

Cavy Genetics: An Exploration

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Introduction

This article is unlikely to help you if your sole focus within the cavy fancy is to make improvements within a well-established, existing breed. Here, tried and tested principles (such as 'Breed to the best to the best and hope for the best' and 'Avoid duplicating faults in the parents and try to ensure that between them they have all the good points you are seeking in the offspring') probably comprise most of the knowledge of genetics that you need.

However, if you are considering how you might improve one of the less popular breeds by crossing to another breed; if you are seeking to create a new breed by recombining genes that are responsible for the existing breeds; or if you are simply curious about how the many different varieties of cavy arise or which new ones may be possible, then hopefully it will be of interest. It should also give you a better understanding about why some 'unexpected' things sometimes happen in matings (e.g. why Rex bred to Teddies produce smooth-hairs), or why there is such a thing as a 'satin carrier' but no such thing as a 'crested carrier'.

The article has not been written by experts on genetics, merely interested individuals who have researched the subject via books, the internet and conversations with other fanciers. However, there were three primary sources of much of this information. The first was Professor Sewall Wright, who did a lot of the detailed work on cavy genetics many decades ago. The others were Roy Robinson and Catherine Whiteway, who wrote books on small livestock genetics and cavy genetics respectively over 30 years ago, which probably did more than anything else to bring Sewell Wright's research to the notice of fanciers.

Roy Robinson's 'Colour Inheritance in Small Livestock', which is still available from 'Fur and Feather' at a very reasonable price, covers much of what is known, with the obvious exception that it has no treatment of genes discovered in recent years. It also shows how much colour inheritance mechanisms are similar across such diverse types of animals as cats, rabbits, mice and cavies, upholding the theory of common ancestors, with predispositions for particular mutations (if not the genes themselves) passing down many generations

Basics

To understand why cavies have particular colours or coat types, it is necessary to start with the basic terms of genetics, for these are the building blocks of the understanding that will follow.

A cavy's body, like that of any animal, is made up of cells. Each of these cells has a nucleus. In the nucleus there are a number of string-like objects called **chromosomes**. There is always an even number of these for the simple reason that half come from one parent and half from the other; and these are aligned in pairs, one of each pair coming from each parent. Lying along each chromosome there are hundreds of smaller pieces of matter called **genes**. It is these genes that are responsible for controlling inherited characteristics. As the chromosomes always come in pairs, so the genes too occur in pairs.

The genes always occur at a given position on a given chromosome, called a **locus** (coming from the Latin word meaning position). Each different form of each gene that can occur at a given locus is properly called an **allele**. For some genes, there can be more than two alleles (forms of the gene) in the general population, but it is important to remember that any one individual never has more than two (one from each parent). If the individual has

received the same allele from both parents, then it is said to be **homozygous**, but if it has different ones from each parent then it is said to be **heterozygous**.

In general English usage the word gene is commonly used to mean a locus and sometimes an allele. This sounds like it should be confusing, but in practice it is not a problem. The word **factor** is commonly used to mean allele. You might hear a fancier say that a given pig is "carrying chocolate factor" for example. In genetic terms this means that the individual is heterozygous for a particular gene affecting colour and one parent has provided an allele that will produce chocolate colouring when in duplicate, this therefore being carried by the cavy even though it may not itself show this characteristic.

Another important matter to consider is that of **dominance**. To explain this, imagine that we only have two Self colours, Purple and Pink. Let us assume that you have both and that they both breed true (that is to say Purples mated to Purples always produce more of the same and similarly for your line of Pinks). The Purples, then, are homozygous for the purple allele and the Pinks are homozygous for the pink one. What happens if you cross a Purple with a Pink? The offspring of this mating will inevitably be heterozygous, which is to say that they will carry purple factor from one parent and pink from the other.

Genetics does not generally work like mixing paint, where you would get an intermediate colour. Normally, one of the genes is '**dominant**' to the other; and the characteristic of this gene is shown by the offspring even though it carries genes for both colours. If Purple is dominant to Pink, then you will get only Purple youngsters (and, in this case, the least dominant, Pink, is said to be 'recessive'). Only if neither is fully dominant to the other will you get some intermediate colour (the 'paint mixing' effect). These cases may show what is called **incomplete dominance** or **co-dominance** (in this case the offspring of our Purple x Pink cross might turn out to be a light purple); but the normal situation is that one gene is dominant and one recessive. When the youngsters are themselves mated there arises the chance that some of the offspring will inherit a double quantity of the recessive Pink gene, as will be explained shortly. In this case a mating of Purple to Purple will produce some Pinks, an apparently surprising result until you remember the origins of the parents.

In real life this is important to remember when you cross one strain of a breed with another to improve a specific feature. The genes that you want to keep in your stock may be recessive (and often are). In this case the first generation arising from the cross may look awful. But if you persevere and interbreed these 'ugly ducklings', a percentage of the second generation will have the recessive genes in duplicate and will thus show the required characteristics from the parent strains.

As a matter of **convention**, the most dominant allele is written with a capital letter, say 'P' in the case of our imaginary purple gene. The least dominant (most recessive) form is always written with the same letter in lower-case, for example 'p' for the 'non purple' (pink) form. If there are more than two alleles, then the ones of intermediate dominance are written with a superscript, for example p^x .

Finally, the genetic composition of the animal is known as its **genotype**. Its physical characteristics (i.e. what you actually see) are termed its **phenotype**.

To see what happens when our crossbred, heterozygous Purple x Pink stock, each carrying both P and p alleles, are interbred, it is often helpful to draw a small diagram indicating the different combinations of alleles that can arise in the offspring, dependant on whether the boar passes on P or p and the sow passes on P or p.:

Sow's genes	P	p
P	PP	Pp
p	Pp	pp

From this you can see at a glance that 1 in 4 (25%) of the offspring will be true breeding, homozygous Purples; 1 in 4 (25%) will be (homozygous) Pink; whilst 2 of the 4 (50%) will again be heterozygous. Whether you can distinguish the heterozygous Purples from the homozygous ones by physical appearance will depend on the degree to which Purple factor is dominant. If Purple is completely dominant you will only be able to deduce this from what happens in future breeding results, for a homozygous Purple will never throw a Pink.

Note that these figures of 25% and 50% are averages. What happens in any one litter is a result of random chance. Further note that this relatively simple picture is often clouded in real life because there may be two or more genes at work to create the visible feature that you are considering. In this case the number of possibilities multiplies up (and often, therefore, the percentage of young that the fancier may be interested in will go down).

Generally, it can be assumed that genes are inherited independently of each other: for example a gene for one colour feature is passed on independently from one for another colour feature or for coat. However, each chromosome passed to an offspring by a parent is made up of strands of genes made up from parts of each of the two chromosomes that it in turn possesses - in effect the two parent chromosomes 'break' and recombine' to form single chromosomes that can be passed onto each offspring.

