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Coat Colour Inheritance in Dogs: Determination of Genotype from Phenotypic Observations

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Summary. The determination of partial genotype, *B*/*b* and *D*/*d*, for coat colour in dogs, from phenotypic observations, is discussed. It is shown that the probability of a given genotype can be reliably determined where multiple observations on the mating of a given dog are available.

Key words: Coat colour – Colour inheritance – Genotype – Dogs – Dobermanns

Introduction

Attention was focussed on this problem by recent controversy over the fawn Dobermann. The basic coat colour in this breed, excluding the tan-points and variations in the shades of the non-black colours, is determined by the interaction of two Mendelian genes, *B*/*b* and *D*/*d* (Little 1979). There are, thus, nine genotypes, as set out in Table 1. We identify each genotype by a Type number, following the notation of the Doberman Pinscher Club of America (Walker 1977).

Table 1. Genotypes and phenotypes in Dobermann coat colours

Type number	Genotype	Phenotype
1	*BBDD*	Black
2	*BBDd*	
3	*BbDD*	
4	*BbDd*	
5	*BBdd*	Blue
6	*Bbdd*	
7	*bbDD*	Liver
8	*bbDd*	
9	*bbdd*	Fawn[a]

[a] The genetic name of this phenotype is lilac, but fawn (Isabella) is most commonly used in this breed

Some current opinion among breed fanciers indicates that the blue and fawn colours are indicative of inferior animals. However, relatively few Dobermanns of these colours exist among the breeding population, so that it is very unlikely that significant deductions about them can have been made. Some current practice eliminates blues and fawns by culling. A move to have the fawn declared as highly undesirable has been rebuffed recently (The Kennel Club 1982).

An informed approach to breeding for colour requires that the genotypes of sufficient of the breeding population be known. Generally, this information is not available, and it is the purpose of this paper to show that such knowledge is ascertainable from phenotypic data on matings, provided that satisfactory approximations to the genotype distributions (prior probabilities) in the breeding population can be made.

Evaluation of Probability

In this work, data have been collected for two sires that have exerted an important influence on the current breeding population in England; the sires will be identified as H (a liver dog) and R (a black dog). The data have been collected from different parts of the country, and consisted, for the two sires, of information on the pedigree and colour of the breeding dam, the numbers and colours of the progeny resulting from each mating, and the colours of the sire and dam of the breeding dam. From this data (Tables 2 and 3), together with that in Table 4, we know that since sire H is liver he must be either Type 7 or Type 8, and because sire R has produced some liver progeny, and is himself black, he must be either Type 3 or Type 4. From this point, and using the progeny data, the probabilities attached to the possible genotypes of the sires can be determined, and also those of the breeding dams, albeit less reliably than those of the sires.

We let Y represent the total series of matings given in Table 2 (for sire H) or Table 3 (for sire R), and we let Z_k represent the situation that a sire is of Type k, ($k = 1, 2, \ldots, 9$). We need to determine the probability that the sire is of Type k, conditional upon the results of the experiment. We symbolize this probability as $P\,(Z_k \mid Y)$. It is a posterior prob-

Table 2. Data on sire H (Type 7 or 8) matings

Litter number	Colour and possible Types of dam[a]	Number of black progeny	Number of liver progeny	Total progeny
1	Black 1, 2, 3, 4	9	0	9
2	Black 1, 2, 3, 4	8	0	8
3[b]	Black 3, 4	8	6	14
4	Black 3, 4	7	3	10
5	Black 3, 4	4	6	10
6[b]	Black 3, 4	5	9	14
7	Black 3, 4	0	5	5
8	Black 1, 2, 3, 4	8	0	8
9[b]	Black 3, 4	5	5	10
10	Black 1, 2, 3, 4	10	0	10
11	Black 3, 4	4	3	7
12[b]	Black 1, 2, 3, 4	5	0	5
13	Black 3, 4	5	5	10
14	Liver 7, 8	0	10	10

[a] In this and subsequent tables, the 'possible Types' were determined by the considerations set down under Evaluation of Probability

