

The Inheritance of Coat Colour in the Cardigan Welsh Corgi

by Ken Linacre

In a working dog, colour is undoubtedly of secondary importance to construction, but the wide range of colours found in the Cardigan Corgi is one of the attractive features of the breed, on which observers often comment. Red, sable, brindle of various shades, tricolour with both clear red and brindled points, black and blue merle, all attractively set off with white, gives something for all tastes. While other breeds have red, sable, tricolour and blue merle and several have red and brindle, no other breed to my knowledge has the same combination of colours as the Cardigan.

What determines these colours? This article gives the outline of a genetic scheme which, I believe, accounts adequately for the main features of colour inheritance in the breed. It is based on the work of Little¹ and on a study of pedigrees and of the history of the breed. It is a personal view and does not express the opinion of, nor does it commit, the Cardigan Welsh Corgi Association. There is room here to give only the main conclusions of the study and not the detailed justification of some points of the argument. Also, more work is required to check the scheme against breeders' experience and to add other points of detail.

It is hoped that breeders will find the subject interesting and that the article may alike help those who wish to concentrate on certain colours and those who seek to understand the colours they obtain.

The Rules of the Game

The inheritance of coat colour, like the inheritance of all other features, is governed by the genes which a dog carries. Genes are essentially signal units which control development and are transmitted unchanged from parents to offspring - we need not be concerned here how nor concerned further with the detailed nature of genes.

¹ Clarence C. Little, 'The Inheritance of Coat Colour in Dogs', Howell Book House, New York, 1973.

A dog carries two genes relating to each single inherited feature. It receives one from each parent (irrespective of sex²) and transmits one to each offspring (again irrespective of sex). The two genes may be the same or different. Different genes produce differing forms of the feature (for example short and long coats). If the two genes are the same, the dog shows the feature in the form these genes dictate, and transmits only that form. If the genes are different, then the dog will show the feature in the form dictated by one of the genes, which is said to be dominant with respect to the other, which is recessive: however, the dog transmits the feature in both forms. The diagrams below show this pattern of inheritance, considering crosses between animals carrying genes represented by ● and ⊗, where ● is dominant over ⊗.

There are three possible gene pairs:

- ●● shows the feature in the ● form
- ●⊗ shows the feature in the ● form but transmits both the ● and ⊗ form
- ⊗⊗ shows the feature in the ⊗ form.

A. ●● x ●● can produce only ●●

B. ⊗⊗ x ⊗⊗ can produce only ⊗⊗

C. ●● x ●⊗ can produce the following gene pairs, using one gene in turn from each parent

●●
●⊗
●●
●⊗

D. ●⊗ x ●⊗ can produce the following gene pairs, using one gene in turn from each parent

●●
●⊗
⊗●
⊗⊗

(N.B. ●⊗ and ⊗● are identical)

In this article we will refer to genes which relate to the control of the same inherited feature as being in the same group.

² This is in general true, but the inheritance of some features is linked to sex and differs in the male and female. However, colour inheritance in the dog is not sex-linked.

The complication of this simple pattern in colour inheritance arises from two causes.

- We have to consider several groups of genes to describe the range of colours and patterns of inheritance we observe.
- There are several different genes in some groups, though any one animal carries only two (which as we have seen may be the same or different) from the range present in the breed.

The Genes which Matter In Determining Colour in the Cardigan Corgi

In the Cardigan Corgi we have to consider five groups of genes to account for the main features of coat colour.

- The A group and the E groups interact, and control the basic colour patterns found in the breed - red, brindle, and tricolour.
- The S group controls the white markings.
- The T group controls the ticking with colour that we see on the white paws and noses in some dogs.
- The M group controls the merle pattern, which is a modification of the basic tricolour pattern.

There are other groups of genes which control some of the colours found in other breeds. The Cardigan carries only the 'normal' gene in these groups and not the variant gene, and these groups need not be considered further in relation to the Cardigan Corgi.

The A and E Groups

The A and E groups control the distribution of dark (black) and light (red) pigment in the coat. The interaction between the groups is particularly important. In the Cardigan there are two genes operative in the A group: a^y restricts the formation of dark pigment and a^t produces the 'tan point' pattern, i.e. leaving tan on the face and eyebrows, chest and lower

legs: a^y is dominant. In the E group, two genes are operative: E allows the full extension of dark pigment according to the control of a^y and a^t , e^{br} allows the dark pigment to appear as brindle markings. Using these four genes we can account for the basic coat colours, as follows. We can distinguish nine patterns of coat colour - several produce the same appearance, but the dogs transmit different colours to their offspring.

