

Hybridisation between the dingo, *Canis lupus dingo*, and the domestic dog, *Canis lupus familiaris*, in Victoria: a critical review

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Abstract. This paper reviews two separate population models proposed for a group of wild canids inhabiting the Victorian eastern highlands and re-analyses some of the data used. The first model was based upon two studies that used eight skull measurements in a canonical variate equation. Those studies classified population samples into three separate groups consisting of dingoes, feral domestic dogs and their hybrids. The second model, based upon a later study, classified a separate and additional population sample on the basis of both coat colour and physical appearance, but also cross-referenced the classifications to their canonical scores. That study rejected the model of three separate canid groups and the ability of the canonical variate equation to differentiate 'pure' dingoes from other canids. Instead the population was classified as a single group of dingo-like wild canids with an increased range in the variability of their physical characteristics compared to the original dingo population. After a re-evaluation of the data from the latter study and careful examination of the limitations of the canonical variate equation, the evidence presented here supports the population model of a single group of wild canids. Theoretical considerations associated with these two population models are discussed, as are the limitations of the canonical variate equation to classify the Victorian eastern highlands and other Australian wild canid populations.

Additional keywords: canid taxonomy, Canidae, canonical variate analysis, cross breeds, hybrids, Victorian eastern highlands, wild canids.

Introduction

In Victoria, Australia, the distribution of wild canids, commonly termed dingoes, *Canis lupus dingo*, has been reduced since European settlement and they are now largely restricted to more heavily forested ranges of the eastern highlands located in the east and north-east of the state. Their distribution is thus contiguous with wild canids inhabiting the similar forested areas of south-eastern New South Wales (collectively the south-eastern highlands). Large areas remain as crown land, including state forests and national parks. Thus, extensive areas remain relatively unaffected by human settlement and wild canids of disputed taxonomic status are abundant.

From the 1830s pastoralists began moving stock into some of these areas, and fencing of stock runs began from the 1860s after land tenure laws were enacted (Anon. 1974). Hybridisation between the wolf-like canids is common (Wayne 1993), so it can be reasonably assumed that hybridisation between dingoes and domestic dogs, *Canis lupus familiaris*, commenced from the 1830s, because the pastoralists of the day used these dogs as both work and companion animals. Since the 1970s there has been much discussion on the possibility and extent of hybridisation between dingoes and domestic dogs in both the Victorian eastern highlands and elsewhere in Australia.

To investigate this hybridisation further, a group of morphological discriminants was identified to separate dingo and

domestic dog skulls (Newsome *et al.* 1980) and those discriminants were then refined and used to develop a canonical variate equation to differentiate between dingoes, domestic dogs and their hybrids (Newsome and Corbett 1982). This equation was then used to classify a group of 50 canids collected from the Victorian eastern highlands as 36% dingoes, 52% hybrids and 12% feral domestic dogs. The possibility of dingoes becoming locally extinct through a process of hybridisation with domestic dogs was also raised. A further consolidation and refinement of the morphological discriminants followed and a group of 354 canids from the same general area were classified as 60.2% dingoes, 30.5% hybrids and 9.3% feral domestic dogs (Newsome and Corbett 1985: Table 3, regions 8, 9 and 10 combined).

A further sample of 554 wild canids was collected from the Victorian eastern highlands between 1981 and 1985 (Jones and Stevens 1988). Reproductive studies on that sample showed a single annual autumn and winter breeding season, similar to that of dingoes, with no evidence of females producing more than one litter per year, as has been reported for captive-bred hybrids (Catling *et al.* 1992). A detailed analysis of the coat colours and physical conformation of 338 adults from this group of canids, cross-referenced to their canonical scores was also carried out (Jones 1990). However, no statistically valid relationship between canonical score and any coat colour or conformation class was found and many classification anomalies were

encountered. There were canids with the appearance and coat colours of dingoes (Category G1 canids), yielding canonical scores within the ranges of either hybrids or domestic dogs. Other canids judged on conformation and coat colour as least likely to be dingoes (Category 3 canids) had canonical scores within the range of dingoes and canids classified as having the appearance and coat colours of hybrids also had canonical scores within the ranges of either dingoes or domestic dogs. Further, no feral domestic dogs were identified as such, either on the basis of physical confirmation, or on the basis of identifiable domestic dog skull characteristics.

