Genetics can be intimidating, but they are essential in breeding programs especially in marked breeds such as the Dwarf Hotot. This article will answer all your genetics questions and maximize potential for marked offspring in litters through understanding of genetics.

**Basic Terminology and Eyeband Colors**

First things first! While there are not the number of color genes in the Dwarf Hotot to be concerned about as say, Netherland Dwarfs, it still helps to have a basic understanding of how genetics work. There are two main types of genes, **dominant** genes which are always displayed if present, and **recessive** genes which can only be displayed if there is no dominant gene present. Dominant genes are written in capital letters, recessive in lower case. There are other types of genes, such as **incompletely dominant**, where there is a blending of the two traits, such as if you took red paint and white paint and mixed them, getting pink. Yet another is **co-dominant** where both dominant traits are displayed, like if you took those red and white paints and splattered them on a canvas without mixing, so both red and white were separate yet intermingled.

There are many color genes in rabbits, but for Dwarf Hotots we needn’t be concerned with all of them, so I will simply describe relevant ones here. Genes come in pairs, and each offspring gets one gene for the pair from each parent. For the eyeband color, currently recognized are both black and chocolate so let’s start here. **B** is the symbol we use for black, and **b** is the symbol we use for brown, aka chocolate. Since capital letters mean dominance, black is dominant to chocolate, which is symbolized with a lower case letter. This gives us the following options for **genotypes**, the genetic code:

- **BB** – this is called **homozygous**, homo meaning “same”, because the animal has two of the same gene. In this case, they are homozygous for black, which is dominant, so we can call this **homozygous dominant**. There is no choice here but for the rabbit to have black eyebands.

- **Bb** – this is called **heterozygous**, hetero meaning “different”, as the animal two different genes. Because black is dominant, this rabbit will also have black eyebands.

- **bb** – this is again homozygous, but because both genes are recessive, we call it **homozygous recessive**, specifically. Because there is no black gene to hide the chocolate, this rabbit will have chocolate eyebands.

Another set of genes that may be useful to know for the future are for dense and dilute. Dense colors are ones such as black and chocolate, and dilute colors are ones such as blue
and lilac. To change black to blue, and chocolate to lilac, we need another gene. These genes are not connected with the black/chocolate gene, as they are on a completely separate locus, meaning location, on the chromosome. All genes are grouped into loci (plural for locus) and the loci are usually not connected as they will be on different chromosomes or far away from each other on the same chromosome, so we can look at them independently.

The dense/dilute genes work just like the black/chocolate genes. D is dense color (black and chocolate) and d is dilute (blue and lilac). Now we have a few more combinations to look at, but for simplicity let’s use an underscore after the dominant genes, because the gene the rabbit carries, or hides behind the dominant gene, doesn’t matter in the color seen on the animal. This is why in the prior example BB and Bb were the same color!

<table>
<thead>
<tr>
<th>B_D_ is black banded</th>
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</thead>
<tbody>
<tr>
<td>bbD_ is chocolate banded (so far so good, it’s all the same as before!)</td>
</tr>
<tr>
<td>B_dd is blue banded, the dilute changes the black to blue</td>
</tr>
<tr>
<td>bbdd is lilac banded, the dilute changes the chocolate to lilac</td>
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And now you have the four eyeland colors we are concerned with in the Dwarf Hotots!

**Determining Outcomes of Crosses: Punnett Squares**

To determine possible band colors in litters, we use what is called a **Punnett Square** which is simply a chart to predict the probabilities of each color. So for example, let’s say we are working on a lilac banded COD, but we don’t have any lilac banded Dwarf Hotots. We do have a chocolate banded buck who carries dilute (bbDd) and a blue banded doe who carries chocolate (Bbdd).

1) Because only one gene per loci from each parent is passed on, we have to figure out all possible combinations for this. Take the chocolate banded buck, bbDd. He could pass on bD, bd, bD, or bd (there are four possible combinations, as each b gene is considered separately). The doe, Bbdd, could pass on therefore Bd, Bd, bd, or bd.

2) Take these possible combinations and put the doe on one side of the chart and the buck on the other, filling across and down. I chose to put the buck on the top and the doe on the left side, but it doesn’t matter which you chose.

3) When filling across and down, remember to write the genes from the same locus next to each other, and always put the dominant gene first.