$a^y a^y EE$	This gives a red - or tan – dog
$a^y a^t EE$	This gives a red or sometimes sable dog, who can produce tricolour offspring (because he transmits a^t)
$a^t a^t EE$	This produces a tricolour with clear red points
$a^y a^y E e^{br}$	This produces a brindle, who can produce red offspring (because he transmits E)
$a^y a^t E e^{br}$	This produces a brindle who can produce red and tricolour offspring (because he transmits E and a^t)
$a^t a^t E e^{br}$	This produces a tricolour with brindling on the red points: it can produce red offspring (because it transmits E)
$a^y a^y e^{br} e^{br}$	This produces a brindle dog, who will produce all brindle offspring (because he transmits only e^{br})
$a^y a^t e^{br} e^{br}$	This produces a brindle dog: all its offspring will show brindle (because it transmits only e^{br}): it can produce tricolour offspring (because it transmits a^t)
$a^t a^t e^{br} e^{br}$	This produces a tricolour with brindling on the red points: all the offspring will show brindle.

Because a dog receives one gene of each group from each parent the following simple rules follow:

- If one of a dog's parents was red, it must carry E and must be capable of producing reds (with a suitable mate)
- If one of a dog's parents was tricolour (with red or brindle points) it must carry a^t and be capable of producing tricolours (with a suitable mate)
- A brindle dog always has at least one brindle parent. (The breed history suggests only one or two exceptions to this, which require further investigation)
- Red may be carried through generations of brindles and tricolour through generations of brindles and/or reds
- It is necessary for a dog to produce only one red offspring to prove that it carries the E gene, or one tricolour offspring to prove that it carries the a^t gene.

It is relatively simple, using these formulations and 'rules', to determine the genes in these groups carried by most of the well known dogs, both those with us today and those in the past. Consider their parents and more particularly their offspring. You should also be able, if you have sufficient data, to determine the formulation for your own dogs.

It is also quite simple, if the formulations for each dog are known, to predict what offspring might be expected from a mating. For each of the parents, one is concerned with four genes, two in the A group and two in the E group. To each offspring it transmits one gene from each group, and this pair may be selected in four ways. Hence in principle, there are sixteen possible formulations of the offspring. This is best illustrated by considering an example.

Consider the mating of the following dogs:

- $a^y a^t E e^{br}$ a brindle animal, capable of producing tris and reds
- $a^y a^t EE$ a red or sable animal capable of producing tris.

We may expect $a^y a^y EE$ red
 $a^y a^y EE$ red

$a^y a^t EE$	red/sable
$a^y a^t EE$	red/sable
$a^y a^y E^{br}$	brindle
$a^y a^y E^{br}$	brindle
$a^y a^t E e^{br}$	brindle
$a^y a^t E e^{br}$	brindle
$a^y a^t EE$	red/sable
$a^y a^t EE^{br}$	red/sable
$a^t a^t EE$	red point tri
$a^t a^t EE$	red point tri
$a^y a^t E e^{br}$	brindle
$a^y a^t E e^{br}$	brindle
$a^t a^t E e^{br}$	brindle point tri
$a^t a^t E e^{br}$	brindle point tri

(It will be seen that some of the formulations are repeated in this case: this is because one of the parents carries identical genes in one group.)

One must bear in mind that while this exercise shows what puppies may result, it only indicates the chances that puppies of a certain genetic formulation may be expected. Thus, in this case, we have a six in sixteen chance of brindles, four in sixteen chance of red/sable and two in sixteen chance of red, red point tricolour or brindle point tricolour. But in a given litter of six to ten puppies, the ratios may be very different, and some possible variants may not appear at all.

While this scheme describes the basic colours in the breed one should add the following points in qualification.

- There are variations in the shades of red and — and this is particularly important - wide variations in the intensity of the brindle markings from very dark to very light shading. These features are governed by secondary groups of genes called modifiers. The inheritance of these features and the details of the modifier groups have yet to be determined and more work is required here.

- Modifiers are also responsible for the degree of sabling in an $a^y a^t EE$ dog. Such dogs may vary from almost clear red to quite heavily marked sable. If a sable is heavily marked then it is certain the dog carries a^t . But dogs which are reasonably described as red may carry a^t too. The test is in the offspring produced. The inheritance of this feature also requires further work.
- While there are dogs in the breed which are reasonably described as black, I contend that they are either a very dark brindle, or a tricolour with very dark brindle points. The former will usually show some brindling on the back. The latter will have a black back, but brindling will usually be found on the face and more particularly on the limbs. The observed breeding patterns support this view.
- In the Pembroke Corgi one frequently sees a tricolour with a black saddle, the remainder of the dog being red - and of course with white markings. I have never seen and do not know of this pattern in the Cardigan Corgi.

The S Group

The S group controls the white markings. There are several genes present, given in the order of dominance. However, the dominance is not very clear and dogs which carry two differing genes may show a median condition. S gives very little white marking, perhaps a spot on the chest and white on the toes; s^i allows larger areas of white on chest, muzzle, head, neck, legs, flanks and tail tip; s^P produces separated patches of colour in an otherwise white coat; s^w produces extreme piebald with only a few patches of colour, generally around the eyes and on the ears.

The British standard for the Cardigan Corgi states that white should not predominate in the coat: $s^P s^P$, $s^P s^w$ and $s^w s^w$ dogs are therefore not shown. They are known and called 'whiteleys'. The s^P and s^w genes can be carried through generations and whiteleys produced from normally marked dogs. The early brood bitch Cassie was white with brindle eye patches and ears.

