

CRESTED GENETICS OLD THEORIES, NEW IDEAS, BETTER PREDICTIONS?

By Ken Yorke (2014)

Back in 2002 I wrote an article “The Crested Budgerigar in Australia” in which I expressed my opinions on Crested budgerigars, including genetics, based on my own personal experience with the variety. That article included my own summarised breeding statistics of about 400 Crested related progeny. A couple of years later when perusing my library of Crested trivia I came across some 1960s breeding statistics (about 1200 progeny) from the UK in an article by Alan Fullilove.

Recently, I found some more UK breeding data (about 1400 progeny) from the mid-1980s. This new data was the impetus to revisit my own breeding data (both old and new) and see how it stacks up against my previous thoughts from 2002 and also against the various theories on Crested genetics which have been published by others. I managed to collate an additional 400 progeny from my own post-2002 breeding.

A few quick points from my 2002 article probably should be restated here as they have some bearing on the remainder of this article:-

- All visual types of crests are caused by a swirling mechanism of the feather quills resulting in existing feathers being misdirected from their usual direction.
- The more feathers affected by the swirl, the stronger its visual appearance.
- Swirls and partial swirls located near skin boundaries such as the cere and eye cause tufts and stray feathers.
- Small “disappearing” (or temporary) crests and stray feathers around the eye have similar genetic potential to Tufteds.
- The crested variety is likely to be a polygenic variety caused by two or more separate genes at least one of which is dominant or partially dominant.
- The nice neat categories of Tufted, Half Circular and Full Circular have little relevance in predictive genetic theories.

Hair Whorls

In 2011 Don Burke published an article “Crested Budgerigars - A New Whorled View” in which he made the astute observation that the swirl of feathers of a crest parallels hair whorls in mammals. Hair whorls are swirls of hairs which can appear on the head or other body parts, singly or in multiple and vary in size and shape.

Numerous studies into the genetics of hair whorls in mammals have been undertaken with varying degrees of success. One of the more promising studies by Julius Nordby on swine in 1932 showed a likely mode of inheritance being an interaction between two complementary dominant genes. In 1933 C Warner and W Craft further tested this theory on 438 swine and produced staggeringly accurate results compared to the Nordby predictions. This theory accurately predicted the presence or absence of a hair whorl. It did not predict the location of the whorl. Nordby’s swine had a whorl on the neck. Warner and Craft’s swine had whorls on the rump, loin and face. It was noted that parents with a whorl in a particular location tended to produce offspring with a whorl in the same location. In short, the genes controlling presence or absence of a whorl are different to the genes which control the location of the whorl. Warner and Craft tried to apply the same principle to cattle and horses without success. So a one theory fits all species may not be possible.

They proposed two separate dominant genes S_1 and S_2 (the letter “S” for Swirl) and their wild

alleles S_{1+} and S_{2+} . To have a visible swirl (whorl) the animal required a minimum of one S_1 and one S_2 gene. All other genetic combinations lacking both of these genes had no swirl.

The promising part of this theory is that if we rename the gene symbol S_1 to C_d and S_2 to C_i and the respective wild alleles to C_{d+} and C_{i+} , this theory (that works for swine) is identical to J.E. Fox's existing Initiator Theory for Crested budgerigars. The difference is the swine theory predicts PRESENCE OR ABSENCE ONLY and the Initiator Theory additionally tries to incorporate the type of swirl (e.g. tuft, half circle, full circle crest). Despite that, the Initiator Theory predictions for crest type are actually reasonably close.

I am proposing a slight modification to the Initiator Theory to remove the nice distinct types of crest, as in practice there are actually many more variations in size and shape. I will use the swine gene notation "S" for consistency and also to easily differentiate my theory from the Initiator Theory.

As such, the visual Cresteds have the following genotypes:- $S_1S_{1+}S_2S_{2+}$, $S_1S_{1+}S_2S_2$, $S_1S_1S_2S_{2+}$, $S_1S_1S_2S_2$. These genotypes have two, three, three and four swirl genes respectively. I propose to call the first one "Low₁₂ Crest" the next two, "Medium₁₂₂ Crest", "Medium₁₁₂ Crest" and the last "High₁₁₂₂ Crest" (The subscripts in the names refer to which and how many S_1 and S_2 genes the types have). The higher the order of the crest the more swirl genes it has AND the more individual feathers form the crest feather swirl.

As a starting point, the Low₁₂ Crest category has the lowest number of swirled feathers and certainly includes tufts, "disappearing" (or temporary) crests and stray feathers around the eye and perhaps weak half circulars. At the other end of the scale the High₁₁₂₂ Crest category has the highest number of swirled feathers and contain very strong crests (predominantly, if not exclusively, strong full circular crests).