When all of these results were considered, Jones (1990) concluded that the canonical variate analysis developed to discriminate between dingoes from arid central Australia and dingo-sized domestic dogs was not appropriate for the Victorian eastern highlands population. Rather, it was considered that the results could be satisfactorily explained only if that population was regarded as a single group of dingo-like wild canids sharing a common gene pool, with an expanded range of morphological characteristics to that of the original dingo population. Although not specifically stated at that time, the major consequence of this population model was to exclude the concept of the 'pure' dingo as an identifiable separate or distinct entity within the broader canid population, even though dingo-like canids were present. However, no specific criticisms of the canonical variate equation were made at that time, and no explanations were given as to the reasons why the canonical variate equation did not accurately classify the Victorian eastern highlands population.

In later literature the failure of the canonical variate equation to accurately classify the Victorian eastern highlands canids and the resultant population model proposed by Jones (1990) has been either overlooked, not understood, or misquoted and the canonical variate equation has been used to classify further Australian canid populations without qualification. For example, the equation was used to classify dingoes, cross breeds and domestic dogs for reproductive studies on canids from four regions across Australia, including the Victorian eastern highlands (Catling *et al.* 1992). In that paper the authors also noted that Jones and Stevens (1988) did not separate dingoes from cross breeds, in their earlier paper on reproduction.

Corbett (1995a) used the canonical variate equation to analyse additional canid populations when comparing regional differences in canonical scores, and Woodall *et al.* (1996) also used this technique to classify 110 canids from four separate locations in Queensland. In that study they cited the study of Jones (1990) as supporting the dingo, feral domestic dog and hybrid population model for the Victorian eastern highlands canid population, when in fact it did not. In a subsequent study, Corbett (2001) quoted the canids classified by Jones (1990) as comprising 17% dingoes, when no such conclusion was reached by Jones. This incorrect interpretation of the conclusions of Jones (1990) was repeated by Daniels and Corbett (2003).

Debate on the need for the conservation of dingoes and research into their identification towards that end, has also intensified in recent times. Both the canonical variate equation of Newsome and Corbett and DNA analysis (Wilton 2001) have been proposed as techniques for the identification of dingoes. This literature has been comprehensively reviewed by Elledge *et al.* (2006).

In Victoria, the Scientific Advisory Committee, created under the Flora and Fauna Guarantee Act of 1988, recently issued a *Final Recommendation Report*, which recommended the nomination of the dingo as a threatened native species (Anon. 2007). When making that determination, the Scientific Advisory Committee accepted a submission based upon the Victorian eastern highlands population model of a mixed group of dingoes, feral domestic dogs and their hybrids (Newsome and Corbett 1982, 1985; Corbett 2001), and ignored a submission based upon the conclusions of Jones (1990) that the population consisted of a single group of wild canids, from which 'pure' dingoes could not be differentiated. The significance here is that if legislation enacted regarding the conservation or management of the current Victorian wild canids is based upon incorrect scientific data, it could face legal challenge by those who may be disadvantaged by, or opposed to, such laws or management plans. Further, a lack of reliable diagnostic criteria for the identification of dingoes would make any such plans unworkable.

This paper examines the respective merits of these two different population models for the Victorian eastern highlands canids, presents a more detailed analysis of the data from Jones (1990) and examines in detail the limitations of this particular canonical variate equation to classify the Victorian eastern highlands and other Australian wild canid populations.

Methods and results

The canonical variate equation (Newsome *et al.* 1980; Newsome and Corbett 1982, 1985) was based upon eight variables refined from the skull measurements of two separate groups of animals – 50 presumed pure dingoes collected from remote central Australia, and 43 domestic dogs collected from the Canberra dog pound (Blue-healers, Kelpies, Border Collies and their crosses) – and tested against a group of 41 captive-bred hybrids. The hybrids were bred by crossing eight captive animals, presumed to be pure dingoes and collected as pups from remote central Australia, with seven domestic dogs of five breeds (Blue-heeler, Kelpie, Labrador, Doberman Pinscher and Beagle) over six years (1969–75). Note that the 50 dingoes and 43 domestic dogs used as reference groups for the skull variables were not the parents of the reference hybrids. The skull variables for the eight parental dingoes of the hybrid reference group were also measured, but those for the parental domestic dogs were not.

