C O A T   C O L O R   G E N E T I C S

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GENETIC TERMS AND REFERENCES

ALLELES Gene pairs

CHROMOSOMES Small rod-shaped bodies found within the nucleus of each cell. Each Chromosome contains many genes.

DNA The complex chemical which controls the chemical development of an organism.

DOMINANT GENE One which has such a powerful influence that it will overshadow the effect of a recessive gene.

GENES The basic units of heredity, composed of DNA and located on the chromosomes.

INCOMPLETE DOMINANCE When a dominant gene, combined with a recessive gene produces a trait which is intermediate or a blending of the two genes.

MULTIPLE ALLELES or Gene Series. When there are more than two kinds of genes which may occur on a given spot of a chromosome, each causing a different expression of a trait.

MUTATION A sudden structural change in a gene which causes a different expression of a trait. It may be inheritable.

POLYGENIC TRAIT A trait controlled by a number of gene pairs.

RECESSIVE GENE One which does not exhibit its trait in the presence of a dominant gene.

REFERENCES: Hutt, F.B. 1964 "Animal Genetics". New York, Ronald Press

Burns, M. and Fraser, M.N. 1966 "Genetics of the Dog, the Basis of Successful Breeding". Philadelphia, J.B. Lippincott Co.

COAT COLOR INHERITANCE

Dr. Clarence C. Little in his book The Inheritance of Coat Color in Dogs mentions the following allelic series concerned with the inheritance of coat color. Remember a dog will carry two genes from each of the series, one on each chromosome, with one being derived from each parent. They may be the same gene (homozygous) or they may be two different genes (heterozygous). The G, P, R, and T gene loci have been omitted from discussion since almost all Danes are homozygous for one gene in each series and so are not important in determining different colors in Danes. In the G series they are homozygous for the recessive non-greying gene (gg) and in the P series homozygous for the ~~recessive~~ dominant non-pink-eyed dilution maybe gene (PP). In the R series they are probably homozygous for the recessive non-roan gene (rr) and in the T series they are probably homozygous for the ~~recessive~~ non-ticking gene (tt). It should be noted, however, that there is some slight question involving the T and R genes and there is a slight possibility that merle or harlequin Danes may carry the T and or R genes.

A SERIES influences the distribution of dark and light pigment. In order of dominance:

$\underline{A^s}$ allows distribution of dark brown or black all over the body.

$\underline{a^w}$ a possible allele which would produce the wild agouti type of color.

$\underline{a^y}$ restricts dark and produces tan or fawn or sable.

$\underline{a^t}$ produces bicolor (black and tan, etc.)

A further gene in this series is postulated by some writers, but not by Little. It would resrtict dark to a saddle pattern.

PRESENT IN DANES--A^s and a^y. (and a^t has appeared)

B SERIES in order of dominance:

$\underline{B}$ = black

$\underline{b}$ = liver or chocolate.

PRESENT IN DANES--B and occasionally b. (Little does not include "b" in Danes but new evidence indicates that it does exist in Danes.)

C SERIES in order of dominance:

$\underline{C}$ = full depth of pigment.

$\underline{c^{ch}}$ = chinchilla, reduces the red or yellow pigment more than the black.

$\underline{c^a}$ = complete albinism.

PRESENT IN DANES--C and probably c^{ch}. Little does not include c^{ch} in Danes, but new evidence suggests it may exist.

D SERIES in order of dominance:

$\underline{D}$ allows dense pigmentation.

$\underline{d}$ = dilution of pigment

PRESENT IN DANES--D (e.g. black Danes) and d (e.g. blue Danes).

E SERIES in order of dominance:

$\underline{E^m}$ = black mask

$\underline{E}$ allows formation of dark pigment (black or brown) over entire body.

$\underline{e^{br}}$ = brindle

$\underline{e}$ restricts dark pigment to red, orange or yellow.