Both types of Medium Crest contain all the other visual crest types with a medium number of swirled feathers (e.g. probably strong half circulars, weaker full circulars and perhaps even extremely strong tufts). At this stage I do not propose any obvious visual difference between the two Medium Crest types. There are no strict visual demarcation lines between each category as it is based solely on the number of swirled feathers, no matter where they are located or what they look like.

Many experienced Crested breeders have long used a similar ranking for crest breeding potential, even using a pointscore system (e.g. 0 points for Normal, 1 for Crestbred, 2 for Tuft, 3 for Half Circular etc). The aim being to make pairings based on the scores of both parents to maximise the strongest type of crest in the progeny. This old system, despite not being based on sound science, is actually similar to the above, where we are counting genes and hence in effect counting swirled feathers.

Inheritance of the Locus (Crest Location)

The swine study showed that the location of a swirl is inherited separately to the genes which cause presence or absence of a swirl. I propose a new rare recessive gene L_S and its common wild allele L_+ ("L" stands for "Locus" with the subscript "S" for "Skull"). The L_S gene is responsible for putting a locus on the skull so a swirl can potentially form. It is not important at this stage to identify exactly where on the skull the locus lies, just that it is somewhere on the skull.

The following genotypes are possible:-

- $L_S L_S$ POTENTIALLY creates a visible locus on the skull;
- $L_S L_+$ wild type split for skull locus (no visible locus in most cases);

- L_+L_+ wild type (no visible locus)

I have emphasised the word “potentially” above because a visible swirl on the skull of any type requires two recessive L_S genes AND at least one each of the dominant S_1 and S_2 genes. This added complication to crested genetics increases the number of crest related genotypes from the 9 used in the Initiator Theory to 27 in my theory. Table 1A gives a full list of all the genotypes and possible matings.

Based on real breeding statistics, it is likely that a small percentage (**approximately 20%**) of the Crestbred no.s 10-13 may in fact show a swirl or disappearing swirl. Even though they only have one L_S gene it may be similar to the way that some Normals split Danish Recessive Pied show a visible head spot.

Recent research undertaken at the University of Utah identified the EphB2 gene which acts like an on-off switch to create a head crest on pigeons. It is believed to be a recessive gene. They also believed other genetic factors (which they did not study in detail) determined the shape of crest.

Overestimation of Visual Cresteds

Table 1A is still only one piece in a larger puzzle that is Crested genetics. One of the major criticisms of the Initiator Theory has been that it generally overestimates the percentages of the visual crest types in many matings.

One of my favourite benchmark matings to test any Crested genetic theory is the mating of Full Circular Crest x Normal. Using the Initiator Theory we have two possible matings:-

Full Circular(df) x Normal = 100% TuftMating(1)
and Full Circular(sf) x Normal = 50% Tuft + 50% CrestbredMating(2)

In my own breeding results I have achieved 13% Tuft plus 8% small disappearing crests and permanent stray feathers at various locations on the skull plus 79% birds with no swirls. The UK results that I have were 17% Tuft, 8% Half Circular, 9% Full Circular (some of the Halves being attributed to misidentification of very strong Tufts and the remaining appearance of Halves and Fulls being attributed to the Normal parent being a misidentified Crestbred and not a pure Normal). In any case the percentage of visual Cresteds does not approach either 50% or 100% as suggested by the Initiator Theory.

In my theory using Table 1A, Mating (1) becomes:-

No. 1 High₁₁₂₂ Crest x No.27 Normal(pure)
= 100% No.13 Crestbred_{12S}Mating(1A)
= 80% No.13 Crestbred_{12S} (no swirl) + **20% No.13 Crestbred_{12S} (small swirl)**

Mating (2) becomes:-

No. 2 Medium₁₂₂ Crest x No.27 Normal(pure)
= 50% No.13 Crestbred_{12S} + 50% No.17 Crestbred_{2S}Mating(2A)
= 40% No.13 Crestbred_{12S} (no swirl) + **10% No.13 Crestbred_{12S} (small swirl)**
+ 50% No.17 Crestbred_{2S} (no swirl).

and/or No. 3 Medium₁₁₂ Crest x No.27 Normal(pure)

= 50% No.13 Crestbred_{12S} + 50% No.15 Crestbred_{1S}Mating(2B)
= 40% No.13 Crestbred_{12S} (no swirl) + **10% No.13 Crestbred_{12S} (small swirl)**
+ 50% No.15 Crestbred_{1S} (no swirl).