The equation is $Y = 0.249X1 - 0.261X2 + 1.999X3 - 1.137X4 + 0.318X5 + 0.475X6 - 0.205X7 + 0.136X8 - 3.717$, where $X1$ = length of the auditory bulla, $X2$ = maximum maxillary width, $X3$ = mid-crown width of tooth upper P4, $X4$ = basal crown length of tooth upper C1, $X5$ = opisthion to inion height, $X6$ = width of nasal bones at the premaxilla–maxilla suture, $X7$ = cranial height from the external auditory meatus to the bregma, and $X8$ = distance between the posterior alveolar rims of teeth upper C1 to P4. The relative importance of the skull measurements is in the order given in the equation. A skull is from a domestic dog if $Y \leq -1.394$, from a hybrid if Y is between -1.393 and 1.270 , or from a dingo if $Y \geq 1.271$. The values of the eight skull variables for the parental dingoes and the canid reference groups are given in Table 1.

The reference dingoes had longer auditory bullae ($X1$), a smaller maxillary width ($X2$), thicker carnassial teeth upper

Table 1. Values of the eight skull variables for the parental dingoes and canid reference groups

From Newsome and Corbett (1982) table 3, including Corrigenda Amendments for table 3, from Newsome and Corbett (1985). All measurements are in millimetres. Values are means \pm s.e. Significant differences between the variables of the parental and reference dingoes are shown in bold

Skull variable	Parental dingo (<i>n</i> = 8)	Dingo (<i>n</i> = 50)	Dog (<i>n</i> = 43)	Hybrid (<i>n</i> = 41)
<i>X1</i> = Length of the auditory bulla	25.7 \pm 0.4	25.1 \pm 0.2	20.8 \pm 0.3	22.1 \pm 0.3
<i>X2</i> = Maximum maxillary width	63.6 \pm 0.9	60.3 \pm 0.4	62.8 \pm 0.7	60.1 \pm 0.5
<i>X3</i> = Mid-crown width of upper P4	7.3 \pm 0.11	7.5 \pm 0.06	6.8 \pm 0.06	6.8 \pm 0.07
<i>X4</i> = Basal crown length of upper C1	9.7 \pm 0.24	9.5 \pm 0.09	9.8 \pm 0.12	9.4 \pm 0.12
<i>X5</i> = Opisthion toinion height	33.0 \pm 0.5	33.5 \pm 0.3	28.4 \pm 0.4	30.3 \pm 0.4
<i>X6</i> = Width of the nasal bones	12.4 \pm 0.3	11.6 \pm 0.1	10.2 \pm 0.2	10.7 \pm 0.2
<i>X7</i> = Auditory meatus to bregma height	56.8 \pm 0.9	55.9 \pm 0.3	58.2 \pm 0.6	55.2 \pm 0.5
<i>X8</i> = Distance between upper C1 to P4	48.2 \pm 0.8	54.6 \pm 0.3	50.5 \pm 0.6	49.8 \pm 0.7

P4 (*X3*), thinner canine teeth upper C1 (*X4*), a greater opisthion toinion height (*X5*), wider nasal bones (*X6*), a smaller cranial height from the external auditory meatus to the bregma (*X7*), and a greater distance between teeth upper C1 to P4 (*X8*) than the reference domestic dogs. The reference hybrids had values that were mainly intermediate, but their population scores overlapped those of the other two groups. An unpaired *t*-test carried out on the skull variables between the parental and reference dingoes found that there were significant differences in three of the eight variables tested (*X2*, *X6* and *X8*). The parental dingoes had a greater maxillary width ($P = 0.003$), a greater width of the nasal bones ($P = 0.005$) and a shorter distance between teeth upper C1 to P4 ($P \leq 0.0001$). Two of these variables (*X2* and *X8*) were dog-like rather than dingo-like, while the third variable (*X6*) was dingo-like.