PRESENT IN DANES--E^m and E and e^{br}. There is a slight possibility that ee exists in a few Danes. This could possibly account for the production of blacks from "fawn to fawn". If the two dogs involved were $a^y a^y E^m E^m$ x $A^s A^s ee$ it would be probable that all $A^s a^y E^m e$ would result and they would be black.

M SERIES in order of dominance:

$\underline{M}$ = merling, produces irregular patches of dark pigment on a lighter background of the same pigment. Homozygous MM is semilethal and animals are often blind or deaf and/or sterile. They are usually mostly white. The M genes also tend to add white.

$\underline{m}$ = non merle.

PRESENT IN DANES--M and m.

S SERIES in order of dominance:

S = solid coat, no white except possibly a small amount on chest and toes.

s^i = "irish" spotting (so-called after a strain of mice)--white on one or more of the following: muzzle, forehead, feet, neck, tail tip, chest, belly, throat.

s^p = piebald spotting, similar to irish, though only 15% or 20% pigmented.

s^w = extreme white spotting, all or almost all white.

There is some confusion in distinguishing animals in this series phenotypically due to the action of plus and minus modifying factors (various genetic factors independent of the main gene). There are also frequently situations of incomplete dominance occurring in this series.

PRESENT IN DANES--S and s^i and s^p and probably s^w.

There must also be at least one other gene and possibly more, to account for the difference between merles and harlequins. Little attempts to explain the difference by an interaction of M and s^p and s^w genes but this seems to be an inadequate explanation. Burns and Fraser suggest harlequins are EE Mm and that merles are E_{br} Mm_{br} or Ee^{br}Mm but this also would seem unlikely, since the occurrence of eemm or $e^{br}e^{br}$mm dogs is infrequent in merle to merle breedings and even more so because it does not explain how two harlequins can produce a merle which they frequently do. Dr. Bagala, in 1966, hypothesised another gene series which he entitled the W series (not to be confused with the W series of Iljin). This seems to possibly provide an explanation for the genetic difference between harlequin and merle:

This is only a possibility, not yet an accepted theory:

W SERIES in order of dominance:

W clears ground grey color of merle to white, harlequin. Lethal in the homozygous state and death occurs in ~~the embryo~~ utero.

w = non clearing gene.

Since homozygous W is lethal, all harlequins must be Ww and all merles must be ww. This explains why we get no true-breeding harlequins. There is a question as to what effect W would have on fawns, brindles, blues, and blacks, but for the time being we will assume they could be ww or Ww and be phenotypically the same.

There is a crying need for more research to be done on the inheritance of harlequin color. Even if Bagala's hypothesis is correct and we assume that the S series is quantitative in nature and that a number of situations of incomplete dominance exists, there are still some unexplained problems--i.e., the ss harlequin, which we assume most are, being bred to the same and producing blacks with little or no white. If we assume then that harlequins must be Ss to produce such blacks, then what is happening to our ss harlequins? There must be cooperation among harlequin breeders in gathering data on harlequin and merle and black crossings so something concrete may be established.

Some Sample Genotypes	Phenotype
$A^s a^y$BBCCCdEEmmww	black
$A^s A^s$BbCCDDE^mEmmww	black
$A^s A^s$bbCCDDEEmmww	chocolate or liver
$a^y a^y$BBCCDD$E^m E^m$mmww	masked fawn
$A^s A^s$BBCCDDEEMmWw	harlequin
$a^y a^y$BBCCdd$E^m e^{br}$mmww	masked dilute brindle ("blue-brindle")

Remember, for one phenotype, there may be many genotypes.

Below is a list of what a dog must carry to be a certain color. It is not what it would necessarily be BEST for it to carry as far as a breeding program is concerned. For example, a dog may carry one liver (chocolate) recessive and still phenotypically be a good color, but HE WOULD NOT BE A GOOD DOG TO USE IN A BREEDING PROGRAM. All dogs carry two genes in each series.

When the terms, fawn, brindle, blue, black, and harlequin are used, it refers to the color as described in the Standard unless otherwise noted.