[b] Combination of two litters with the same sire, H

Table 3. Data on sire R (Type 3 or 4) matings

Litter number	Colour and possible Types of dam[a]	Number of black progeny	Number of liver progeny	Total progeny
1	Black 1, 2, 3, 4	5	0	5
2[b]	Black 3, 4	17	8	25
3	Black 1, 2, 3, 4	5	0	5
4	Black 3, 4	11	1	12
5	Black 1, 2, 3, 4	1	0	1
6	Black 3, 4	10	3	13
7	Liver 7, 8	4	4	8
8	Liver 7, 8	5	2	7
9	Liver 7, 8	3	7	10
10	Liver 7, 8	6	2	8
11	Liver 7, 8	7	2	9
12	Liver 7, 8	2	2	4
13	Liver 7, 8	6	4	10
14	Liver 7, 8	1	2	3

[a] See footnote to Table 2

[b] Combination of two litters with the same sire, R

ability (see, for example, Elandt-Johnson 1971), and its calculation requires the knowledge of certain prior probabilities. Let the prior probability that a sire or dam is of Type k be π_k, where the assumption that the prior probabilities are the same for sires and dams is deemed to be reasonable. We let p_{1jk}, p_{2jk}, p_{3jk} and p_{4jk} be, respectively, the probabilities that given offspring of a Type j × Type k mating are liver, black, blue and fawn. They are obtainable from Table 4, the directions given in the legend being based on Mendelian predictions, and assuming that all genotypes have equal fitness and that the two loci B and D are unlinked. For example, $p_{148} = \frac{1}{8} + \frac{2}{8} = \frac{3}{8}$. Let l_i, m_i, n_i and q_i be, respectively, the numbers of liver, black, blue and fawn progeny in litter i (that is, from dam i). For our data n_i and q_i are zero, although blue and fawn progeny are possible for several mating combinations, as Table 4 indicates.

In the Mathematical Appendix (equation A5), a general expression is derived for $P(Z_k \mid Y)$, which reduces, for our data, to

$$P(Z_k \mid Y) = \frac{\prod_{i=1}^{i=14} \left[\sum_{h(i)} p_{1hk}{}^{l_i} p_{2hk}{}^{m_i} \pi_h \right] \pi_k}{\sum_j \left\{ \prod_{i=1}^{i=14} \left[\sum_{h(i)} p_{1hj}{}^{l_i} p_{2hj}{}^{m_i} \pi_h \right] \right\} \pi_j} \tag{1}$$

where the sum in the numerator is over all Types h consistent with the phenotype of dam i, subject to any other relevant restriction. For sire H, the sum over j in the denominator includes $j = 7$ and 8 only; indeed, the formula is needed only for $k = 7$ and 8, because $P(Z_k \mid Y) = 0$ for $k \neq 7$ and 8, sire H being liver. It is necessary to calculate only $P(Z_7 \mid Y)$ from the formula because $P(Z_8 \mid Y) = 1 - P(Z_7 \mid Y)$. Sire R is black, so $P(Z_k \mid Y) = 0$ for $k \neq 1, 2, 3, 4$. However, as remarked previously, the presence of liver progeny among the litters from this sire means that $P(Z_1 \mid Y) = P(Z_2 \mid Y) = 0$ also, because $p_{1h1} = p_{1h2} = 0$, from Table 4. Thus, the sum in the denominator of equation (1) is here for $j = 3$ and 4, and we compute $P(Z_3 \mid Y)$, $P(Z_4 \mid Y)$ being given as $1 - P(Z_3 \mid Y)$. As explained in the Appendix, equation (1) is justified within the assumption that the dams are independent, which is true if the dams are drawn at random from a large population, but not if they are closely related. A study of the pedigrees of the dams used in the experiments indicated that the independence assumption was justified; some data collected were rejected from the calculations by this criterion.