In order to make a direct comparison with the three canid reference groups of Newsome and Corbett (1982, 1985), a sample of 338 adult wild canids from the 554 collected by Jones (1990) was classified by the canonical variate equation into three groups corresponding in canonical values to the dingo, domestic dog and hybrid groups of Newsome and Corbett. An unpaired *t*-test was carried out on every pair of skull variables between each canid reference group and the equivalent wild canid group. These data are presented in Table 2.

For this comparison, the wild canids in the group for which $Y \geq 1.271$ were significantly different from the reference dingoes

with respect to five of the eight skull variables. The wild canids were similar in length of auditory bullae (*X1*), had a greater maxillary width (*X2*), were similar in width of teeth upper P4 (*X3*), had a greater basal length of teeth upper C1 (*X4*), a greater opisthion toinion height (*X5*), a greater width of nasal bones (*X6*), a greater cranial height from the external auditory meatus to the bregma (*X7*) and a similar distance between teeth upper C1 to P4 (*X8*).

The wild canids in the group for which $Y \leq -1.394$ were significantly different from the reference domestic dogs with respect to four of the eight skull variables. The wild canids had longer auditory bullae (*X1*), had a similar maxillary width (*X2*), were similar in width of teeth upper P4 (*X3*), had a greater basal length of teeth upper C1 (*X4*), a greater opisthion toinion height (*X5*), a greater width of nasal bones (*X6*), had a similar cranial height from the external auditory meatus to the bregma (*X7*) and a similar distance between teeth upper C1 to P4 (*X8*).

The wild canids in the group for which $Y = -1.393$ – 1.270 were significantly different from the reference hybrids with respect to all of the eight skull variables. The wild canids had longer auditory bullae (*X1*), had a greater maxillary width (*X2*), were greater in width of teeth upper P4 (*X3*), had a greater basal length of teeth upper C1 (*X4*), a greater opisthion toinion height (*X5*), a greater width of nasal bones (*X6*), a greater cranial height from the external auditory meatus to the bregma (*X7*) and a greater distance between teeth upper C1 to P4 (*X8*).

Table 2. Comparisons of the eight skull variables between the three canid reference groups of Newsome and Corbett (Table 1), and the wild canids of Jones (1990) classified into the same three corresponding groups

All measurements are in millimetres. Values are means \pm s.e. Significant differences between the skull variables of the canid reference groups of Newsome and Corbett and the equivalent wild canid groups of Jones are shown in bold

Skull variable	Canid ≥ 1.271 (<i>n</i> = 111)		Canid ≤ -1.394 (<i>n</i> = 13)		Canid -1.393 to 1.270 (<i>n</i> = 214)	
	Mean \pm s.e.	<i>t</i>	Mean \pm s.e.	<i>t</i>	Mean \pm s.e.	<i>t</i>
<i>X1</i>	25.0 \pm 0.12	0.65	22.6 \pm 0.52	0.005	24.2 \pm 0.09	<0.0001
<i>X2</i>	63.0 \pm 0.29	<0.0001	62.4 \pm 0.98	0.77	63.2 \pm 0.19	<0.0001
<i>X3</i>	7.4 \pm 0.04	0.17	6.6 \pm 0.12	0.12	7.1 \pm 0.03	<0.0001
<i>X4</i>	10.0 \pm 0.07	<0.0001	10.3 \pm 0.17	0.04	10.1 \pm 0.05	<0.0001
<i>X5</i>	35.8 \pm 0.23	<0.0001	32.3 \pm 0.89	<0.0001	34.0 \pm 0.18	<0.0001
<i>X6</i>	12.6 \pm 0.11	<0.0001	11.8 \pm 0.26	0.0001	12.2 \pm 0.07	<0.0001
<i>X7</i>	58.8 \pm 0.26	<0.0001	58.2 \pm 0.83	1.0	58.8 \pm 0.19	<0.0001
<i>X8</i>	54.1 \pm 0.28	0.28	49.5 \pm 1.16	0.43	52.7 \pm 0.21	<0.0001