<table>
<thead>
<tr>
<th></th>
<th>bD</th>
<th>bd</th>
<th>bD</th>
<th>bd</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bd</td>
<td>BbDd (black)</td>
<td>Bbdd (blue)</td>
<td>BbDd (black)</td>
<td>Bbdd (blue)</td>
</tr>
<tr>
<td>Bd</td>
<td>BbDd (black)</td>
<td>Bbdd (blue)</td>
<td>BbDd (black)</td>
<td>Bbdd (blue)</td>
</tr>
<tr>
<td>bd</td>
<td>bbDd (chocolate)</td>
<td>bbdd (lilac)</td>
<td>bbDd (chocolate)</td>
<td>bbdd (lilac)</td>
</tr>
<tr>
<td>bd</td>
<td>bbDd (chocolate)</td>
<td>bbdd (lilac)</td>
<td>bbDd (chocolate)</td>
<td>bbdd (lilac)</td>
</tr>
</tbody>
</table>

The nice thing about Punnett Squares is that they give you the probability of each color as well. Now of course, probability isn’t frequency, but it still gives a general idea. It’s like if you flip a coin 100 times, it won’t necessarily be 50 heads and 50 tails.
So let’s tally the times each color shows up:
Black: 4, Blue: 4, Chocolate: 4, Lilac: 4

Each color occurs 4 times out of 16 possible outcomes. $\frac{4}{16} = \frac{1}{4}$, or 25%, so each color has a 25% chance of popping up in the litter.

**Dwarf Hotot Markings**

So that is how the eyband color works, what about the pattern itself? This is where it starts to get a lot trickier. I often hear that the Dwarf Hotot pattern is caused by the Broken gene in combination with the Dutch gene. While this is true, it’s slightly more complex than simply being a Broken Dutch, and understanding this bit of genetics will help maximize the number of properly banded baby Dwarf Hotots in your litters!

First let’s look at the Broken gene, technically called the English Spot gene, hence the codes of En for Broken and en for solid. If you are familiar with the Broken pattern you may recall the term Charlie which is used to describe a rabbit with very little, often less than 10%, coloring on their Broken pattern. This lightly marked Broken is caused when the rabbit has two Broken genes. A properly marked Broken has one copy of each gene, and a solid of course has both recessives.
- EnEn – Charlie, usually less than 10% color
- Enen – Broken, usually between 30-70% color
- enen – Solid, no white in the pattern

Well, that’s not so complicated, but now let’s study the Dutch gene. There are actually three different versions of it.
- Du – normal, non-Dutch (aka no Dutch pattern)
- du" – Dark Dutch, a more heavily marked Dutch pattern with more color in it
- du" – White Dutch, a lighter marked Dutch pattern with more white in it

The two Dutch variations, Dark Dutch and White Dutch, will mix much like the Broken and solid genes do.

The Dutch and Broken genes work together to create the Dwarf Hotot pattern. The Broken is needed to “clear off” the rest of the color on the body, ears, and head that the Dutch pattern leaves behind. However, both the Dutch and Broken patterns are additionally influenced by modifying genes. If you think about it, no two Brokens really ever look alike, they may be more blanketed, more spotted, more or less color, etc. even though they are all genetically Enen. The Dutch pattern also has variances, not every Dutch rabbit born has the proper pattern to show. These modifications really aren’t controllable, as they are likely caused by many genes interacting and as such are at this time impossible to characterize. But, putting the right Broken and Dutch gene combinations together, we can maximize the chance for properly banded offspring in our Dwarf Hotot litters.
The banding pattern on the Dwarf Hotot has the basic genotype En_du^wdu^w ideally. There are other combinations, due to modifying genes, that could also produce eyebands causing large variance in the actual genotype of the Dwarf Hotot. For example, a classic Dutch-marked animal is generally du^d du^w (although again, due to modifying genes du^w du^w is also possible) but they are solids. So it makes sense that in Dwarf Hotot litters, we see Dutch-marked animals as Dwarf Hotots can carry solid.

There is definitely a gradient, which is further affected by modifying genes, as to the amount of pigment on the Dwarf Hotot. You can think of it in terms of the follow chart, from least (as we strive for very little pigment) to most pigment:

<p>| | |</p>
<table>
<thead>
<tr>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>EnEn</td>
<td>Enen</td>
</tr>
<tr>
<td>du^w du^w</td>
<td>du^d du^w</td>
</tr>
</tbody>
</table>

The trick is figuring out which combination of the above your Dwarf Hotots are. Here are some examples of the various gradients of color seen, and what possible genotypes they may be as a reference. A bolded genotype is the most likely for that pattern, but others are possible due to the modifying genes present.

<p>| | |</p>
<table>
<thead>
<tr>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>enendu^d du^d or enendu^d du^w</td>
<td>“Booted”</td>
</tr>
<tr>
<td>enendu^d du^w or enendu^w du^w</td>
<td>“Dutch”</td>
</tr>
<tr>
<td>En_du^d du^w or En_du^w du^w or enendu^w du^w</td>
<td>“Broken Dutch”</td>
</tr>
<tr>
<td>En_du^w du^w or EnEndu^d du^w</td>
<td>“Marked”</td>
</tr>
</tbody>
</table>
You can use mismarks easily in breeding programs, however, I would not recommend the enen versions of mismarks to be used, as you do need at least one Broken gene to create the Dwarf Hotot pattern. The “Broken Dutch” mismarks can and do produce many properly marked kits. In fact, one variation not shown in the above images is the “Brown Eyed White”. These animals with no coloration or eyebands are EnEndu^wdu^w so the breeding of one to a Broken Dutch will generally result in 100% properly marked kits.