A^s - all blacks, blues, harlequins and merles must have one or two.

a^y - all fawns and brindles must have two. Blacks, blues, harlequins and merles may carry one recessively. (also could be $a^t a^t$)

b - all chocolates or livers (dogs with liver nose) must have two. Blacks, blues, harlequins, merles, fawns and brindles may carry one recessively.

B - all blacks, blues, harlequins, merles, faws and brindles must have one or two.

C - all fawns and brindles must have one or two. Blues, blacks, harlequins and merles may have 0 or 1 or 2.

c^{ch} - possibly some of the very light background fawns and brindles have two. Blues, blacks, harlequins and merles may carry 0 or 1 or 2.

D - all blacks, harlequins, fawns, brindles, and merles with black pigment must have one or two.

d - all blues, dilute fawns, dilute brindles, dilute harlequins and dilute merles must have two.

E^m - all masked fawns have at least one. Most masked brindles have 1, but there is some confusion since the striping can tend to give the appearance of a mask when genotypically there is no masking gene. Blacks, blues, harlequins and merles may have 0 or 1 or 2.

E - all maskless fawns have 2. Brindles can have 0 or 1. Blacks, blues, merles and harlequins can have 0 or 1 or 2. Masked fawns may carry 1 recessively to E^m.

e^{br} - all brindles must have at least 1. Blues, blacks, harlequins and merles could carry 0 or 1 or 2. Fawns can't carry any. It must be remembered that E^m is ~~dominant to~~ [epistatic] e^{br} but E^m only affects a small area on the dog and e^{br} expresses itself on the rest of the dog. Hence, an $E^m e^{br}$ animal will be a masked brindle providing, of course, that the genes in the other series also allow this.

M - all harlequins and merles have 1. Only the defective can have 2.

m - blacks, blues, fawns, and brindles can all carry 2. Harlequins and merles carry 1.

There is considerable confusion in this next series, since plus and minus modifying factors (various genetic factors independent of the main gene) are operative. So there is aome overlap between the genes. There are also frequent fluctuations of incomplete dominances.

S - all fawns, brindles, blues, and blacks must have 2. Merles may have 0, 1 or 2. Harlequins can have 0 or 1.

s^i - harlequins and merles can carry 0, 1 or 2. Fawns, brindles, blacks and blues could carry one recessively, but if they did, they probably would have too much white. [eg - Bostons]

s^p = same as s^i.

s^w - almost-all-white or white probably have 2. The MM defective dogs will be mostly white and they need not carry 2. Harlequins and merles carry 0 or 1. Fawns, brindles, blacks, and blues could carry 1 recessively but they almost certainly would have too much white.

Proposed W^h - all harlequins have 1. Assume fawns, brindles, blues and blacks could have 1 undetected.

w - all Danes must carry 1. Merles must have 2. Fawns, brindles, blacks, and blues could have 2.

BREEDING PROGRAMS

(NOTE: THIS WAS WRITTEN BEFORE THE GREAT DANE CLUB OF AMERICA COLOR CODE WAS REVISED TO THE WAY IT READS NOW. CONSEQUENTLY SOME TENSES IN THE TEXT HAVE BEEN CHANGED IN THE INTEREST OF BEING CONSISTENT WITH MATTERS AS THEY STAND IN 1973. SOME COMMENTS HAVE ALSO BEEN ADDED TO THE SECTIONS ON EACH OF THE COLORS TO INDICATE THE VIEW OF THE GREAT DANE CLUB OF AMERICA AND ITS AFFILIATES AS WELL AS THAT OF OTHER GREAT DANE CLUBS.
FOR REFERENCE TO THE PRESENT COLOR CODE, SEE THE BACK COVER OF THE ILLUSTRATED STANDARD IN ITS CURRENT EDITION).