Discussion

The canonical variate equation

The study by Jones (1990) clearly demonstrated that the canonical variate equation of Newsome and Corbett did not accurately classify the Victorian eastern highlands wild canid population, and there must be reasons for this. The canonical variate equation produces a numerical value by adding together the products of all those skull variables and their weightings that are larger for the reference dingoes ($X1$, $X3$, $X5$, $X6$ and $X8$) (dingo-like variables), and subtracting the products of all those skull variables and their weightings that are larger for the reference domestic dogs ($X2$, $X4$ and $X7$) (dog-like variables). The variables are also ranked in order of importance. Thus the equation is very specific, and the limitations to its use are that the dingoes in the population being analysed and the domestic dogs that mate with them must have similar skull shapes to those of the reference dingoes and reference domestic dogs.

Hence, before this equation can be used to classify any other wild canid population, it should be established that these similarities exist. If these similarities cannot be established but the equation is applied anyway, then it must be assumed that the canid groups under test have comparable skull shapes to the canid reference groups. The process of classification then relies upon untested *a priori* assumptions, and hence loses much of its scientific validity. Further, the additional assumption must be made that the numerical range of the hybrids remains mutually exclusive over time (i.e. overlap between the ranges of the hybrids and reference groups cannot occur). It should also be noted that this equation is attempting to differentiate two groups of canids that are separate, only at the subspecies level, and both groups have undergone differing degrees of modification by domestication (Scott 1968; Elledge *et al.* 2006). The equation is further complicated because, while the dingo skull can be regarded as a type, strictly speaking the domestic dog skull does not represent a specific type, but a subset of types.

Variations in dingo skulls

The 50 reference dingoes were collected from arid central Australia, a vastly different habitat to that of the Victorian eastern highlands and the sample size was small. Of further concern were the unexplained differences in the maxillary width ($X2$), width of the nasal bones ($X6$) and the distance between teeth upper C1 to P4 ($X8$) of the reference dingoes compared with the parental dingoes. These differences may indicate a greater range of variability in the shape of the dingo skull than the reference dingo population suggests. This, in turn, must limit the reliability of the method to discriminate between other wild canid groups. These factors were briefly discussed by Newsome and Corbett (1982), and Woodall *et al.* (1996) reported differences in the dimensions of some dingo skulls from four regional Queensland groups.

Variations in the skulls of hybridising domestic dogs

The selection of domestic dogs used for both the reference group and for breeding the reference hybrids was limited to dingo-sized animals, after it was found that size played an important part in the value of the various skull measurements (Newsome *et al.* 1980). However, in addition to the breeds mentioned previously, the

farms, residences and smaller townships adjacent to or near the surrounding timbered areas of the Victorian eastern highlands would contain a much larger variety of domestic dog breeds than those chosen for either the reference population or for breeding the reference hybrids. The composition of those domestic dogs breeding with dingoes could influence the skull shape and therefore the classification of the hybrids and this could be a further influence in applying the canonical variate equation to the Victorian eastern highlands canids, although size restraints would discount the more extreme breeds from mating. For example, when selecting the character set from dog skulls for the original equation, two Australian cattle dogs were excluded because of their large auditory bullae (Newsome *et al.* 1980). This illustrates the difficulty of the selection process, which was subjective in nature, given the great variety of skull shapes now present in modern domestic dogs. The possible effect of such factors should therefore be considered.

The hybrid reference group

The breeding of the hybrid reference group (Newsome and Corbett 1982) was by a captive breeding program of relatively short duration. There were approximately equal numbers of dingoes and domestic dogs and the hybrids were produced in captivity over a period of six years so that none of the natural biological processes that occur in the wild were duplicated. In addition, the skulls of the parental domestic dogs were not measured, so comparisons with the other groups could not be made. The artificial nature of the breeding process was a flaw in the development of the canonical variate equation; put simply, it did not duplicate the hybridisation processes that occur in wild canid populations over extended periods, and therefore could not be expected to produce or reflect the skull shapes of the resultant hybrids that now occur in the wild.