It remains to supply values for the π_k. Of the possible matings implied by Table 4, we have eliminated any involving Type 5, 6 and 9 in our evaluation of the π_k because dogs of these Types (blues and fawns) are used as parents only very rarely relative to those of the other Types. We have assumed that the genotypes in our breeding population have arisen through the other possible matings. We have taken π_k as $S_k/36$, where S_k is the sum of the fractional contributions of each Type k, $(k = 1, 2, \ldots, 9)$ from the 36 matings, excluding reciprocal crosses, involving Types 1, 2, 3, 4, 7 and 8. The following results, which should be regarded as approximate, were obtained:

k	1	2	3	4	5	6	7	8	9
π_k	0.141	0.094	0.281	0.188	0.016	0.031	0.141	0.094	0.016

Obviously, an erroneous value of π_k can lead to incorrect final results. However, as described below, we did examine our findings in respect of their sensitivity to variations, in π_k. Moreover, the phenotype probabilities implied by our π_k agree well with the experimental population data given by Gruenig (1959). Our ratio black:blue:liver:fawn, represented by $(\pi_1 + \pi_2 + \pi_3 + \pi_4) : (\pi_5 + \pi_6) : (\pi_7 + \pi_8) : \pi_9$, is 0.70:0.05:0.23:0.02 whereas Gruenig's ratio is 0.75:0.03:0.21:0.01.

Discussion of Numerical Results

We outline first the calculation of $P(Z_7 \mid Y)$ for sire H. Dams 1 to 13 are black while dam 14 is liver. Thus, for $i = 1, 2, \ldots, 13$, the $h(i)$ sums range over $h = 1, 2, 3$, and 4 in general, but over $h = 3$ and 4 only where it is known from pedigree data that one of the parents of the dam is liver; for $i = 14$, we have $h = 7$ and 8. From

Table 4. Dobermann coat colour chart. The broad band in any Type box indicates the phenotype, and the other (narrow) bands indicate the phenotypes that can be produced by appropriate matings. The probability that a Type *j* × Type *k* mating produces a Type *i* offspring is obtained from the (*j*, *k*)th box by dividing the number in italics opposite Type *i* by the sum of the numbers in italics in that box. For example, the probability that a Type 4 × Type 8 mating produces a Type 3 offspring is 1/8. These probabilities depend, for their accuracy, on large numbers of offspring for the two Types mated. Any given litter may deviate from the given Mendelian predictions. If any Type *i* does not appear in a box, its probability from the given mating is identically zero