Accordingly, genes that occur close together on a parental chromosome are usually passed on together to any offspring. This is termed 'linkage'. When two characteristics appear to be passed on together, e.g. predisposition to OCD with satinisation, it is important to know whether this is due to the action of a single gene or whether two 'linked' genes are working together. In the second case, with enough matings and a little luck, the link can be broken. In the first case it never will, and the best you will be able to do is to select stock and employ management techniques that mitigate the undesirable side-effect.

Genetics isn't everything

- and we don't know everything about genetics

Before anyone gets the impression that cavy genetics is a well-understood science, some things have to be recognised. The first is that there are over 20,000 gene loci in the cavy. However, only a few of the ones producing the most obvious effects have been properly studied. For example, it is undoubtedly true that genes control an animal's type; but nobody has yet taken the trouble to study and document what and how many genes do this. Only the principal genes affecting colour, markings and coat type are understood to any significant extent. Even in these areas, the genes affecting exact shade of colour or exact length of coat etc. are not understood in scientific terms.

Another problem, which concerns the marked varieties in particular, is that it is believed that random environmental factors facing the developing embryo can have a significant effect on markings. To what extent this is true is unknown; but it certainly would account for the fact that producing a BIS winner in some breeds has long been known to require a healthy chunk of luck and an even larger chunk of perseverance.

A final issue that is inadequately understood is that genes for factors such as colour also appear to have unexpected effects on other features, e.g. the lethal effects of the gene producing Dalmation or Roan cavies, or the apparently adverse effect of the 'mahogany red factor' on size.

So, be warned that genetics isn't everything; and that there are large areas of cavy genetics that we don't know everything, or even very much, about. Bear this in mind as you read on...

Colour genetics in the cavy

Black and related colours

Let us take as our first building block in cavy genetics the colour Black and the other colours that are derived from it.

There are, principally, two genes that affect Black. These are the so-called 'Black gene' (which has two generally encountered forms) and the 'Pink Eye gene' (which has at least three forms in this country).

These different alleles (most dominant first) are:

BLACK

- B Black. Produces normal colouring in the coat. Unless affected by other genes (see below) a BB individual will have dark eyes and dark skin.
- b Chocolate. Causes a modification to the normally black pigment granules of the coat producing a chocolate effect. A bb individual also normally has a slight ruby cast to the eye and much lighter skin, whereas BB individuals may have a relatively matt version of the same colour.

There also appears to be a further form, recessive to b, giving a pale, milky chocolate and a 'red' rather than 'ruby' eye, as seen in some Abyssinians.

PINK EYE

- P Normal Eye. Normal coat colour.
- p^g The partial pink eye (or grey) dilution gene. Dilutes black by about 50% and produces a distinctly ruby cast to the eye. Has little, if any, effect on the coat colour of Red cavies, but does affect eye colour in these.
- p The pink eye dilution gene. Dilutes black by about 80% and produces a pink eye. Has little, if any, effect on the coat colour of red cavies, but still affects the eye colour of these.

Combining the established forms of these genes gives the following possibilities

	BB	bb
PP	Black	Chocolate
p ^g p ^g	Slate	'Caramel'
pp	Lilac	Beige

We have to be clear what is meant by 'Slate'. Slate is a term used by longhair fanciers to basically mean 'Black'. However, with a longhair one mainly sees the undercolour rather than the top colour. Consequently black appears as a dark, slate grey. This is not what is meant when people talk of a Self Slate, which arises due to partial pink eye dilution occurring in combination with Black. Slates may vary between a dark grey down to a bluish lilac.

This variation in shade has given rise to claims that there are further forms of the pink eye gene; but it is more likely that some are p^gp heterozygotes (possibly distinguishable by their 'red' rather than 'ruby' eyes), whilst others may be carrying cream dilution genes (see below). At times the lighter colour has been called 'blue'; but 'blue' varieties in other species (for example cats) get their colour from a different gene that has not yet shown itself in cavies, which distributes pigment irregularly within each hair, giving greater reflection of white light and a slate blue appearance. The gene 'd', as used in

cats etc., has been 'reserved' for the potential discovery of the 'blue dilution' gene in cavies.

Chocolates with the partial pink eye dilution have been variously referred to as 'Toffee', 'Coffee' and most recently 'Caramel'.

Red and related colours

Cavies are capable of producing just two different basic pigment colours for their coat, black and red (often referred to as 'yellow' in genetic literature). Up to now we have only considered those colours where the black pigment is seen. However, we now turn to two more genes, one called the 'Extension' gene that allows black pigment or suppresses it, allowing the red (or yellow) to show through; and another called the Colour Intensity or 'C Series', which affects colour intensity particularly in reds.

EXTENSION

E The Extension gene. Allows black pigment to extend throughout the coat. All the black varieties so far considered are EE.

e^p Partial Extension. Allows black pigment to appear in parts of the coat. This leads to tortoiseshell and brindle markings. We will consider this gene later when dealing with marked varieties.

e Non-Extension. Allows red pigment to be seen in the coat. However, black pigmentation of the eye and skin is not affected; and red (ee) cavies may betray whether they carry a black or chocolate base by skin and eye colour. In ee cavies a small amount of the black pigment still appears in the coat, often giving a muddy appearance in old age. Thus whether a red cavy carries black or chocolate can slightly affect its coat colour too.

E is not completely dominant over e^p so Ee^p animals typically have small red patches, blazes or odd red feet.

C (Colour dilution) Series (incompletely dominant in many situations)

C Intense colour. No dilution of either black or red. Black eyes.

c^d Light dilution. Black diluted very slightly in intensity. Red diluted to Buff. May give a very slight ruby cast to the eye. A dark dilution gene, c^k, has also been mentioned, but there is no evidence that it is present in the UK; and consideration of only the c^d light dilution gene is sufficient to explain the colours encountered here.

c^r Ruby eyed dilution. Red diluted to white. Black only marginally diluted. Very dark ruby eyes.

c^h Sometimes known as the Himalayan dilution (also sometimes referred to as ca). This is not the 'true albino' gene found in some species (which is normally written c). The true albino gene, although thoroughly recessive, cuts off all pigment production and produces an animal that has poor eyesight. The c^h gene cuts off production of all red pigment, but permits temperature sensitive synthesis of black pigment, hence the coloured points of the Himalayan. Himalayans carry EE at the extension locus, thus allowing the black or chocolate points, while PEWs carry ee, which also cuts off production of black pigment, thus producing the apparent albino appearance. Therefore, there is not and cannot be any such thing as a Red Himalayan.

Use of these genes gives the following colours:

	CC	$c^d c^d$	$c^d c^h *$	$c^r c^r$	$c^h c^h$
eeBBPP	Red			BEW**	
eebbPP	DEG	Buff	Cream	DEW***	PEW
eebbpp	PEG	Saffron	P.E. Cream		

* A $c^d c^r$ Cream is also possible but is not normally encountered.

