo purity: implications for dingo conservation. *Wildlife Research* **35**, 812–820. doi:10.1071/WR07056

Evanno, G., Regnaut, S., and Goudet, J. (2005). Detecting the number of clusters of individuals using the software STRUCTURE: a simulation study. *Molecular Ecology* **14**, 2611–2620. doi:10.1111/j.1365-294X.2005.02553.x

Fedriani, J. M., Fuller, T. K., and Sauvajot, R. M. (2001). Does availability of anthropogenic food enhance densities of omnivorous mammals? An example with coyotes in southern California. *Ecography* **24**, 325–331.

Fleming, P. J. S., Corbett, L. K., Harden, R., and Thomson, P. (2001). 'Managing the Impacts of Dingoes and Other Wild Dogs.' (Bureau of Rural Sciences: Canberra.)

Fleming, P. J. S., Allen, B. L., and Ballard, G. (2012). Seven considerations about dingoes as biodiversity engineers: the socioecological niches of dogs in Australia. *Australian Mammalogy* **34**, 119–131. doi:10.1071/AM11012

Francisco, L. V., Langston, A. A., Mellersh, C. S., Neal, C. L., and Ostrander, E. A. (1996). A class of highly polymorphic tetranucleotide repeats for canine genetic mapping. *Mammalian Genome* **7**, 359–362.

Fredholm, M., and Winterø, A. K. (1995). Variation of short tandem repeats within and between species belonging to the Canidae family. *Mammalian Genome* **6**, 11–18. doi:10.1007/BF00350887

Gibson, D.F. (1986). 'A Biological Survey of the Tanami Desert in the Northern Territory.' (Parks and Wildlife Commission of the Northern Territory: Alice Springs, NT.)

Handel, C. M., Pajot, L. M., Talbot, S. L., and Sage, G. K. (2006). Use of buccal swabs for sampling DNA from nestling and adult birds. *Wildlife Society Bulletin* **34**, 1094–1100. doi:10.2193/0091-7648(2006)34[1094:UOBSFS]2.0.CO;2

Hardaker, J. (2012). Aspects relating to pets, people and indigenous communities and how to work together for a sustainable way forward. In 'Proceedings of the Australian Institute of Animal Management Annual Conference on Animal Management, 2012'. (Ed. D. Murray.) pp. 48–53. (The Australian Institute of Animal Management: Canberra.)

Holmes, N. G., Dickens, H. F., Parker, H. L., Binns, M. M., Mellersh, C. S., and Sampson, J. (1995). Eighteen canine microsatellites. *Animal Genetics* **26**, 132–133. doi:10.1111/j.1365-2052.1995.tb02659.x

Hubisz, M. J., Falush, D., Stephens, M., and Pritchard, J. K. (2009). Inferring weak population structure with the assistance of sample group information. *Molecular Ecology Resources* **9**, 1322–1332. doi:10.1111/j.1755-0998.2009.02591.x

Ivanova, N. V., Dewaard, J. R., and Hebert, P. D. N. (2006). An inexpensive, automation-friendly protocol for recovering high-quality DNA. *Molecular Ecology Notes* **6**, 998–1002. doi:10.1111/j.1471-8286.2006.01428.x

Jakobsson, M., and Rosenberg, N. A. (2007). CLUMPP: a cluster matching and permutation program for dealing with label switching and multimodality in analysis of population structure. *Bioinformatics* **23**, 1801–1806. doi:10.1093/bioinformatics/btm233

Johnson, C. N., Isaac, J. L., and Fisher, D. O. (2007). Rarity of a top predator triggers continent-wide collapse of mammal prey: dingoes and marsupials in Australia. *Proceedings. Biological Sciences* **274**, 341–346. doi:10.1098/rspb.2006.3711

Jones, E., and Stevens, P. L. (1988). Reproduction in wild canids, *Canis familiaris*, from the eastern highlands of Victoria. *Wildlife Research* **15**, 385–394. doi:10.1071/WR9880385

Jost, L. (2008). GST and its relatives do not measure differentiation. *Molecular Ecology* **17**, 4015–4026. doi:10.1111/j.1365-294X.2008.03887.x

Konovalov, D. A., Manning, C., and Henshaw, M. T. (2004). KINGROUP: a program for pedigree relationship reconstruction and kin group assignments using genetic markers. *Molecular Ecology Notes* **4**, 779–782. doi:10.1111/j.1471-8286.2004.00796.x

Mahood, M. (1996). 'Icing on the Damper.' (Central Queensland University Press: Rockhampton, Qld.)