**Optimizing Chances for Marked Offspring**

So why do some Dwarf Hotot breeders seem to rarely deal with Broken Dutch and other mismarks, other than the occasional random spots, while others do? Why do some crosses give close to 100% marked kits, while others throw a ton of mismarks? Well, the modifying genes do play a role, however, we can breed to get the most marked kits even without knowing about the modifires. Keeping the White Dutch (du^w) homozygous helps a lot, so try and get rid of the Dark Dutch (du^d) by culling animals producing Booted and Dutch mismarks. Also, if Broken Dutch are consistently popping up, again, that is more likely due to the Dark Dutch gene. If you keep all your marked animals EnEndu^wdu^w or EnEndu^wdu^w you will have much better luck pulling out a high rate of marked babies.

Getting rid of bad combinations of the Broken and Dutch genes can be difficult, as they are actually linked. This is why culling is important for markings and not just type. There are many many loci per chromosome, and if they are close enough together, they often get passed on together. The closer they are the more often this occurs. This is called linkage because the genes are “linked” via the same chromosome. Normally, it is assumed that the loci are on separate chromosomes. This means they can each have an equal chance of being passed on as only one chromosome from each parent is passed on; this is why there is one copy of each gene from each parent. This assumption allows us to determine probabilities like we did with the Punnett Square. However, this is not always the case, and it turns out the Broken and Dutch genes are linked pretty closely to each other.

When someone talks about a crossover percent or a map unit, these are ways of saying how close the two loci are. This number is the gene’s chance, the percentage, of being passed on independently, as “normal” genes would be.

Example: the En (English Spot aka Broken) locus and the Du (Dutch) locus. These loci have a map unit of 13, which equals a crossover percent of 13%, meaning that the genes will be passed on independently of one another only 13% of the time, not like the random chances you would expect. The other 87% of the time, they remain connected.

Remember, this is two different genes from two different loci, this is not the gene pair. This does not mean that both Broken and solid (Enen) will come from one parent. Instead, it means if you have, for example, a solid gene linked with a Dark Dutch (en & du^d), 87% of the time those genes will be passed on together, which is bad because it creates a much higher chance to get mismarked offspring because a Broken gene is needed, and
homozygous for White Dutch is preferred. In fact, if the Dark Dutch is involved, the rabbit has to be homozygous for Broken to get a properly marked Dwarf Hotot, so from the outset a rabbit with en & du linked will produce at minimum 44% mismarked kits! (50% of the time this “bad” chromosome is passed on, so 0.50 * 0.87 = 0.44, or 44%)

**Eye Specs & Blue “China” Eyes**

It has been determined that the reason for specs and blue eyes in the Dwarf Hotot coloration comes as a potential by-product of linkage. Specifically, it is caused by linkage between the White Dutch and Broken genes following a crossing over event. Remember, chromosomes come in pairs, and paired chromosomes often exchange data between themselves. This data exchange is called **crossing over**. Here’s a picture to illustrate:

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[| | → \( \text{\rotatebox{90}{\(\mathbf{\wedge}\)}}\) → | |]
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As you can see, it actually “swapped” bits of itself with its partner chromosome. This happens multiple times, and it is why even when loci are on the same chromosome, we can usually assume they are still passed on independently because they are far enough apart that a crossover will happen between them. But of course, sometimes that isn’t the case, as is with the Broken and Dutch loci which are rarely “mixed up” by this process and are passed on together 87% of the time.

On the rare occasion a crossover event does happen, that puts a Broken and White Dutch gene onto the same chromosome, that is when specs and blue “China” eyes occur. China eye blue coloration is paler than the typical blue-eyed white coloration, and neither it nor specs is something that cannot be avoided, but this is why it occurs.

**Conclusions**

Breeding for the highest ratio of marked offspring is possible. The key things to remember are: 1) keep the Broken gene in play by not using solid based mismarks and 2) weed out the dark Dutch gene. Blue “China” eyes and eye specs actually show that a Broken and White Dutch gene are on the same chromosome, and this being ideal, they actually make good use in breeding programs as you know what at least one chromosome is, and that it is the best combination you could hope for.

**Sources**

Castle, W.E. *Studies of color inheritance and of linkage in rabbits*. Carnegie Inst. No. 337
Castle, W.E., Hadley, P.B. *The English Rabbit and the Question of Mendelian Unit-Character Constancy*. PNAS. 1915; 1(1).