Since all ethical dog breeders strive to produce as few mismarked puppies as possible and to produce as many correctly marked as possible (looking ahead as many generations as possible) there is a need to understand and apply the knowledge of color inheritance to a breeding program. The breeder should have clearly in mind which colors he wishes to produce and strive to upgrade their quality. All breeders should be concerned with the upgrading of all five colors. In order to do this, he must not only know the phenotype of his animal but also the genotype. This was one of the problems with the Great Dane Club of America's previous Code, in that it only took into account the phenotype of the dog. For example, it allowed blue to black breeding and then allowed those resulting blacks to be bred to harlequins, thereby introducing the dilution gene into harlequins. This gene, in the homozygous state, leads to dilute harlequins (i.e. with blue patches instead of black). To have a truly effective code or breeding program, one must take into account genotype rather than just phenotype. A black is a black is a black is just not the case. There are many genetically different blacks and they must be treated as such.

If a breeder is to produce correctly marked offspring, he must know which genes to avoid when breeding. Below are some basic guidelines to producing correctly marked dogs. Remember, only color is being considered. It should be noted, however, that color is only woth eight points out of a hundred in our Standard, and it would be wrong to look at only color and forget the rest of the dog. Sometimes, for the sake of upgrading conformation in a particular dog, otherwise undesirable crossings may be done. <u>However, they should only be attempted by the experienced breeder who has a thorough knowledge of color genetics and is willing to cull, control, and test breed</u> the dogs he is working with until the undesirable color gene or genes have been eliminated from his new hopefully upgraded stock. The following is an outline for an ideal situation and would only be completely practical if all colors were of equal quality and popularity.

<u>FAWNS</u>: Since it is undesirable to have dilute fawns or fawns with considerable white or merled fawns it would be best not to breed fawns to blues, harlequins, or merles, or to any other color which carried a dilution "d", white spotting "s^1" or "s^p" or "s^w", or merling "M" allele. They could safely be bred to fawns, brindles, and blacks <u>who did NOT carry those undesirable genes</u> ("non-carrier blacks" for the sake of this discourse, meaning <u>non-carriers of undesirables</u>. Even these can be carriers of desirable fawn and brindle). These fawns resulting from fawn x brindle, brindle x brindle, fawn x"non-carrier black", and "non-carrier black" x "non-carrier black" are just the same as those from fawn x fawn breeding since they could not carry the dominant brindle or black genes and still be fawn. It might be noted that the old idea of fawn x fawn breeding over several generations washing out color is not true providing that well pigmented fawns are always selected. (NOTE: the above assumes the existence of blacks which are not carriers of the undesirable alleles, which would require considerable test breeding to ascertain. At this time there are virtually no blacks without the presence of the undesirable genes' being a distinct

possibility according to their pedigrees. THE GREAT DANE CLUB OF AMERICA STILL DOES NOT CONDONE THE CROSSING OF FAWNS OR BRINDLES TO BLACKS since it is obviously unsafe for most people to try it.)

BRINDLES: Like fawns, the dilution, white spotting and merling genes are to be avoided. Brindles can be bred to fawns, to brindles, and to blacks <u>which do not carry those undesirable genes</u> (SEE NOTE ABOVE).

<u>BLUES</u>: Fawn, brindle, merle, and white spotting genes should be avoided. Hence, blues should be bred to blues or blacks not carrying those genes. Because of the scarcity of top quality blues, it is sometimes necessary to do other breedings that ordinarily would be undesirable. It should be noted, however, that blue bred to black from black breeding only, and hence not carrying a dilution gene, will yield only blacks. It may be necessary for the blue breeders to breed to fawns and brindles to upgrade the conformation of their dogs but the dogs resulting must be carefully controlled and test-bred until the undesirable gene has been eliminated (from all the resulting colors) and the desired conformation upgrading has been achieved. (N.B. This is the opinion of the writer of this article, Jane Chopson of California).