Mayr, E. (1954). Change of Genetic Environment and Evolution. In 'Evolution as a Process.' (Eds J. Huxley, A. C. Hardy and E. B. Ford.) pp. 157–180. (Allen and Unwin: London.)

Meek, P. D. (1999). The movement, roaming behaviour and home range of free-roaming domestic dogs, *Canis lupus familiaris*, in coastal New South Wales. *Wildlife Research* **26**, 847–855. doi:10.1071/WR97101

Meggitt, M. J. (1965). The Association between Australian Aborigines and Dingoes. In 'Man, Culture and Animals'. (Eds A. Leeds and A. Vayda.) pp. 7–26. (American Association for the Advancement of Science: Washington, DC.)

Mellersh, C. S., Langston, A. A., Acland, G. M., Fleming, M. A., Ray, K. W., Wiegand, N. A., Wiegand, N. A., Francisco, L. V., Gibbs, M., Aguirre, G. D., and Ostrander, E. A. (1997). A linkage map of the canine genome. *Genomics* **46**, 326–336. doi:10.1006/geno.1997.5098

Mooney, H. A., and Cleland, E. E. (2001). The evolutionary impact of invasive species. *Proceedings of the National Academy of Sciences, USA* **98**, 5446–5451. doi:10.1073/pnas.091093398

Moore, W. S. (1977). An evaluation of narrow hybrid zones in vertebrates. *The Quarterly Review of Biology* **52**, 263–277. doi:10.1086/409995

Newsome, T. M. (2011). The ecology of the dingo (*Canis lupus dingo*) in the Tanami Desert in relation to human resource subsidies. Ph.D. Thesis, The University of Sydney.

Newsome, A. E., and Corbett, L. K. (1982). The identity of the dingo II. Hybridization with domestic dogs in captivity and in the wild. *Australian Journal of Zoology* **30**, 365–374. doi:10.1071/ZO9820365

Newsome, A. E., and Corbett, L. K. (1985). The identity of the dingo III. The incidence of dingoes, dogs and hybrids and their coat colours in remote and settled regions of Australia. *Australian Journal of Zoology* **33**, 363–375. doi:10.1071/ZO9850363

Newsome, A. E., Corbett, L. K., and Carpenter, S. M. (1980). The identity of the dingo I. Morphological discriminants of dingo and dog skulls. *Australian Journal of Zoology* **28**, 615–625. doi:10.1071/ZO9800615

Newsome, T. M., Ballard, G.-A., Dickman, C. R., Fleming, P. J. S., and van de Ven, R. (2013). Home range, activity and sociality of a top predator, the dingo: a test of the Resource Dispersion Hypothesis. *Ecography* doi:10.1111/j.1600-0587.2013.00056.x

Ostrander, E. A., Sprague, G. F., and Rine, J. (1993). Identification and characterization of dinucleotide repeat $(CA)_n$ markers for genetic mapping in dog. *Genomics* **16**, 207–213. doi:10.1006/geno.1993.1160

Ostrander, E. A., Mapa, F. A., Yee, M., and Rine, J. (1995). One hundred and one new simple sequence repeat-based markers for the canine genome. *Mammalian Genome* **6**, 192–195. doi:10.1007/BF00293011

Peakall, R., and Smouse, P. E. (2006). GENALEX 6: genetic analysis in Excel. Population genetic software for teaching and research. *Molecular Ecology Notes* **6**, 288–295. doi:10.1111/j.1471-8286.2005.01155.x

Pople, A. R., Grigg, G. C., Cairns, S. C., Beard, L. A., and Alexander, P. (2000). Trends in the numbers of red kangaroos and emus on either side of the South Australian dingo fence: evidence for predator regulation? *Wildlife Research* **27**, 269–276. doi:10.1071/WR99030

Primmer, C. R., and Matthews, M. E. (1993). Canine tetranucleotide repeat polymorphism at the VIAS-D10 locus. *Animal Genetics* **24**, 332. doi:10.1111/j.1365-2052.1993.tb00334.x

Pritchard, J. K., Stephens, M., and Donnelly, P. (2000). Inference of population structure using multilocus genotype data. *Genetics* **155**, 945–959.