Sire → Dam ↓	TYPE 1 *BBDD* Black	TYPE 2 *BBDd* Black Blue	TYPE 3 *BbDD* Black Liver	TYPE 4 *BbDd* Black Blue Liver Fawn	TYPE 5 *BBdd* Blue Black	TYPE 6 *Bbdd* Blue Black Liver Fawn	TYPE 7 *bbDD* Liver Black	TYPE 8 *bbDd* Liver Black Blue Fawn	TYPE 9 *bbdd* Fawn Black Blue Liver
TYPE 1 *BBDD* Black	TYPE 1 - *1*	TYPE 1 - *1* TYPE 2 - *1*	TYPE 1 - *1* TYPE 3 - *1*	TYPE 1 - *1* TYPE 2 - *1* TYPE 3 - *1* TYPE 4 - *1*	TYPE 2 - *1*	TYPE 2 - *1* TYPE 4 - *1*	TYPE 3 - *1*	TYPE 3 - *1* TYPE 4 - *1*	TYPE 4 - *1*
TYPE 2 *BBDd* Black Blue	TYPE 1 - *1* TYPE 2 - *1*	TYPE 1 - *1* TYPE 2 - *2* TYPE 5 - *1*	TYPE 1 - *1* TYPE 2 - *1* TYPE 3 - *1* TYPE 4 - *1*	TYPE 1 - *1* TYPE 2 - *2* TYPE 3 - *1* TYPE 4 - *2* TYPE 5 - *1* TYPE 6 - *1*	TYPE 2 - *1* TYPE 5 - *1*	TYPE 2 - *1* TYPE 4 - *1* TYPE 5 - *1* TYPE 6 - *1*	TYPE 3 - *1* TYPE 4 - *1*	TYPE 3 - *1* TYPE 4 - *2* TYPE 6 - *1*	TYPE 4 - *1* TYPE 6 - *1*
TYPE 3 *BbDD* Black Liver	TYPE 1 - *1* TYPE 3 - *1*	TYPE 1 - *1* TYPE 2 - *1* TYPE 3 - *1* TYPE 4 - *1*	TYPE 1 - *1* TYPE 3 - *2* TYPE 7 - *1*	TYPE 1 - *1* TYPE 2 - *1* TYPE 3 - *2* TYPE 4 - *2* TYPE 7 - *1* TYPE 8 - *1*	TYPE 2 - *1* TYPE 4 - *1*	TYPE 2 - *1* TYPE 4 - *2* TYPE 8 - *1*	TYPE 3 - *1* TYPE 7 - *1*	TYPE 3 - *1* TYPE 4 - *1* TYPE 7 - *1* TYPE 8 - *1*	TYPE 4 - *1* TYPE 8 - *1*
TYPE 4 *BbDd* Black Blue Liver Fawn	TYPE 1 - *1* TYPE 2 - *1* TYPE 3 - *1* TYPE 4 - *1*	TYPE 1 - *1* TYPE 2 - *2* TYPE 3 - *1* TYPE 4 - *2* TYPE 5 - *1* TYPE 6 - *1*	TYPE 1 - *1* TYPE 2 - *1* TYPE 3 - *2* TYPE 4 - *2* TYPE 7 - *1* TYPE 8 - *1*	TYPE 1 - *1* TYPE 2 - *2* TYPE 3 - *2* TYPE 4 - *4* TYPE 5 - *1* TYPE 6 - *2* TYPE 7 - *1* TYPE 8 - *2* TYPE 9 - *1*	TYPE 2 - *1* TYPE 4 - *1* TYPE 5 - *1* TYPE 6 - *1*	TYPE 2 - *1* TYPE 4 - *2* TYPE 5 - *1* TYPE 6 - *2* TYPE 8 - *1* TYPE 9 - *1*	TYPE 3 - *1* TYPE 4 - *1* TYPE 7 - *1* TYPE 8 - *1*	TYPE 3 - *1* TYPE 4 - *2* TYPE 6 - *1* TYPE 7 - *1* TYPE 8 - *2* TYPE 9 - *1*	TYPE 4 - *1* TYPE 6 - *1* TYPE 8 - *1* TYPE 9 - *1*
TYPE 5 *BBdd* Blue Black	TYPE 2 - *1*	TYPE 2 - *1* TYPE 5 - *1*	TYPE 2 - *1* TYPE 4 - *1*	TYPE 2 - *1* TYPE 4 - *1* TYPE 5 - *1* TYPE 6 - *1*	TYPE 5 - *1*	TYPE 5 - *1* TYPE 6 - *1*	TYPE 4 - *1*	TYPE 4 - *1* TYPE 6 - *1*	TYPE 6 - *1*
TYPE 6 *Bbdd* Blue Black Liver Fawn	TYPE 2 - *1* TYPE 4 - *1*	TYPE 2 - *1* TYPE 4 - *1* TYPE 5 - *1* TYPE 6 - *1*	TYPE 2 - *1* TYPE 4 - *2* TYPE 8 - *1*	TYPE 2 - *1* TYPE 4 - *2* TYPE 5 - *1* TYPE 6 - *2* TYPE 8 - *1* TYPE 9 - *1*	TYPE 5 - *1* TYPE 6 - *1*	TYPE 5 - *1* TYPE 6 - *2* TYPE 9 - *1*	TYPE 4 - *1* TYPE 8 - *1*	TYPE 4 - *1* TYPE 6 - *1* TYPE 8 - *1* TYPE 9 - *1*	TYPE 6 - *1* TYPE 9 - *1*
TYPE 7 *bbDD* Liver Black	TYPE 3 - *1*	TYPE 3 - *1* TYPE 4 - *1*	TYPE 3 - *1* TYPE 7 - *1*	TYPE 3 - *1* TYPE 4 - *1* TYPE 7 - *1* TYPE 8 - *1*	TYPE 4 - *1*	TYPE 4 - *1* TYPE 8 - *1*	TYPE 7 - *1*	TYPE 7 - *1* TYPE 8 - *1*	TYPE 8 - *1*
TYPE 8 *bbDd* Liver Black Blue Fawn	TYPE 3 - *1* TYPE 4 - *1*	TYPE 3 - *1* TYPE 4 - *2* TYPE 6 - *1*	TYPE 3 - *1* TYPE 4 - *1* TYPE 7 - *1* TYPE 8 - *1*	TYPE 3 - *1* TYPE 4 - *2* TYPE 6 - *1* TYPE 7 - *1* TYPE 8 - *2* TYPE 9 - *1*	TYPE 4 - *1* TYPE 6 - *1*	TYPE 4 - *1* TYPE 6 - *1* TYPE 8 - *1* TYPE 9 - *1*	TYPE 7 - *1* TYPE 8 - *1*	TYPE 7 - *1* TYPE 8 - *2* TYPE 9 - *1*	TYPE 8 - *1* TYPE 9 - *1*
TYPE 9 *bbdd* Fawn Black Blue Liver	TYPE 4 - *1*	TYPE 4 - *1* TYPE 6 - *1*	TYPE 4 - *1* TYPE 8 - *1*	TYPE 4 - *1* TYPE 6 - *1* TYPE 8 - *1* TYPE 9 - *1*	TYPE 6 - *1*	TYPE 6 - *1* TYPE 9 - *1*	TYPE 8 - *1*	TYPE 8 - *1* TYPE 9 - *1*	TYPE 9 - *1*