HARLEQUINS: It is undesirable to have fawn, brindle, and dilution genes in harlequins. Hence, fawns, brindles, blues and blacks carrying fawn, brindle, and blue dilution recessives must be avoided in breeding harlequins, if we are to obtain the highest degree of correctly marked offspring. If the proposed "W" is lethal in the homozygous state, and MM is semi-lethal, we <u>will</u> never have true-breeding harlequins since they would be MMWW. If they didn't die in ~~embryo~~ utero, they would be defective. Hence, we must realize there will probably always be a certain number of merles and mismarked blacks resulting from harlequin breeding. It would seem that there should be serious thought given to recognizing these colors since they are evidently unavoidable. The harlequin breeder is already breeding the toughest color and perhaps this would aid him in giving him a wider range of breeding stock to choose from. It also seems needlessly cruel to destroy otherwise healthy puppies for a color which probably cannot be avoided if harlequin breeding is to continue. (N.B. Also the opinion of the writer, Jane Chopson of California).

Since W is lethal in the homozygous state, it might be wisest to avoid producing WW dogs. One must also keep in mind that MM is semi-lethal and hence harlequin to harlequin breeding or harlequin to merle breeding will yield some defectives also.

Let us look at some results from harlequin, merle, and black breeding. We will assume that WW is lethal, MM is semi-lethal. These are theoretically what should result:

Phenotype - Harle x Harle

Genotype - MmWw MmWw

Possible gametes - MW, Mw, mW, mw

Punnett Square

(gametes of dam)	MW	Mw	mW	mw (gametes of sire)
MW	MMWW	MMWw	MmWW	MmWw
Mw	MMWw	MMww	MmWw	Mmww
mW	MmWW	MMMw	mmWW	mmWw
mw	MmWw	Mmww	mmWw	mmww

MmWw = Harlequin

Mmww = Merle

mmww = Black

mmWw = Black

Offspring:

Blacks	3/16
Merles	1/8
Dead in Embryo	1/4
Defective	3/16
Harlequins	1/4

TOTAL ACCEPTABLE COLORS - 7/16

(Note: No consideration is given to the amount of white on these blacks and harlequins, hence some may not be correctly marked.)

Harlequin (MmWw) to Merle (Mmww) by the same method yields:

Blacks	1/4
Merles	1/4
Defective	1/4
Harlequins	1/4

TOTAL ACCEPTABLE COLORS - 8/16 or 1/2 (no regard to amount of white)

Harlequin x Black with W gene (MmWw x mmWw) yields:

Blacks	3/8
Merles	1/8
Dead	1/4
Harlequins	1/4

TOTAL ACCEPTABLE, marked without regard to white - 10/16

Harlequin x Black without W gene (MmWw x mmww):

Blacks	1/2
Merle	1/4
Harlequins	1/4

TOTAL ACCEPTABLE, marked without regard to white - 12/16

Merle x Black with W gene (Mmww x mmWw):

Blacks	1/2
Merle	1/4
Harlequins	1/4

TOTAL ACCEPTABLE, marked without regard to white - 12/16

It can be seen from the above that 1/4 harlequins is yielded from all these breedings, so it would seem that as far as the production of harlequins alone, it would make little difference which of these breedings were done. But there are obvious differences in the percentage of merles, blacks, and defectives produced and the number lost in embryo. It should be noted that the fractions are what can be conceived, not actually whelped. In breedings in which there is a loss of puppies in embryo, there would be more than 1/4 harlequins actually whelped, but only 1/4 harlequins actually conceived. (NOTE: in all such predictions these are possible combinations, not what actually comes together in any one breeding).

BLACKS: The black Dane can no longer be treated without regard to its genotype and have only its phenotype considered. Blacks should probably be divided into 5 groups as far as breeding is concerned: (1) Fawn or brindle and black-bred blacks, (2) Harlequin-bred blacks, (3) Blue and black-bred balcks, (4) Black-bred blacks, (5) Combinations of the above.

(1) Blacks with fawn or brindle genes should not be used on blues, blue-bred blacks, harlequins, or harlequin-bred blacks. If fawn and brindle genes are combined with dilution genes, there is a risk of producing dilute fawns and brindles. Harlequin white spotting factors can also produce undesirable effects on fawns and brindles. These blacks may safely be bred to fawns, brindles, blacks like themselves, and blacks who are only black-bred, providing none of them are carrying genes such as dilution, white spotting, or liver (chocolate). (NOTE: this would require extensive test-breeding to determine).