Size and shape of the Victorian wild canid skull

When the comparisons between the reference and wild canid groups (Table 2) are considered, the evidence indicates significant differences in the skull shape of the Victorian eastern highlands wild canids compared with those of the corresponding canid reference groups. There is a common pattern in the shape of the wild canid skull in which, over the three groups classified, 17 of the 24 total variables were significantly larger than those of the corresponding canid reference groups, and none were significantly smaller. All three wild canid groups had a larger basal crown length of tooth upper C1 ($X4$), a greater opisthion to inion height ($X5$) and wider nasal bones ($X6$) when compared with their respective canid reference groups. In addition, both groups with a score >-1.393 had a greater maxillary width ($X2$) and a greater cranial height from the external auditory meatus to the bregma ($X7$) than the reference dingoes and hybrids. The group with a score of ≤ -1.394 also had similar values for a greater maxillary width ($X2$) and a greater cranial height from the external auditory meatus to the bregma ($X7$), but in this case there were no significant differences found because they were tested against the reference domestic dogs. However, this group did have a larger auditory bulla ($X1$) than the reference domestic dogs, as did the canid group with a score of -1.393 to 1.270 over the corresponding reference hybrids.

Corbett (2001) examined the distribution of skull scores of dingoes from seven regions across Australia and found a significant difference for those from the south-eastern highlands region (including the Victorian eastern highlands) when compared with those of the other six regions. He considered the cause to be a greater level of hybridisation there rather than a different skull shape. The data presented in Table 2 suggest a larger skull overall for the Victorian eastern highlands population, but is not conclusive. This is not unexpected, since both regional differences and adaptations to different habitats can influence the size and shape of animals, including their skulls. Given both the mix of skull characters and the greater values of most skull variables now present, there is evidence for a larger original skull that has been further modified by the process of hybridisation. However, regardless of the relative importance of these two influences, it is clear that the wild canid population in the Victorian eastern highlands has a skull that is different in shape to the skulls of the canid reference groups and therefore cannot be classified accurately by the canonical variate equation of Newsome and Corbett.

Characteristics of the skull of Victorian wild canids

In total, over 400 wild canid skulls were examined, and 338 intact adult skulls were measured by Jones (1990). Even though the value of the canonical score for this sample of skulls varied from -3.34 to 4.31 the skulls were of a uniform appearance and type, and the canonical score for any particular skull could not be predicted by a simple physical examination. The most striking characteristics of all these skulls were the elevated heights of the sagittal and nuchal crests, the large size of the auditory bullae, and the well formed tooth row. These differences all fit with what one would expect from wild canids: the sagittal and the nuchal crests respectively form the attachment areas for the muscles that close the jaw and attach the skull to the neck. These muscles need to be strong for animals to catch, kill and devour prey, the large carnassial teeth and well formed tooth row are similarly needed, and the large auditory bulla suggests more acute hearing.

Feral domestic dogs

Newsome and Corbett (1985), in addition to classifying the previously mentioned 354 canids from the Victorian eastern highlands as 60.2% dingoes, 30.5% hybrids and 9.3% feral domestic dogs, also classified 53 canids from a New South Wales south coast population as 22.6% dingoes, 56.6% hybrids and 20.8% feral domestic dogs (Table 3, region 11), and a further 1184 canids from seven regions in northern and central Australia as 97.5% dingoes and 2.4% hybrids, with only one domestic dog present (Newsome and Corbett 1985: table 2, regions 1-7 combined). Woodall *et al.* (1996) also used the same canonical variate equation to classify 110 canid skulls from four separate locations in Queensland. Canids from Augathella and Fraser Island were classified as 95% dingoes and 5% hybrids and 83% dingoes and 17% hybrids respectively. No feral dogs were classified in either location. However canids from western Queensland were classified as 71% dingoes, 19% hybrids and 10% feral domestic dogs and those from south-eastern Queensland were classified as 50% dingoes, 30% hybrids and 20% feral domestic dogs. They also recognised that some

specimens that they classified by the canonical variate equation as dingoes could have been hybrids. Classifying the Victorian eastern highlands population of Jones (1990) using this equation gave 33% of canids in the range of dingoes, 63% in the range of hybrids and 4% in the range of feral domestic dogs. These studies, and later ones by Corbett (1995a, 2001), based on both the regional incidences of pure and hybrid coat colours and also skull score, were taken to suggest that dingo population purity was greatest in more remote northern Australia and least in the more settled southern regions.