Table 4, we obtain:

$p_{117} = p_{127} = 0, \quad p_{137} = p_{147} = 1/2, p_{217} = p_{227} = 1,$
$p_{237} = p_{247} = 1/2, p_{118} = p_{128} = 0, \ p_{138} = 1/2, p_{148} = 3/8,$
$p_{218} = 1, p_{228} = 3/4, p_{238} = 1/2, p_{248} = 3/8, p_{177} = p_{178} = 1,$
$p_{188} = 3/4, p_{277} = p_{278} = p_{288} = 0.$

Thus,

$$P(Z_7 \mid Y) = \frac{C}{C+D}$$

where

$$C = \left\{ \prod_{i=1}^{i=13} \left[\pi_1 + \pi_2 + \left(\frac{1}{2}\right)^{l_i + m_i} (\pi_3 + \pi_4) \right] \right\} \{\pi_7 + \pi_8\} \, \pi_7$$

and

$$D = \left\{ \prod_{i=1}^{i=13} \left[\pi_1 + \left(\frac{3}{4}\right)^{m_i} \pi_2 + \left(\frac{1}{2}\right)^{l_i + m_i} \pi_3 + \left(\frac{3}{8}\right)^{l_i + m_i} \pi_4 \right] \right\} \times \left\{ \pi_7 + \left(\frac{3}{4}\right)^{l_i} \pi_8 \right\} \pi_8$$

whence we derive $P(Z_7 \mid Y) = 0.999$. It may be noted that the black-liver segregation of litters is irrelevant in C, but affects some components of D, the effect of the segregation here being due to the fact that, as Table 4 shows, there are non-zero probabilities of a blue offspring from a Type 2 × Type 8 mating, and of a fawn offspring from a Type 8 × Type 8 mating. If zero probability were assigned to each of these events, then the black-liver segregation would be irrelevant to $P(Z_7 \mid Y)$.

The subject editor proposed to us an alternative, simpler method which computes posterior probabilities conditional only on the total litter sizes, and ignoring the segregation. We have applied his method to our data for sire H, and it leads to a similar result[1] to that obtained here for $P(Z_7 \mid Y)$. The effect of the segregation is dwarfed by that arising from the absence of blue or fawn progeny: the presence of a single such offspring from sire H would give $P(Z_7 \mid Y) = 0$ and $P(Z_8 \mid Y) = 1$.