The precise details of white markings are probably controlled by modifier genes, and some patterns of white markings frequently recur. Apart from the frequent white blaze and white collar, the 'one long sock and one short sock' marking on the front legs is a commonly found pattern.

The T Group

The T group contains two genes: T produces ticking while t produces clear white: T is dominant. Ticking is usually found on the white on the feet and muzzle; I have never seen it on the chest nor on the collar, which is probably an extension of the chest area. The ticking matches the coat colour in a brindle and in a red; in a tricolour it matches the colour of the points, i.e. red in a red point and the appropriate shade in a brindle point. Ticking is a minor point of colouring, of so little significance that it is seldom noted.

The M Group

This group contains two genes: M produces dilution of dark pigment to blue leaving some patches unaffected: m produces normal coat colour: M is dominant.

The blue merle Cardigan is essentially a modified tricolour. A normal tricolour carries two m genes. A blue merle carries the genes Mm. Blue merles frequently have the iris of one or both eyes partially or completely marked with white patches: the eyesight is quite normal. A blue merle may have red points if the foundation is a red point tricolour, and carries the genes $a^t a^t E E M m$, or brindle points, when the dog can appear to be almost totally blue - it carries the genes $a^t a^t E e^{br} M m$ or $a^t a^t e^{br} e^{br} M m$. Red in the undercoat may show through the blue.

It is the usual practice to mate blue merle with tricolours, producing blue merle and tricolour offspring. In describing this we need only be concerned with the M group. We have

$$Mm \text{ (blue)} \times mm \text{ (tri)} \quad \rightarrow \quad Mm \text{ (blue)} + mm \text{ (tri)}$$

If two blue merles are mated we have

$$Mm \text{ (blue)} \times Mm \text{ (blue)} \quad \rightarrow \quad mm \text{ (tri)}$$

→ Mm (blue merle)

→ MM

Dogs carrying two M genes, MM, are blue merles, but will frequently be marked with large areas of white (this is not to be confused with the action of the S group genes) and may suffer from defective development of the eyes and/or defective hearing. In other breeds which have the blue merle colour it has been shown that the proportion of MM dogs from such matings is significantly lower than one would expect, indicating that the MM foetus may be reabsorbed. The same must be true of the Cardigan but numbers are probably too small to establish reliable statistics.

This mechanism of the M and m inheritance accounts for one of the other 'rules' of colour breeding. A tricolour dog can be mated with colours other than blue merle and will not produce blue merle offspring; he cannot do so, even if one or both of his parents were blue merles, because he does not carry the M gene. To produce blue merles, he must be mated to a blue merle, or to a dog carrying the M gene.

Dogs other than blue merles can carry the M gene, that is dogs other than $a^t a^t$ dogs. If the basic coat colour would have carried a large amount of dark pigment, the M gene may produce merle patching, but the ground colour will not be blue - such a dog might for example be $a^y a^t e^{br} e^{br} Mm$, where the mm dog would be a brindle. If the basic coat colour carries little dark pigment, there is nothing to show the presence of the M gene. The merling may be apparent in the dark puppy coat in the nest, but not be apparent in the adult coat. An $a^y a^y EEMm$ dog would not show merle features. Such animals are produced in matings of blue merles with colours other than tricolour. (Blue merles may sometimes be mated with very dark brindles under the view that they are black.) Clearly dogs which carry the M gene can transmit it, even if the dog's coat colour does not indicate its presence. There are recorded instances in the breed of blue merle stock being produced when neither parent was a blue merle. Quite normal blue merles might be produced from blue merle matings with colours other than tricolours if the mates carry the a^t gene

$a^y a^t EE mm$ (red sable) x $a^t a^t EEMm$ (blue merle)

→ $a^t a^t EEMm$ (blue merle)

→ $a^t a^t Eemm$ (tri)

→ $a^y a^t EEmm$ (red sable)

→ $a^y a^t EEMm$ (apparent red or off-colour merle)

There has been a vigorous debate in Cardigan Corgi circles in the USA about the breeding and showing of so-called off-colour merles, and anyone interested should refer to the literature of the American clubs. The standards for many breeds indicate that coat colour is not important, yet there are well recognised colours in such breeds and dogs of other colours are seldom, if ever, seen. The British standard for the Cardigan Corgi allows any coat colour but we do not see colours other than those listed at the start of this article at our shows.

Matings of blue merles to other than tan point or brindle point tricolour dogs are not frequent. The genetic schemes offered for your consideration in this article are believed to be correct and to satisfactorily account for the colours we find in the breed. The starting point in deriving them is our collective experience in the breed over many years. It is the analysis of that experience which reveals the systematic patterns and rules of colour inheritance. Application of the rules therefore does no more than structure our experience and provide a foundation for the projection of experience into prediction.

I am very grateful to many Cardigan friends in this country and overseas for helpful information, discussion and correspondence. Without their help it would not have been possible to make any progress on understanding the colours in our breed.

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