Raymond, M., and Rousset, F. (1995). GENEPOP (version 1.2): population genetics software for exact tests and ecumenicism. *The Journal of Heredity* **86**, 248–249.

Rhymer, J. M., and Simberloff, D. (1996). Extinction by hybridization and introgression. *Annual Review of Ecology and Systematics* **27**, 83–109. doi:10.1146/annurev.ecolsys.27.1.83

Richards, B., Skoletsky, J., Shuber, A. P., Balfour, R., Stern, R. C., Dorkin, H. L., Parad, R. B., Witt, D., and Klinger, K. W. (1993). Multiplex PCR amplification from the CFTR gene using DNA prepared from buccal brushes/swabs. *Human Molecular Genetics* **2**, 159–163. doi:10.1093/hmg/2.2.159

Robley, A., Gormley, A., Forsyth, D., Wilton, A., and Stephens, D. (2010). Movements and habitat selection by wild dogs in eastern Victoria. *Australian Mammalogy* **32**, 23–32. doi:10.1071/AM09030

Rose, D. B. (1992). 'Dingo Makes Us Human: Life and Land in an Aboriginal Australian Culture.' (Cambridge University Press: Melbourne.)

Rousset, F. (2008). GENEPOP'007: a complete re implementation of the genepop software for Windows and Linux. *Molecular Ecology Resources* **8**, 103–106. doi:10.1111/j.1471-8286.2007.01931.x

Rutledge, L. Y., Bos, K. I., Pearce, R. J., and White, B. N. (2010). Genetic and morphometric analysis of sixteenth century *Canis* skull fragments: implications for historic eastern and gray wolf distribution in North America. *Conservation Genetics* **11**, 1273–1281. doi:10.1007/s10592-009-9957-2

Savolainen, P., Leitner, T., Wilton, A. N., Matisoo-Smith, E., and Lundeberg, J. (2004). A detailed picture of the origin of the Australian dingo, obtained from the study of mitochondrial DNA. *Proceedings of the National Academy of Sciences, USA* **101**, 12387–12390. doi:10.1073/pnas.0401814101

Seehausen, O. L. E., Takimoto, G., Roy, D., and Jokela, J. (2008). Speciation reversal and biodiversity dynamics with hybridization in changing environments. *Molecular Ecology* **17**, 30–44. doi:10.1111/j.1365-294X.2007.03529.x

Smith, B. P., and Litchfield, C. A. (2009). A review of the relationship between indigenous Australians, dingoes (*Canis dingo*) and domestic dogs (*Canis familiaris*). *Anthrozoos* **22**, 111–128. doi:10.2752/175303709X434149

Stephens, D. (2011). The molecular ecology of Australian wild dogs: hybridisation, gene flow and genetic structure at multiple geographic scales. Ph.D. Thesis, The University of Western Australia, Perth.

Thomson, P. C. (1992). The behavioural ecology of dingoes in north-western Australia. IV. Social and spatial organisation, and movements. *Wildlife Research* **19**, 543–563. doi:10.1071/WR9920543

Tunbridge, D. (1996). Mammals of the dreaming. Ph.D. Thesis, University of Canberra.

Wallach, A. D., and O'Neill, A. J. (2009). Threatened species indicate hot-spots of top–down regulation. *Animal Biodiversity and Conservation* **32**, 127–133.

Weir, B., and Cockerham, C. C. (1984). Estimating *F*-statistics for the analysis of population structure. *Evolution* **38**, 1358–1370. doi:10.2307/2408641

Wilton, A. N. (2001). DNA methods of assessing dingo purity. In 'A Symposium on the Dingo'. (Eds C. R. Dickman and D. Lunney.) pp. 49–56. (Royal Zoological Society of New South Wales: Sydney.)

Wilton, A. N., Stewart, D., and Zafiris, K. (1999). Microsatelite variation in the Australian dingo. *The American Genetic Association* **90**, 108–111.