The black-liver segregation is more important for the sire R data. We have pointed out earlier that $P(Z_1 \mid Y) = P(Z_2 \mid Y) = 0$: had no liver progeny been recorded for sire R, these probabilities would have been non-zero. In addition to some of the p values listed above, we need (from Table 4):

$p_{133} = p_{134} = 1/4, p_{144} = 3/16,$
$p_{233} = p_{234} = 3/4, p_{244} = 9/16.$

Then,

$$P(Z_3 \mid Y) = \frac{C}{C+D}$$

where now

$$C = \left\{ \prod_{i=1}^{i=6} \left[\left(\frac{1}{4}\right)^{l_i} \left(\frac{3}{4}\right)^{m_i} (\pi_3 + \pi_4) \right] \right\} \times \left\{ \prod_{i=7}^{i=14} \left[\left(\frac{1}{2}\right)^{l_i + m_i} (\pi_7 + \pi_8) \right] \right\} \pi_3$$

and

$$D = \left\{ \prod_{i=1}^{i=6} \left[\left(\frac{1}{4}\right)^{l_i} \left(\frac{3}{4}\right)^{m_i} \pi_3 + \left(\frac{3}{16}\right)^{l_i} \left(\frac{9}{16}\right)^{m_i} \pi_4 \right] \right\} \times \left\{ \prod_{i=7}^{i=14} \left[\left(\frac{1}{2}\right)^{l_i + m_i} \pi_7 + \left(\frac{3}{8}\right)^{l_i + m_i} \pi_8 \right] \right\} \pi_4 .$$

Although the second factor (due to the liver dams) of both C and D depends on the totals $l_i + m_i$, the first factor in both cases does reflect the black-liver segregation, and, indeed, this effect is not merely a consequence of assuming non-zero probabilities of blue and fawn progeny. We obtain $P(Z_3 \mid Y) = 0.998$; again, the presence of a single blue or fawn offspring would have led to $P(Z_3 \mid Y) = 0$, with $P(Z_4 \mid Y) = 1$ instead of its present value of 0.002.

The genotype probabilities for each dam in both experiments were also computed. The method employed Bayes' formula (see Appendix, equation A9), using generally only the data on the litter in question, but

Table 5. Results for sire H and mates

Dog	Types[a]	Probability/%[b]	Dog	Types[a]	Probability/%[b]
Sire H	7	99.9 (99.1)	Dam 8	1	59.6 (74.5)
	8	0.1 (0.9)		2	39.7 (24.8)
Dam 1	1	59.8 (74.7)		3	0.5 (0.5)
	2	39.8 (24.9)		4	0.3 (0.2)
	3	0.2 (0.3)	Dam 9	3	60.0 (75.0)
	4	0.2 (0.1)		4	40.0 (25.0)
Dam 2[c]	1	59.6 (74.6)	Dam 10	1	59.9 (74.9)
	2	39.7 (24.8)		2	39.9 (25.0)
	3	0.5 (0.4)		3	0.1 (0.1)
	4	0.3 (0.2)		4	0.1 (0.0)
Dam 3	3	60.0 (75.0)	Dam 11	3	60.0 (75.0)
	4	40.0 (25.0)		4	40.0 (25.0)
Dam 4	3	60.0 (75.0)	Dam 12	1	56.5 (70.6)
	4	40.0 (25.0)		2	37.6 (23.5)
Dam 5	3	60.0 (75.0)		3	3.5 (4.4)
	4	40.0 (25.0)		4	2.4 (1.5)
Dam 6	3	60.0 (75.0)	Dam 13	3	60.0 (75.0)
	4	40.0 (25.0)		4	40.0 (25.0)
Dam 7	3	60.0 (75.0)	Dam 14	7	60.0 (75.0)
	4	40.0 (25.0)		8	40.0 (25.0)

[a] Only Types with non-zero probabilities are listed
[b] The unparenthesised figures are obtained using the original prior probabilities π_k; the parenthesised results used the π_k values modified as described in the paper
[c] The same dam as 1 in Table 6; the results are for the combination of both litters