** 'Black Eyed' White with dark pads, ears & eyes / rims (rather inappropriately called a 'Panda' in NZ).

*** The usually typier, pink-padded Dark Eyed White, which has distinctly ruby eyes.

A point to note about the chart above is that there are some boxes that are not filled in, including the entire eeBBpp series, which in base form would be a pink-eyed Golden based on Black, with dark skin and pads. Generally, attempting to breed animals that represent these missing 'colours' would not represent a very useful employment of the breeder's efforts. For example, it would be possible to produce a pig that is eebbpp $c^r c^r$. However, this would only turn out to be an alternative way of producing a PEW.

Finer points about colour

There are a number of things to say about the chart of Red colours, and the most controversial point should be mentioned first. **Red** and **D.E. Golden** can actually have the same genotype in terms of the major genes that we understand. The Red colour is produced by selecting for a darker shade. Clearly modifier genes are at work, and the likelihood is that the Self Red (and the Golden Agouti) utilises a 'mahogany' modifying gene.

However, Red and DEG are placed on the chart where many believe that the best coat colours are produced, and as the Self Standard for colour of ears and pads indicates (i.e. Red should be on a BB Black base, while DEG should be on a bb Chocolate base). However, it is equally clear from a look at the ear and eye colour of some of today's Reds and DEGs that stock is being exhibited that would suggest that these positions have been reversed.

The next colour to talk about is the **Cream**. A lot of books for the novice mention that Creams when bred together will throw up the odd Buff in the litter, and further that these should be retained for breeding with 'the lighter coloured Creams from the litters'. What is not pointed out in these books, however, is that Creams are in fact a hybrid breed that will never breed true, and that the 'lighter coloured Creams' are in fact likely to be Whites! Cream x Cream matings will produce an average of 1 in 4 Buffs, 2 in 4 Creams and 1 in 4 Whites. Buff x White will produce 100% Creams; although, if Whites from a strain of Self Whites are used for this purpose, the Creams produced are often darker than those from a Cream breeding line, probably due to the effect of minor genes that are masked in the Self White breeding programme.

There are actually two possible gene combinations at the C locus that will produce Cream (c^d with c^r or c^h , if the dark dilution gene (c^k) is not present in the UK). Of these, it

seems that $c^d c^h$ is relied upon by most top breeders (i.e. their line of Creams throw PEWs not DEWs).

Finally, there have been suggestions, originating in the USA, that Self Chocolates are not simply EEbbPPCC but that the best ones have colour that is actually improved by the presence of $c^d c^d$. However, the colour qualities of the best UK Self Chocolates are very good, and there is no evidence of the presence of $c^d c^d$ within Chocolates here. It is probably the presence of minor recessive modifiers that intensify chocolate colour that explains why Chocolates produced after outcrossing to Blacks are frequently poor in undercolour, since these will have only one copy of these modifiers.

Self colour genotypes at a glance

Here is a summary table for the different colour genotypes.

	Extension	Black	Pink Eye	C Series
Black	EE	BB	PP	CC
Chocolate	EE	bb	PP	CC
Lilac	EE	BB	pp	CC
Beige	EE	bb	pp	CC
Slate	EE	BB	$p^g p^g$	CC
'Caramel'	EE	bb	$p^g p^g$	CC
Red	ee	BB (preferred)	PP	CC
DEG	ee	bb (preferred)	PP	CC
Buff	ee	bb	PP	$c^d c^d$
Cream	ee	bb	PP	$c^d c^h$
DEW	ee	bb	PP	$c^r c^r$
PEW	ee	bb	PP	$c^h c^h$
PEG	ee	bb	pp	CC
Saffron	ee	bb	pp	$c^d c^d$
PE Cream	ee	bb	pp	$c^d c^h$
Silver Dilute	EE	BB	PP	$c^r c^r$
Lemon Dilute(s)	EE	BB	PP	$c^d c^d$, $c^d c^r$ or $c^r c^r$
Cinnamon Dilute	EE	bb	PP	$c^r c^r$
Cream Dilute(s)	EE	bb	PP	$c^d c^d$, $c^d c^r$ or $c^r c^r$

This table covers all of the ESCC recognised colours, as well as some 'dilutes' that are encountered in Agouti breeding but have never been developed as discrete Self breeds.

Marked varieties

HIMALAYANS

Since we have already mentioned all of the genes that are relevant to Himalayans, it is sensible to discuss these first. The PEW, as we have seen, is based on the non-extension genes (ee) which suppresses black pigment. They carry the chocolate genes (bb), which leads to light pads and ears, and also himalayan dilution genes ($c^h c^h$) at the C locus, which prevents all red pigment. It is irrelevant what version of the pink eye gene they have as dark pigmentation of the eye is already impossible by virtue of the himalayan dilution. In practice, they are believed to have the normal version of the pink eye gene (PP).

If a PEW is bred to have the extension gene (EE), dark pigmentation of the points is possible and gives rise to a Chocolate Himalayan. Replace bb with BB and you get a Black Himalayan. Red Himalayans are not possible due the effect of the himalayan dilution gene in suppressing all red pigmentation. In theory, Slate, Lilac and Beige versions should exist, but the evidence so far is that colour is sufficiently eliminated by the $c^h c^h$ genotype that they do not exhibit darker points.

AGOUTIS

A form of Golden Agouti is actually the normal or wild state for a cavy. The ticked effect in Agoutis is produced by having a black or chocolate shaft to the hair, ticked with essentially red, cream or white, and the very extreme end of the hair ticked yet again with the black or chocolate base colour. On the belly of this breed there is a similar situation, but the base is much narrower, the red/cream/white band is broader, and the ticking of base colour at the extreme end of the hair is absent, which yields an apparently solid colour. The gene that controls this appearance is documented as having four forms:

AGOUTI

- A Normal Agouti.
- a^r Ticked belly ('Solid') agouti. The apparently solid belly is replaced by a ticked appearance here as well.
- at Tanned. Produces red (or cream or white) markings around the eyes, nostrils, jowls, chest, throat, belly and inside leg, along with red (or cream or white) ticking on the flanks. Only partially recessive to A, a^r .
- a Non-Agouti. All the Black (and related) Self varieties have this form of the gene. However, it is important to realise that Reds (and related colours) are not necessarily aa at this locus. Despite the fact that the non-extension, red gene (e) is recessive to black (E) and that non-agouti (a) is recessive to agouti (A), when a cavy is homozygous for the red gene (ee) virtually all the black pigment disappears from the coat. Therefore red-based cavies can carry agouti factor unseen. Be aware, then, that a Golden x Black cross may give agouti offspring in the first generation. As a rule of thumb, the vast majority of Whites, Creams, Buffs and Goldens are AA, but for some reason (probably out-crossing to improve type) Reds are usually aa. Whilst it is not necessarily the case that red-based colours carry the agouti gene, it must be true that the Agouti varieties are EE at the extension locus, in order to exhibit black-based colouration (with none of the random red / silver patches that would arise from Ee).