Of interest here is that, with the possible exception of the western Queensland canids, remote and relatively unaltered populations of dingoes classified by the canonical variate equation yielded low numbers of hybrids and no feral domestic dogs, but populations from more settled locations yielded larger numbers of hybrids and also feral domestic dogs. In all of these studies the occurrences of feral domestic dogs have been accepted as normal, without additional comment by the respective authors. However, no canids so classified appear to have been independently identified as feral domestic dogs on either physical appearance, or on observable domestic dog-like skull characteristics. The great diversity in the physical appearance of modern domestic dogs – their coat colours, sizes, body characteristics and wide variety of skull shapes is both well known and documented (Scott 1968) – and the appearance of many of these characteristics in canid populations where they have been classified by the canonical variate equation, should be easily recognised in either individual animals or their skulls.

No feral domestic dogs were recognised by Jones (1990) using these criteria for the Victorian eastern highlands canids, even though 4% of them were placed in the range of feral domestic dogs by the canonical variate equation. He concluded that feral domestic dogs were not present in that sample of canids. It is therefore reasonable to assume that this would also apply to those other canid populations where feral domestic dogs were so classified. No populations of feral domestic dogs have been reported in the general literature, and if true feral domestic dog populations exist, they should be expected to occur in areas other than those localities populated by dingoes where hybrids are also common. However they appear only in wild canid populations analysed by the canonical variate equation after a significant amount of hybridisation has taken place, and are therefore not likely to be feral domestic dogs, but hybrids with canonical scores that have expanded over time to now fall within the range of domestic dogs.

The process of hybridisation in Victoria

In the Victorian eastern highlands hybridisation seems to have proceeded at a low rate for over 170 years, but the mechanisms of hybridisation remain speculative. Jones (1990) suggested that F1 hybrids were more likely produced from matings between wandering male domestic dogs and female dingoes because the progeny from the opposite cross would not survive, due to the difficulty of female domestic dogs raising litters of pups in the wild. Analysis of dingo mitochondrial DNA supports this view (Savolainen *et al.* 2004). Social barriers that restrict matings and therefore gene flow between dingoes and domestic dogs have been reported for central Australian populations (Corbett 1995b)

but no data are available for the Victorian eastern highlands canids. Presumably, the rarity of wandering domestic dogs encountering oestrous female wild canids could also be considered a barrier, but once the F1 hybrids so created reach reproductive age, they may be no more disadvantaged as regards further matings than any other canids. Initially, because F1 hybrids would be few, these animals would be much more likely to breed back to the broader dingo population. The process of gene flow through the population would have become increasingly more complex as domestic dogs of different breeds (or cross breeds) from various locations would have mated, over time, with either female dingoes or hybrids of various types. The adolescents from those matings would have then dispersed and further matings would have occurred between either individuals of further levels of mixed ancestry or the remaining dingoes. Natural selection, that most powerful of biological forces, would have also played a major role in what is essentially an evolutionary process. This complex spread of domestic dog genes throughout the population would have proceeded more rapidly as the number of hybrids increased, and the real driving force of hybridisation was not a group of feral domestic dogs, but the hybrids themselves.

The status of hybrids

Those canids not classified as dingoes or feral domestic dogs by the canonical variate equation and/or those with coat colours reflecting the influences of domestic dogs have been universally referred to as 'hybrids' or 'cross breeds' by authors other than Jones (1990). However, these animals are diverse in both appearance and genotype, do not constitute a uniform group of canids, and in many regions cannot be positively identified as such from dingoes. Several criticisms can therefore be made of classifying them simply as hybrids or cross breeds. First, this group, including those hybrids mistakenly classified as dingoes or feral domestic dogs, is now an important component of the wild canid populations in the more settled regions of Australia, and the fact of their existence, whether we like it or not, needs to be acknowledged. Second, the terms 'hybrid' or 'cross breed' do not accurately describe these animals because they are essentially dingo-like wild canids and most represent the end product of a slow process of change or continuing change, and not the product of a simple cross between a domestic dog and a dingo. Third, in the more settled regions of Australia, as is the case for the Victorian eastern highlands, there is no reliable method of differentiating hybrids from dingoes. All share a common gene pool and 'pure' dingoes may not now exist in these areas at all. Jones (1990) recognised this fact for the Victorian eastern highlands population, calling them simply by the collective term 'wild canids'. Corbett (2001) has also suggested that this population may now contain no 'pure' dingoes. Daniels and Corbett (2003), when discussing future conservation strategies now suggest a broader definition for dingoes, rather than one based upon type.