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[1] 98.7%

Table 6. Results for sire R and mates

Dog	Types[a]	Probabilitiy/%[b]	Dog	Types[a]	Probability/%[b]
Sire R	3	99.8 (98.7)	Dam 6	3	60.1 (75.1)
	4	0.2 (1.3)		4	39.9 (24.9)
Dam 1[c]	1	59.6 (74.6)	Dam 7	7	60.1 (75.1)
	2	39.7 (24.8)		8	39.9 (24.9)
	3	0.5 (0.4)	Dam 8	7	60.0 (75.0)
	4	0.3 (0.2)		8	40.0 (25.0)
Dam 2	3	60.1 (75.1)	Dam 9[d]	7	69.1 (79.1)
	4	39.9 (24.9)		8	30.9 (20.9)
Dam 3	1	40.7 (50.9)	Dam 10	7	60.1 (75.1)
	2	27.1 (17.0)		8	39.9 (24.9)
	3	19.3 (24.1)	Dam 11	7	60.1 (75.1)
	4	12.9 (8.0)		8	39.9 (24.9)
Dam 4	3	60.1 (75.1)	Dam 12	7	60.0 (75.0)
	4	39.9 (24.9)		8	40.0 (25.0)
Dam 5	1	24.0 (30.0)	Dam 13	7	60.1 (75.1)
	2	16.0 (10.0)		8	39.9 (24.9)
	3	36.0 (45.0)	Dam 14	7	60.0 (75.0)
	4	24.0 (15.0)		8	40.0 (25.0)

[a,b,c] See footnotes to Table 5

[d] Includes data from a second mating with another 3, 4 sire that produced 3 black and 3 liver progeny

replacing the sire H prior probabilities π_7 and π_8 by 0.998 and 0.002, these values being those obtained on 13 dams (that is, excluding the dam under investigation). Similarly, for the experiment with sire R, the prior probabilities π_3 and π_4 were replaced by the values 0.997 and 0.003. As a result, only the probabilities relating to matings of black dams with sire R reflect the black-liver segregation of the progeny. In the case of two dams, data on multiple matings were available, and the results were correspondingly strengthened.

The calculations of sire and dam probabilities were carried out with a program written in FORTRAN, the full results being displayed in Tables 5 and 6. The results for sires H and R can be seen to be highly reliable, those for the dams being less reliable because they are less heavily dependent on the experimental data and reflect more the values ascribed to the prior probabilities. Thus, none of the dam posteriors is close to unity, but in the case of black dams the procedure usually narrows the possibilities down from four Types to two, sometimes with just one Type being the more strongly indicated.

The procedure for determining π_k may err in over-estimating π_2, π_4 and π_8. The reason for this view is that the breeding population studied is strongly related to American Dobermann lines, where Types 1, 3 and 7 are known to be prominent. In order to examine the effect of over-estimating these particular π_k values, π_2, π_4 and π_8 were halved, leaving the black : liver ratio at approximately 3 : 1, and probabilities again computed. These results are given in parentheses in Tables 5 and 6. It can be seen that the probabilities for the two sires are not appreciably changed. This desirable insensitivity arises because each sire was investigated through a large number of matings. In the case of the dams, we can only conclude that the larger of unparenthesised values for each dam indicates a minimum for the most probable Type.

A knowledge of this sort of genotype information would permit colour planning in breeding, a process much more desirable than either prohibition or elimination of progeny of unwanted phenotypes. Although considered here in relation to the Dobermann coat colour, it is clear that a similar analysis could be invoked for any di-hybrid inheritance, and in other canine breeds.

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Mathematical Appendix

We shall derive formulae for posterior genotype probabilities that are immediately applicable to our data, and are relevant also to a more general situation than that presented by our experimental results. The basic probability concepts and formulae used here are given, for example, in Elandt-Johnson (1971). Some further notation is needed in order to complement that introduced in the section on Evaluation of Probability.

We represent Y in terms of basic events G, H_i and X_i, $(i = 1, 2, \ldots, N)$, where N is the number of litters in the experiment ($N = 14$ in both of our experiments). Now G is the event that the sire has the observed phenotype, H_i is the event that dam i has the observed phenotype, and X_i is the event that litter i has the observed phenotypic composition, that is, l_i liver, m_i black, n_i blue and q_i fawn offspring. Then Y is the intersection

$$Y = G \cap \prod_{i=1}^{N} [H_i \cap X_i]$$

whence

$$\mathrm{P}(Z_k \mid Y) = P\left(Z_k \mid G \cap \prod_{i=1}^{N} [H_i \cap X_i]\right)$$

which is zero whenever Z_k is inconsistent with G. For those Z_k consistent with G we have, by Bayes' theorem,