In regard to the different colours of the Agouti breed, these are produced by different combinations of the Black and C Series genes, just as for Selves. The six recognised Agouti colours are Golden (Black/Red), Lemon (Black/Cream), Silver (Black/White), Chocolate (Chocolate/Red), Cream (Chocolate/Cream) and Cinnamon (Chocolate/White).

All Agouti breeds (other than most strains of Golden) throw a 'dilute'. These are basically Black or Chocolate-type Selves. Agouti fanciers use these in their breeding programmes to counter the production of excessively light individuals. However, as we have seen, combining genes is not generally a process of 'blending' colours or shades; and to the geneticist it is not immediately obvious that crossing a light Agouti with a dilute black will darken the colour. However, these Agoutis are not necessarily lighter coloured. Rather, the band of ticking is wider, which leads to a lighter, slightly more blotchy, appearance, as well as an undesired light/white belly and a tendency to eye circles and bonnet strings.

These lighter Agoutis are almost certainly homozygous for the Agouti gene (AA), and the darker ones (the showable animals) are heterozygous (Aa). This being so, then if you interbreed the darker ones you should get 50% darker Agoutis (Aa), 25% dilutes (aa) and 25% lighter Agoutis (AA). Interbreeding dilutes with lighter ones would produce 100% darker Agoutis; and this observation has indeed been reported by some Agouti fanciers.

A possible argument against this theory is that Golden do not generally throw a dilute, yet they have what is considered good ticking / colour. However, this is probably due to the fact that selective breeding in the Golden has produced what fanciers consider the correct base colour and the right amount of ticking within the AA genotype. When these cavy are crossed to Self Blacks, which in terms of all major genes are a 'dilute' of the Golden Agouti, the influence of the minor genes producing the desired mahogany colour, along with quality of ticking, is reduced; and Golden Agoutis of a light, brassy colour are the usual result.

Because of the influence of these minor genes in producing quality of ticking in the Agouti, the general principle is that 'pure' Selves should not be used as if they were Agouti dilutes.

ARGENTES

All of the NACC recognised Agouti colours are based around the normal form of the pink eye gene (P). It is, however, possible to breed cavy that are genetically agouti but which have either of the other forms of the pink eye gene. In the case of the pink eye dilution gene p this produces what is referred to as an Argente. The colour combinations that are possible for normal Agoutis are repeated again, but with Lilac or Beige as the base colour. Agouti-types based on the partial pink eye dilution gene that produces Slate and Caramel are also possible.

FOXES & TANS

These are based on $a^t a^t$, in combination with the other colour genes that are possible in Agoutis. Dependent on whether the cavy carries CC, $c^r c^r$ or $c^d c^d$ / $c^d c^r$ at the C locus the cavy would be referred to as a Tan, a Fox or an Otter respectively. (As a developing breed the Otter may be encountered in both buff- and cream-based forms.) Therefore, the Fox is effectively a silvered tan, with the red colour diluted to white by the presence of the silver genotype $c^r c^r$. Pink-eyed (Argente) versions are also possible.

When A is encountered in combination with a^t , the cavy has tan markings on an agouti background, indicating an effective co-dominance of these genes. A Silver Agouti Fox has been referred to as a 'Chinchilla', but it is much simpler to refer to specific Agouti/Argente versions of Tans/Foxes/Otters as such rather than to invent further names for them.

TORTOISESHELLS, BRINDLES, HARLEQUINS, MAGPIES

The partial extension gene (e^p) mentioned earlier is the principal gene responsible for these breeds, for it allows both Black and Red to appear in the coat (on separate hairs unlike in the agouti types). Their full genotype is $aa e^p e^p BBPPCC$. Unfortunately,

experience has shown that removing the brindling from a Tortoiseshell and the patching from a Brindle are both nearly impossible, so relatively few smooth coated versions are seen, though they are popular amongst Abyssinian fanciers (markings being less important on a coated breed).

Variations on the colour theme are clearly possible, so one can have, say, a Black and Buff patched cavy ($aae^p e^p BBPPc^d c^d$) or a Black and White $aae^p e^p BBPPc^r c^r$, which is where the Harlequins and Magpies enter. Harlequin and Magpie breeders have circumvented the problem of how to get properly patched or brindled specimens by allowing a pseudo three-coloured animal in which one of the 'colours' is brindling. This is to say that patches of the darker and lighter colour plus patches of brindling, in a similar pattern to the Tortoise and White, are sought.

TORTOISE & WHITES, TRICOLOURS

It has long been known that the Tortoise & White variety suffers from fewer problems with brindling than their two-colour cousins, the white markings having the effect of breaking up the red and black colours. It is probably for this reason that they are more popular amongst fanciers. But how do you get a third colour on to a cavy? This is where the 'white spotting gene' comes in. The simplest explanation of this (although some sources claim that different versions of this largely recessive gene exist) is:

WHITE SPOTTING (Incomplete dominant)

- S No white spotting
- s White spotting (as in Dutch, most TWs)
- s^b (?) White spotting (as in Belted)

The S gene is incompletely dominant, Ss individuals being likely to show some white markings. The recessive genotype ss has a high degree of randomness in its effects. Studies have shown that less than half the variation in white markings between individuals is genetic (i.e. due to modifier genes); and littermates, even from inbred strains, can show enormous variation in the amount of white.

The full Tort & White genotype is $aae^p e^p BBPPCCss$. By use of the other colour genes that we have already mentioned, other Tri-colour combinations are possible, for example Beige, Golden and White ($aa e^p e^p bbppCCss$)

DUTCH

The first Dutch marked cavies appeared from Tort & Whites (not the other way round as is often thought); but due to the presence of the partial extension gene these were Black, Red and White, though they had the required markings. Today 'Tortoiseshell Dutch' are not a recognised form of the breed. By replacing the partial extension gene with EE you get Black Dutch, and by using ee you get Red Dutch. In fact all of the recognised Self, Agouti and Argente colourings are possible; and most of the more common colours are recognised by the Dutch Cavy Club. So a Black Dutch is $aaEEBCCPPss$ and the red version is $eeBBCCPPss$.

The Dutch pattern appears in other mammals, including rabbits and mice. It is likely that this pattern is the normal manifestation of the white spotting genotype ss; and that the production of ss animals that are not Dutch-patterned involves selection for modifier genes.

Dutch and Tort & White are recognised as being amongst the most challenging of varieties to breed. Part of the uncertainty surrounding the White Spotting gene is the problem that random effects on the markings occur whilst the embryo is developing. However, there certainly are other (minor) genes at work in forming the markings of these breeds.

Experienced Dutch breeders write that one should try not to breed from pairings where both parties are 'unbalanced' (left marked significantly differently to right), have a flesh ear, slipping saddle or missing stops, as these faults tend to 'breed in'. This is 'fancier-speak' for the fact that there are specific genes that tend to produce these faults.