While the recent literature has been aimed at the conservation of 'pure' dingoes (Corbett 1995c, 2001; Dickman and Lunney 2001; Wilton 2001; Daniels and Corbett 2003; Elledge *et al.* 2006), this is not a realistic option for the Victorian eastern highlands canid population, or other similar populations that have undergone extensive hybridisation over a long period.

Management or conservation policies based upon incorrect scientific classification or unrealistic expectations of conserving 'pure' dingoes will not work, and new policies should now be developed to accommodate the present realities.

Failure of the canonical variate equation

Hybridisation over time between dingoes and domestic dogs has clearly increased the degree of genetic diversity in the Victorian eastern highlands canid population as a whole, and changes to the presumed original skull shape simply reflect this. While the canonical variate equation can readily differentiate between the skulls of dingoes and domestic dogs, it cannot do so when the eight skull variables are subject to change over time, caused by hybridisation. This effect would be compounded by any regional or habitat differences in skull shape. Thus, if one of the skull variables of an individual in a population under test was significantly different from its equivalent variable in the corresponding canid reference group, an incorrect classification could result. This effect would be compounded if this difference was large enough to change the ranking order of the variables, or in more extreme cases switched them from dingo-like to dog-like or *vice versa*. These effects would increase as more variables changed in value due to increased genetic diversity; thus the equation becomes less reliable as hybridisation within a canid population increases. The net effect of these changes is to expand the canonical scores of hybrids into the ranges of both dingoes and domestic dogs.

For example, in the Victorian eastern highlands sample of Jones (1990), 58 canids from the 338 classified by physical conformation were placed in the G1 category (ginger animals most likely to be dingoes). When this group was classified by the canonical variate equation, 36% were within the range of dingoes, 60% were within the range of hybrids and 4% were within the range of domestic dogs. In an attempt to refine the canonical variate equation further, Corbett (2001), when classifying dingo skulls from seven regions across Australia, defined a dingo as a canid having a ginger coat colour and with each of the eight skull variables within the 95% confidence limits of dingoes. It was hoped that this stricter definition for dingoes would reduce the possibility of classifying hybrids as dingoes. When this stricter definition was applied to the Victorian eastern highlands sample of Jones (1990), it yielded 19 canids from the 338 classified, 18 of which were female, but only 8 of them were placed in the G1 category. For this canid population the tighter classification technique simply selected a subset of skull variables from a much larger set of skull variables, and the inconsistent results shown above illustrate this. Further, no evidence exists to suggest that an individual so classified could not be a hybrid.

Conclusion

The population model of a single group of wild canids proposed by Jones (1990) for the Victorian eastern highlands is supported by the evidence, and the population model of a mixed group of dingoes, feral domestic dogs and their hybrids proposed by Newsome and Corbett (1982, 1985) is not supported. Thus the eastern Victorian population consists of a group of wild canids, from which 'pure' dingoes (if they exist) cannot be differentiated using skull morphology and coat colour criteria. Feral domestic

dogs are rare or absent. There is also evidence of a larger skull size overall for this population. The classification errors of other studies were caused by the limitations and shortcomings of the canonical variate equation when applied to canids with skulls different in shape to the reference canid groups, and by the unpredictable nature of a prolonged hybridisation process that has expanded the canonical scores of hybrids well into the ranges of both dingoes and domestic dogs. The limitations of the canonical variate equation identified from the study of this wild canid population, would also apply to other wild canid populations that have experienced a significant level of hybridisation with domestic dogs over a prolonged period of time. Therefore studies that have used this technique to classify other wild canid populations for taxonomic, reproductive or other purposes will all suffer from classification errors, which will be greater in populations with higher level of hybridisation.

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