(2) Blacks from harlequin may carry recessive genes for white spotting and hence, it could be unsafe to use them on fawns, brindles, blues, or blacks carrying fawn, brindle, or blue. They can be bred to harlequin, although there will probably be some merles and blacks with too much white produced. They can also be bred to merles to produce harlequin if they are Ww. They could also be bred to blacks like themselves or blacks from black breeding, although again this could produce or eventually produce blacks with too much white. If used on harlequin-bred blacks and both are Ww, 1/4 of the litter will probably die in embryo.

(3) Blue-bred blacks: it is probably wisest to only breed blacks carrying the dilution gene to blues and blacks like themselves to produce blues and blacks--or to black-bred blacks to produce blacks. It would be undesirable to breed them to fawns, brindles, harlequins, or blacks carrying these genes, because of the chance of producing dilutions of these colors in future generations.

(4) Black-bred blacks (A^SA^SBBCCDDEEmmSSww): This is the one dane which can be bred to all five colors with comparative safety. The only real exception lies in breeding to harlequins. Aside from the usual merles and blacks with too much white, some of the resulting harlequins may have too little white. If used on harlequin-bred blacks, the latter may contribute too much white to the offspring. They may safely be bred to fawns, brindles, blues, and blacks carrying these genes or blacks like themselves, but only blacks will be obtained. (NOTE: if they are bred to any color other than black, the offspring become carriers of whatever other color the black was bred to and should be, in turn, bred accordingly. We repeat, IT IS ONLY BY REPEATED TEST-BREEDING THAT IT CAN BE DETERMINED IF A BLACK IS A CARRIER OF SOME OTHER COLOR OR NOT.)

(5) Blacks which carry genes from two of the following categories: (a) fawn and/or brindle, (b) blue dilution, (c) harlequin white spotting. These could be termed problem dogs as far as a breeding program is concerned. (NOTE: this is the category into which so many of today's blacks fall because of past breeding practices). Since dilute or white spotted fawns and brindles are undesirable as are dilute harlequins or white spotted blues, before such a dog is bred, a breeder should seriously ask himself if such a dog has so much to offer that it would be worth the risk. If in spite of the sizeable chance of producing mis-marked pups, he still decides to breed the dog, he should decide which color he wants to produce and breed to a dog pure for that color or carrying recessives for it, and who does not also carry the other undesirable gene that his dog carries. He then must carefully control and cull and test-breed resulting puppies until the undesirable gene has been eliminated.

TEST BREEDING Since the possibility of test breeding being done to determine whether or not a hidden recessive is present has been mentioned, it might be of use to explain how such breedings should be done. If, for example, we had a black from a black (DD) x blue (dd) breeding, there is no need to do a test breeding for the presence of the recessive dilution gene, since one member of each gene pair is derived from each parent. Hence, we know the dog is Dd. But if the dog is a black from parents who are "D?" we would do a test breeding to determine the genotype of the black offspring. Since he is black, we know he is either DD or Dd. To determine which, we breed him to a blue. If any blue (dd) puppies result, we can conclude he was Dd. But if no dilute offspring result among a sufficient number of puppies, we can probably conclude that he was DD. The same method can be used to test for any recessive gene, i.e., by breeding a dominant back to a double recessive. (NOTE: Caution must be exercised in test breeding as to what is done about the resulting puppies, as they may also be carriers of undesirable genes which are not being tested for. Hence it may again be stressed that this type of experimentation is NOT FOR BEGINNERS OR THOSE WITHOUT A THOROUGH KNOWLEDGE OF GENETICS. And it is expensive.

THE SAFEST ROAD TO FOLLOW IS THAT OF THE COLOR CODE OF THE GREAT DANE CLUB OF AMERICA AS REVISED IN 1972.)