There are a few other things that should be noted in relation to Dutch colours:

- 1/ Whilst in Lemon and Cream Agoutis, the genotype is generally that of the 'Cream', $c^d c^h$, giving animals that do not 'breed true', most Cream Dutch are genetically, $c^d c^d$, based on a 'Buff' genotype. Some strains of Cream Dutch have been based on the lighter 'true Cream', $c^d c^h$, genotype. However, these have the disadvantage that, with this lighter shade of colour, it can be difficult to discern some of the markings; whilst the production in Cream Dutch to Cream Dutch matings of circa 25% of 'White Dutch' offspring is also rather undesirable! This is why most Cream Dutch are, in fact, Buff Dutch of various shades.
- 2/ It is doubtful that many Agouti Dutch fanciers would wish to put up with dilutes appearing in their strains, for the simple reason that breeding Dutch is difficult enough without also being unable to show about a quarter of the stock that is produced because they have poor colour. Thus, many Agouti Dutch are probably AA rather than Aa at the Agouti locus. This means that the colour is likely to be lighter than in the corresponding Agouti breed.

BELTEDS

Restriction of white spotting to a belt of colour circling the body just behind the shoulders, and including the front legs and feet, produces the Belted cavy. Similar markings are found in mice, pigs and cattle. The Belted originated from a line of T/Ws, some strains of which do produce less white and bicolour / solid heads; and, when Belteds are crossed to Sels, offspring with no white markings are produced. Since Ss always tends to produce some white markings, this suggests that a further allele of the white spotting gene may be responsible, producing more restricted white markings and entirely recessive to S. We might term this s^b .

BI-COLOURS

We have seen that other tri-colour combinations than the normal Black, Red and White of the Tort & White are possible; and clearly other variations on the Tortoiseshell and Brindle themes are possible too. A true bi-colour cavy (other than Harlequin and Magpie that are pseudo three coloured) can be bred in the same way. However, the problem of how to eliminate brindling again rears its ugly head. However, by taking a line of Tortoiseshell & White selected for patchwork rather than Dutch-type markings, and by introducing EE (black) or ee (red) in place of the partial extension gene e^p , one could obtain a line of two-colour patched cavies that are 'Something and White'. These would be genetically similar to Dutch but selected for the required bi-colour patching.

DALMATIANS AND ROANS

This provides one of the most controversial areas of cavy genetics, in that it involves the appearance of a 'lethal' gene, whilst two different explanations have been advanced for the Roan. The most widely accepted (by UK fanciers at least) explanation is as follows:

WHITE LETHAL (Incomplete dominant)

Wh The 'Dalmation gene'. In the heterozygous (Whwh) condition, this produces a cavy with a face that is often similar to a Dutch (solid cheeks with a white blaze), but the body is primarily white with coloured spotting (the Dalmation). Eyes are ruby. In the homozygote (WhWh) the gene produces white babies, typically with no eyes (anophthalmic); often the individual has deformed or missing teeth, and there may be deafness. Mostly such babies die as foetuses or at or soon after birth.

wh^{mi} The 'Roan gene' A lot of the homozygous representatives of this gene die young too, though some do live and are not infertile (contrary to popular belief). They are white and with very small (microphthalmic) eyes. In the heterozygous form the gene leads to roaning on the body of the cavy, with generally solid head and feet (the **Roan**).

wh Normal form of the gene, producing no white markings or lethal effects.

In order to avoid the production of non-viable white babies, many breeders recommend that you should breed Dalmations with Dalmation-bred Selves. This will give an average of 50% Dalmations and 50% Dalmation-bred Selves. The difficulty with this method is that you cannot see the quality of the minor genes affecting the potential spotting quality in the Dalmation-bred Self.

Other Dalmation breeders breed Dalmation with Dalmation. This still only gives 50% Dalmations, so has no advantage from this point of view; but it does allow the breeder to select for spotting quality in both parents, which matters if minor genes affecting spotting quality are inherited independently of the major gene for spotting itself. The disadvantage is that you get some non-viable white babies. In theory there should be 25% of these, but in practice it may be less than this (probably due to the fact that some of these young die and are reabsorbed before birth).

In regard to Roans, it is generally agreed that there is a similar situation as with Dalmations. However, Professor Sewell Wright reported that the roan cavies in his work arose as a result of a largely recessive 'silvering' gene, si, found in combination with a modifier. Since the commonly-encountered Roans in Abyssinians and Smooths produce an average of 50% Roans when mated to cavies not carrying roan, it is likely that today we are not dealing with the largely recessive gene encountered by Sewell Wright. In addition, 'silvered' or 'grizzled' cavies tend to have as many white hairs in the head as the body, and also to show an increase in effect as they mature.

Further light may be cast on this in any particular strain of Roans by asking:

- 1/ What happens when breeding the particular line of Roans with a Self? If you get an average of 50% Roan and 50% non-Roan, then you have got wh^{mi} or at least a dominant roan gene in your stock. If you get cavies that are mainly Self, but with roan patches, then you have got the partially recessive 'si'
- 2/ What happens if a Roan is crossed to a Dalmation? If any sickly white young are produced then you are more likely to have Wh wh^{mi}, since it would be unlikely that the combination of heterozygous genes on different loci would produce such offspring.

The 'Dalmation gene' seems to inhibit the production of red / yellow pigment, especially on the belly, the tendency being for no belly spotting. This factor reduces the show potential of cavies dependent on red belly spots, such as the Red / Golden Dalmation, 'normal' Golden Agouti Dalmation, 'Black & Tan Dalmation' and, to an extent, what could be an interesting breed, the 'Black/Red Tricolour Dalmation'. There does not appear to be a problem with the combination of red / yellow pigment and the 'roan gene'.

SABLE

The essential feature of the Sable breed is that it is a dark coloured cavy with still darker points similar to those on a Himalayan. Unlike Sable rabbits, which are homozygotes based upon a chinchillation gene not yet found in cavies, these have a single allele for Himalayan dilution (c^h) in combination with another of the C series genes, either c^r or c^d.

The c^hc^r genotype is readily produced by crossing Black Himalayans to Silver Agouti dilutes, or Chocolate Himalayans to Cinnamon Agouti dilutes, to create forms of Black

(known as 'Seal') or Chocolate Sable respectively. Introducing the partial or full pink eye dilution genes can produce other variants such as Slate, Lilac or Beige Sables.

c^{hc^d} can be most easily produced by crossing Black Himalayans to a sufficient number of Lemon Agouti dilutes that c^dc^r or c^dc^d is likely to be present in the mix, or similarly Chocolate Himalayans to Cream Agouti dilutes. It is also likely to be produced in the second generation after crosses of Chocolate Himalayans with Buff, in this case being encountered in the chocolate-based form. It has been suggested that the c^{hc^d} genotype may give more pronounced markings than c^{hc^r} , which would explain why only the chocolate-based form, probably derived from Chocolate Himalayan / Buff crosses, has been given a full standard in Australia.