$$P(Z_k \mid Y) = \frac{P\left(\prod_{i=1}^{N} [H_i \cap X_i] \mid Z_k\right) \pi_k}{\sum_j' P\left(\prod_{i=1}^{N} [H_i \cap X_i] \mid Z_j\right) \pi_j} \tag{A1}$$

where the prime on the sum in the denominator indicates only those Types j that are consistent with G. We assume that the events H_i are independent (see discussion under Evaluation of Probability). Thus, although the X_i are not themselves independent, because a common sire is involved, they are independent conditional on Z_k. Thus,

$$\begin{aligned} P\left(\prod_{i=1}^{N} [H_i \cap X_i] \mid Z_k\right) &= \prod_{i=1}^{N} P(H_i \cap X_i \mid Z_k) \\ &= \prod_{i=1}^{N} \sum_{h(i)} P(W_h \cap X_i \mid Z_k) \end{aligned} \tag{A2}$$

where W_h is the event that a dam is Type h, and the sum is over those Types h such that W_h is consistent with H_i. But

$$P(W_h \cap X_i \mid Z_k) = P(X_i \mid W_h \cap Z_k)\, \pi_h \tag{A3}$$

where

$$\begin{aligned} P(X_i \mid W_h \cap Z_k) &= \frac{(l_i + m_i + n_i + q_i)!}{l_i!\, m_i!\, n_i!\, q_i!} \\ &\quad \times p_{1hk}{}^{l_i} p_{2hk}{}^{m_i} p_{3hk}{}^{n_i} p_{4hk}{}^{q_i} \end{aligned} \tag{A4}$$

a multinomial probability, the p terms being defined under Evaluation of Probability. It remains to insert (A4) into (A3) into (A2) into (A1); in the process, the factorial terms cancel and we obtain

$$P(Z_k \mid Y) = \frac{\prod_{i=1}^{N} \left[\sum_{h(i)} p_{1hk}{}^{l_i} p_{2hk}{}^{m_i} p_{3hk}{}^{n_i} p_{4hk}{}^{q_i} \pi_h\right] \pi_k}{\sum_j \left\{\prod_{i=1}^{N} \left[\sum_{h(i)} p_{1hj}{}^{l_i} p_{2hj}{}^{m_i} p_{3hj}{}^{n_i} p_{4hj}{}^{q_i} \pi_h\right]\right\} \pi_j}. \tag{A5}$$

This formula gives the posterior sire genotype probabilities.

To find the posteriors for the dams, we do not condition fully on the event Y, but adopt the computationally simpler approach of conditioning only on the phenotype information of the dam and sire, and then replacing the sire prior probabilities by the posterior probabilities computed first, using equation (A5). Thus, for dam i, the required probability for the dam, $P(W_h \mid G \cap H_i \cap X_i)$, is zero if W_h is inconsistent with H_i, and $P(W_h \mid G \cap X_i)$ otherwise. Developing (A6) by Bayes' theorem, we have

$$P(W_h \mid G \cap X_i) = \frac{P(G \cap X_i \mid W_h)\, \pi_h}{\sum_j' P(G \cap X_i \mid W_j)\, \pi_j} \tag{A7}$$

the sum in the denominator being taken over all j such that W_j is consistent with H_i. But

$$\begin{aligned} P(G \cap X_i \mid W_h) &= \sum_{k(i)} P(Z_k \cap X_i \mid W_h) \\ &= \sum_{k(i)} P(X_i \mid W_h \cap Z_k)\, \pi_k \end{aligned} \tag{A8}$$

where the sum is taken over those Types k for which Z_k is consistent with G. It remains to insert (A4) into (A8) into (A7) into (A6) to obtain

$$P(W_h \mid G \cap H_i \cap X_i) = \frac{\sum_{k(i)} p_{1hk}{}^{l_i} p_{2hk}{}^{m_i} p_{3hk}{}^{n_i} p_{4hk}{}^{q_i} \pi_k \pi_h}{\sum_j' \sum_{k(i)} p_{1jk}{}^{l_i} p_{2jk}{}^{m_i} p_{3jk}{}^{n_i} p_{4jk}{}^{q_i} \pi_k \pi_j}. \tag{A9}$$

The final step is to replace the sire prior probabilities π_k by the posteriors given by (A5).

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