As Sables are heterozygotes they will not breed true, producing mixtures of Sables, Himalayans and slatey Black/Chocolate 'Dilutes' in their litters.

A combination of c^hc^r with a^ta^t , the tan genotype, produces a Sable Fox (any red colouration being suppressed by c^hc^r), this being known as the 'Martin Sable' from the nomenclature of a similarly marked rabbit.

Marked genotypes at a glance

Here is a listing of many of the genotypes of marked breeds. It is not exhaustive, but application of what we have discussed so far will allow the genetics of other breeds to be deduced. 'n/r' is used in cases where it does not matter which specific alleles are used.

	Agouti	Extension	Black	C Series	Pink Eye	Spotting	'White'
Black Himalayan	aa	EE	BB	c ^h c ^h	n/r	SS	whwh
Choc Himalayan	aa	EE	bb	c ^h c ^h	n/r	SS	whwh
Golden Agouti	AA/Aa	EE	BB	CC	PP	SS	whwh
Lemon Agouti	Aa	EE	BB	c ^d c ^r	PP	SS	whwh
Silver Agouti	Aa	EE	BB	c ^r c ^r	PP	SS	whwh
Cinnamon Agouti	Aa	EE	bb	c ^r c ^r	PP	SS	whwh
Gold/Lilac Argente	Aa	EE	BB	CC	pp	SS	whwh
Black Tan	a ^t a ^t	EE	BB	CC	PP	SS	whwh
Silver Fox	a ^t a ^t	EE	BB	c ^r c ^r	PP	SS	whwh
Chocolate Otter	a ^t a ^t	EE	bb	c ^d c ^r or c ^d c ^d	PP	SS	whwh
Tort/Brindle	aa	e ^p e ^p	BB	CC	PP	SS	whwh
Tort & White	aa	e ^p e ^p	BB	CC	PP	ss	whwh
Choc/Buff Tricolour	aa	e ^p e ^p	bb	c ^d c ^d	PP	ss	whwh
Harlequin	aa	e ^p e ^p	BB	c ^d c ^d	PP	SS	whwh
Magpie	aa	e ^p e ^p	BB	c ^r c ^r	PP	SS	whwh
Black Dutch	aa	EE	BB	CC	PP	ss	whwh
Red Dutch	n/r	ee	BB	CC	PP	ss	whwh
Cream Agouti Dutch	AA	EE	bb	c ^d c ^d	PP	ss	whwh
Black Dalmation	aa	EE	BB	CC	PP	SS	Whwh
Black Roan	aa	EE	BB	CC	PP	SS	wh ^{mi} wh
Chocolate Sable	aa	EE	bb	c ^r c ^h or c ^d c ^h	PP	SS	whwh

Genetics of coated varieties

Let us start here with the oldest of the various coat types, Abyssinians, Peruvians and Shelties, not forgetting ordinary smooth-coated cavies. To begin with a slight oversimplification, just two genes account for the most significant differences between these four different forms of coat:

LENGTH

L Normal coat length

I Long hair

L appears to be incompletely dominant to I, the heterozygote LI being a semi-longhair.

In addition, there also appears to be a discrete 'semi-longhair' gene, which is dominant to shorthair, and which is encountered along with a rexoid-type gene in the Swiss Teddy. It is not known whether this gene occurs on the same locus as the longhair gene.

ROUGH

R Rough coated, rosettes. Unlike many mutations, this is dominant.

r Normal coat, no rosettes

Combining these we get:

	RR	rr
LL	Abyssinian	Smooth
II	Peruvian	Sheltie

In the case of Abyssinians and Peruvians, however, things are not quite as simple as they first appear, for a modifier gene is known to have an effect.

MODIFIER OF ROUGH

M Normal coat - rosette formation largely suppressed, but with rough coat on head.

m Rosette formation permitted.

M may be only partially dominant to m, with Mm individuals having only hip rosettes and a form of ridge. In addition, there may be an intermediate allele m^h that suppresses all rosettes other than those on the hips, accounting for the presence of hip rosettes in Peruvians (see below).

Abyssinians are LLRRmm. Cavies that have the Rough gene without the recessive modifier (RR or Rr with MM) can usually be recognised by the fact that they have the hair on the feet growing backwards or in whorls; and there will be a ridge down the back. Cavies that are RR or Rr with Mm nearly always have two rudimentary rosettes on the rump and a form of ridge. Cavies with rr are smooth, no matter what modifier they possess.

With **Peruvians** one only wants the two rosettes on the rump that help to produce density of sweep. Thus Peruvians require a form of the modifier gene that inhibits rosette production other than on the hips. This may be M itself or an intermediate modifier that permits hip rosette production. It cannot be that both M and m need to be present, otherwise Peruvians would not breed true, which they do. An Mm Peruvian relying on the presence of both modifier alleles for its hip rosettes would throw multi-rosetted longhairs (mm, see below) and non-rosetted Peruvians (MM) in their litters as well as Mm Peruvians.

M is usually supposed to be present in Peruvians, largely suppressing the effects of R but still permitting rough coat on the head and the two hip rosettes (but see under Ridgebacks

below for further discussion of this point), making the genotype IIRRMM. Those occasional Peruvians that throw Shelties are then IIRrMM.

In Australia a variety with the intriguing name of the 'Sheba Mini Yak' was developed in the 1960s and 1970s from a cross between what were described by the Australian Standards Review Committee as 'poor quality' Abyssinians and 'very poor quality Shelties' (known as 'Wombat-faced Peruvians'). It is described as a 'coarse semi-longhair', with the aim being the appearance of a 'tousled, rough-hair day', with 'longish hair covering the feet but no more; a fringe lying forward on the face; a mutton-chop moustache; rosettes on the shoulders, sides and rump; and a plume of hair coming up from the rump.'

Genetically, the first representatives would have been LIRrMm, rough-coated semi-longhairs. A true-breeding strain would, however, be IIRRmm, 'long-haired Abyssinians', but selected for coarse texture, density such as to cause the hair to stick out rather than fall flat, and moderate length of coat (indeed, the reverse of the selection in Peruvians). However, over the years many were crossed with Peruvians, resulting in longer, flatter coats and softer texture; and the resulting controversy over the standard then led to its withdrawal in 2005. The original breeds from which the Sheba Mini Yak was created are long gone, and its re-establishment will require rigid selection for coarser, shorter coats and more random rosettes. A variety of the same genotype, but with the longer, less coarse hair that is more likely with the genes around today, is known as the 'Sheba'.

The Ridgeback variety has a pronounced ridge with a short coat and no hip rosettes. First-generation 'Ridgeback-types' originating from an Aby/Smooth cross will be LLRrMm (or from a Peruvian /Smooth cross LIRrMM); but these would produce a proportion of Abys (or Peruvians) and smooths when crossed together. As the Ridgebacks being shown today, selected for pronounced ridges and no hip rosettes, were originally produced after Peruvian/Smooth crosses but now 'breed true', their genotype must be LLRRMM.

However, Peruvians exhibit no signs of a ridge but do have hip rosettes, the opposite of the Ridgeback. A possible explanation is that there is an additional modifier gene that is present in Peruvians to allow hip rosettes (this could be an intermediate version of M and m, which might be referred to as m^h), but that the effect of the long coat genotype II is to suppress ridge production (which also appears to be the case in the Sheba breeds, which too have rosettes but no ridge). If such a modifier gene is not present in smooth-hairedes, as is likely, then you would by selection obtain cavyes with a ridge but no rosettes.

If this is so, it would similarly be possible to produce Peruvian-type longhairs with rough coat on the head giving a frontal, but no hip rosettes; though it is doubtful whether these would represent a particularly interesting addition to the fancy. However, it is not known whether the m^h hypothesis does offer the correct explanation for the 'Peruvian: no ridge, hip rosettes', 'Ridgeback: ridge, no hip rosettes' conundrum. Unless someone does want to cross Ridgebacks with Shelties to try for the 'Non-Rosetted Peruvian', we may have to await a cavy genome project to find out!

Moving through the other genes that affect coat type we have:

CRESTED (or Star gene)

St A single rosette on the forehead. Another dominant mutation.

st Normal coat, no forehead rosette.

The crested gene has been breed into smooth cavyes, producing regular Cresteds, and Shelties, producing the Coronet.

Cresteds are normally either of Self colouration (the English Crested) or have the crest in a white colour (American Crested). The latter are carrying a white spotting gene, which may be partially dominant, but is probably not the major White Spotting gene seen in Tort & Whites and Dutch, which would produce far too much white.

REX

Rx Normal coat, no rexing

rx Rex coat, by which is meant hair with a kink in the shaft.

The rex gene has been bred into otherwise smooth coated cavies, producing the **Rex**, and into Shelties, Coronets and Peruvians, producing **Texels**, **Merinos** and **Alpacas** respectively.

TEDDY

T Normal coat, no rexoid characteristics

t Teddy coat

The rex type coat in the **Teddy** is produced by a different recessive gene on a different locus to the Rex, which produces a plusher feel to the coat. Thus a Rex x Teddy cross produces cavies carrying single copies of the recessive rex and teddy genes, thus giving smooth coated offspring in the first generation - something that is hard to explain without an understanding of genetics! The Teddy gene too can be bred into long-coated cavies, but it is not yet established whether the resulting varieties are sufficiently distinguishable from Texels, Merinos and Alpacas as to constitute discrete show varieties.

SWISS TEDDY

Yet another rexoid gene occurs in the **Swiss Teddy**, again recessive and again on a different locus, so that crossing to Rex or Teddies once more gives smooth-coated cavies. Here, though, the gene is encountered along with a dominant 'semi-longhair gene' to give the desired 'puffball' effect. It would be possible to produce both non-rexoid semi-longhairs or Swiss Teddy-type rexoid shorthairs using these genes, but it is uncertain whether either of these have any potential as show exhibits.

CURLY

There is another rexoid mutant, known as the 'curly gene', Cu, which first showed up in Sweden. This one differs in that it is dominant. The curly gene can be encountered in combination with the shorthair genotype LL. These are called 'Curlies' and are yet another variant on the Rex / Teddy theme. However, it is more commonly found with the Peruvian genotype IIRMM, producing the variety known as the **Lunkarya** (Lunkarya litters sometimes contain Peruvians). 'Sheltie-type' equivalents, CuCullrMM, are also possible, but it is not known how distinctively these vary from the normal type.

A similar (or possibly the same) dominant rexoid gene is responsible for the '**Lakeland**' cavies that have appeared in breeding programmes for hairless cavies.

SATIN

Sn Normal coat, no satinisation.

sn Satin coat, having a hollow shaft to the hairs that produces a satin sheen to the coat.

In this country the satin gene is encountered mainly in combination with short-haired, smooth-coated cavies as the fully standardised **Satin**. In other parts of the world such breeds as Satin Shelties, Peruvians, Teddies and Abyssinians are found. Because the fundamental coat features of these breeds are modified by satinisation, these varieties are not recognised as having either full or guide standards in the UK.

The frequently-reported incidence of OCD in Satins is due either to a potential side-effect of the satin gene (most likely) or to 'linkage' with a gene occurring close by on the same chromosome.

Coated genotypes at a glance

	Rough	Modifier	Length	Rex	Teddy	Curly	Star	Satin
Smooth	rr	MM	LL	RxRx	TT	cucu	stst	SnSn
Rex	rr	MM	LL	rxrx	TT	cucu	stst	SnSn
Teddy	rr	MM	LL	RxRx	tt	cucu	stst	SnSn
Sheltie	rr	MM	ll	RxRx	TT	cucu	stst	SnSn
Texel	rr	MM	ll	rxrx	TT	cucu	stst	SnSn
Coronet	rr	MM	ll	RxRx	TT	cucu	StSt	SnSn
Merino	rr	MM	ll	rxrx	TT	cucu	StSt	SnSn
Peruvian	RR	MM (or m ^h m ^h)	ll	RxRx	TT	cucu	stst	SnSn
Alpaca	RR	MM (or m ^h m ^h)	ll	rxrx	TT	cucu	stst	SnSn
Satin	rr	MM	LL	RxRx	TT	cucu	stst	snsn
Sheba	RR	mm	ll	RxRx	TT	cucu	stst	SnSn
Crested	rr	MM	LL	RxRx	TT	cucu	StSt	SnSn
Abyssinian	RR	mm	LL	RxRx	TT	cucu	stst	SnSn
Ridgeback	RR	MM	LL	RxRx	TT	cucu	stst	SnSn
Lunkarya	RR	MM (or m ^h m ^h)	ll	RxRx	TT	CuCu	stst	SnSn

Other combinations are possible, although how desirable they are is open to debate. For example, a **Somali** cavy has been described in the USA, this being a rexoid Abyssinian. However, there do not appear to be Crested Abyssinians, as the effects of the Rough and Star genes do not appear to be additive. This is because Abys are already 'pseudo crested'. - they have a relatively large bald patch in the centre of their foreheads where a crest would be!

Potential new breeds

In the above we have examined the major genotypes of all of the breeds of cavy that are recognised today and a few that aren't. Nonetheless, there are many other possibilities. Over thirty years ago a fancier named Geoff White created a minor stir by penning an article in 'Fur & Feather' claiming that: "There are 256 theoretical breeds of cavy." He arrived at this sum by looking at all of the possible combinations of different genes that were known at that time.

Looking at all of the genes that we have mentioned in this article (including such obscure ones as the 'Swiss semi-longhair dominant' but ignoring more speculative ones such as a 'Belted' spotting gene, a 'Peruvian hip rosette modifier' or the white spotting one encountered only in American Cresteds), and treating all genes as either dominant or recessive (when in fact some are only partially so, thus increasing the number of possibilities), a similar calculation today would lead to the headline: "There are 1,769,472 theoretical breeds of cavy." As there aren't quite that many fanciers, clearly some rationalisation is necessary if we are to have a sensibly-organised fancy.

The first part of the rationalisation comes naturally, in that many of the possible gene combinations (genotypes) give the same physical appearance (phenotype). For example, Red, Golden and Buff Himalayans all bear a remarkable resemblance to each other and to Whites, though not to Himalayans as we know them. Other combinations are likely to give such similar results that no judge would be able to distinguish one 'breed' from another, if breeds were defined on the basis of genotype. These considerations underpin the first obvious definition of what constitutes a recognised breed. Since judges must operate by considering phenotype not genotype, breeds must be readily distinguishable from each other.

A second principle underpinning the recognition of a breed is that the features distinguishing the breed must be significant in fancy terms. Within Selves colour alone is enough to constitute the definition of the breed. In breeds where markings or coat are more significant, colour is at best used to split classes and in some cases is ignored altogether (as in longhairs). The sole exception is a historical one, made in the case of the Black/Red Tricolour, which is better known as the Tortoise and White and afforded its own classes and its own Breed Club.

Next, it must be possible to define a standard of excellence for the breed in which aspirations for each significant feature can be defined, and against which cavies can readily be judged. This involves establishing a clear vision of what the ideal specimen should look like, with the ideal attributes likely to be achievable only after a sustained process of selection by the breeders concerned.

The final requirement is that the new breed should be a 'desirable addition' to the fancy. Clearly, desirability, like beauty, is in the eye of the beholder; and, to a large extent, when a proposed breed proves sufficiently popular it implies a degree of desirability. However, there will be situations, particularly when the genes responsible for producing breed features have highly undesirable side effects, where a degree of popularity is not always considered sufficient by a majority of the fancy. For this reason the UK fancy has determined that 'Skinnies' and 'Baldwins', just like Microphthalmic Whites, have no place within it.

As well as the possibility of new breeds' being created by the recombination of existing genes in different ways, these can also occur as a result of the creation of new genes by genetic mutation. All of the genes found in the cavy fancy today originally occurred as mutations of the original 'wild' forms. Although such mutations are rare, and potentially significant ones even rarer, several important mutations have been discovered within the memory of many of today's fanciers, such as those producing Dalmations, Cresteds, Rex, Satins, Tans etc. More colour genes are known in mice and rabbits that have been identified in cavies, and some would provide desirable additions to the cavy fancy - so if a 'sport' crops up in one of your litters look at it carefully. It is not likely to, but might just, be such a desirable mutation.

However, if you have a vision of a new breed that might be created by recombining various genes in existing breeds, please remember that you will not only have to cope with the cynicism of many fanciers and overcome the hurdles on distinctiveness, desirability and definition of standard described above, it might also be very difficult.

Intermixing a number of genes to produce the desired result could take several generations before you get anywhere near a line that consistently produces the features that you are aiming for. When you are working with recessive genes, which will often be the case, large numbers of 'carriers' may have to be bred together before you produce the homozygotes that you seek. This process is not a prospect for the faint of heart!

'Cross breeds'

'Cross-bred' is a term that is often used as a derogatory term by traditionalists to describe some new variety of which they disapprove. If the phrase means anything, it describes the products of a mating between two different breeds, which might be the results of an accident or a pet-breeding enterprise, or alternatively might be steps along the route described above to create a new breed. However, it has frequently been used to describe breeds such as Dalmations, Cresteds, Satins etc. that no amount of cross-breeding from non- Dalmations, Cresteds or Satins / Satin carriers would produce unless the extremely rare accident of a genetic mutation occurred.

The situation is further complicated in that some traditional standardised breeds of cavy can be produced by 'cross-breeding', the best example being the Self Cream, which can be produced 100% of the time by crossing Buffs to Whites but only 50% of the time by crossing Cream to Cream, as we have discussed above. Accordingly, 'Cross-bred' is a term that should only be used, if at all, when the user is aware of the exact mating used to produce the cavy referred to. Those fanciers who use it to describe new varieties of which they disapprove are, in doing so, generally demonstrating their ignorance rather than the wisdom and experience that they believe they are displaying.

Indeed, in other fancies, 'cross breeding is regularly undertaken as a means of revitalising or improving breeds; and, when carried out in a careful and controlled manner, this is an accepted and respected part of the breeder's 'toolkit'. The loss of viability of some breeds of cavy, as a result of using too limited a gene pool over many generations, seems to indicate that similar practices may be beneficial within the cavy fancy.

'True breeding' or 'pure-breeding'

When they refer to a particular breed, these terms are used with rather the opposite connotation to that above, to indicate that the breed always throws the key features for which it is known. This situation will arise only when the breed is based entirely on homozygous gene combinations, such as occurs in the Self Black or the Sheltie. The need to be 'true breeding' is a desirable feature within a fancy breed, as it increases the numbers of animals that can be considered for showing; but it is not essential.

A perfectly reputable breed such as the Crested can regularly throw non-Crested offspring due to the legitimate breeding technique of regular crosses to Selfs (although the breed can also be 'true breeding'). Some other breeds rely on heterozygosity for their very existence, such as Self Creams, Roans, Dalmations and probably show-quality Silver and Cinnamon Agoutis; so that when mated together they always produce two other varieties as well as the desired breed, in the well known 1/2/1 ratio (although in the case of Agoutis one of these 'varieties' is simply an Agouti that is excessively light). In other breeds that are based on the white spotting gene, *s*, such as Tricolours, the results of a cross between representatives of the breed should always belong to the breed concerned, but may show such a considerable variance to the standard that very few offspring are showable.

For these reasons, and due to the fact that a judge can only assess the cavies before him, not their ancestors, the question of whether it is 'pure-breeding' is not one of the explicit criteria for breed recognition. However, unless a proposed new breed produces enough representatives of show quality that it can be properly assessed, it is unlikely to be recognised. Accordingly, a degree of 'consistent breeding' of the desired qualities is generally required.

Prologue

Finally, regardless of the reason for the interest in cavy genetics that you have clearly shown by reading this article, you should recognise that, whilst science is a useful adjunct

to your knowledge, it is not a substitute for good stockmanship. Breeding winners remains to a large extent an art; and is the product of common sense, intuition, perseverance and the essential slice of luck. The authors wish the best of luck to all three of you that have now successfully made it to.....THE END.

Note (by BM): *This article relies heavily on one produced by Nick Warren for CAVIES in 1999. Whilst I have modified some of the text, and with Simon Neesam's help updated it where necessary to cover new breeds or the latest ideas on the genotypes of particular breeds, the credit for its structure and clarity should go entirely to Nick. However, any errors in the revised text should be attributed to me; and I should similarly be castigated for any opinions with which you disagree.*