Notice there are NO TRUE CRESTED genotype progeny in the above example matings, only Crestbred genotypes, some of which show a swirl (i.e. birds which look like Low₁₂Crest but are not). The overestimated values of 50% and 100% are now only 10% and 20% respectively in my theory.

Population Genetics

I will diverge slightly now to discuss population genetics which is probably more easily discussed using a simple example of the Danish Recessive Pied. In the total worldwide population of budgerigars there will be a small percentage which are Recessive Pies (with two pied genes), a bigger number of Normals / Recessive Pied (with one pied gene) and the vast majority of birds are Normals (with no pied genes). So if you grab a random normal looking bird from the large population there is a high probability that it has no pied genes and a small probability that it has one pied gene (i.e. split recessive pied). In an ideal world the relative proportions of each type might reach some equilibrium based on their genetic breeding rules. However man interferes with this by arbitrarily applying selection processes to his matings (e.g do you only breed with visuals and not the splits etc). If you did the same example using Green, Green/Blue and Blue you would get entirely different relative proportions of each compared to that of the Recessive Pied. So the moral of the story is that in a captive breeding situation like ours the frequency of variety genes is heavily influenced by how popular is the variety, its genetic rules, how recently the mutation occurred and personal preferences of how we breed them.

This principle will now be applied to the L_S gene. In Table 1A there are three different genotypes for Normal (i.e. a bird with no S₁ or S₂ genes). They are:-

- i. No. 27. S₁₊S₁₊S₂₊S₂₊L_{S+}L_{S+} - the true pure Normal with no skull locus genes. This would be the majority of Normals in our worldwide population.
- ii. No. 18. S₁₊S₁₊S₂₊S₂₊L_SL_{S+} - a Normal that is split for the skull locus gene.
- iii. No. 9. S₁₊S₁₊S₂₊S₂₊L_SL_S - a Normal having 2 L_S genes but still does not display a skull locus because it also has no S₁ and S₂ genes.

Let's now revisit the benchmark Full Circular x Normal mating and for brevity I will only look at the equivalent of Mating (1) above. In my theory Mating (1) becomes any of the following:-

- | | |
|---|-------------------|
| No. 1 High ₁₁₂₂ Crest x No.27 Normal (pure) | Mating (1A) |
| = 100% No.13 Crestbred _{12S} | |
| No.1 High ₁₁₂₂ Crest x No. 18 Normal _S | Mating (1B) |
| = 50% No.4 Low ₁₂ Crest + 50% No.13 Crestbred _{12S} | |
| No.1 High ₁₁₂₂ Crest x No.9 Normal _{SS} | Mating (1C) |
| = 100% No.4 Low ₁₂ Crest | |

Any single mating will be any one of Matings (1A), (1B) or (1C).

For demonstration purposes only, let's assume that the general population of "Normal" budgerigars has 75% No.27 Normal (pure), 20% No.18 Normal_S and 5% No.9 Normal_{SS}. That means that taken across the whole population of every Full Circular x Normal mating, 75% will be mating (1A), 20% will be mating(1B) and 5% will be mating (1C). The resulting average percentage of No.4 Low₁₂ Crest progeny is (75% x 0) + (20% x 50) + (5% x 100) = **15%**. In addition the percentage of No.13 Crestbred_{12S} with a small swirl will be ((75% x 100) + (20% x 50) + (5% x 0)) x 20% = **17%**. Thus the grand total of birds showing a swirl is 15 + 17 = **32%**. The equivalent overestimated figure using the Initiator theory is 100%.

To be more complete you could add in the possibility that the Full Circular parent could also be a No.2 Medium₁₂₂ Crest or No.3 Medium₁₁₂ Crest. In that case the grand total of birds showing a swirl across all 9 possible matings = **21%** . The equivalent overestimated figure using the Initiator Theory is 75%.

- Any Crestbred progeny from any true visual Crested x pure Normal (no.27) mating are guaranteed to have one L_S gene. Any Crestbred progeny from a true visual Crested x true visual Crested mating are guaranteed to have two L_S genes. Therefore the latter Crestbreds will on average subsequently produce more visual Cresteds than the former Crestbreds.
- The Initiator Theory does not cover the impact of the L_S gene on the Crestbreds and on average, overestimates percentages of the visual Cresteds bred from the general Crestbred population.
- Crestbred birds with a swirl will, on average, produce less visual Cresteds than true visual Cresteds.

The above examples show how the inclusion of the L_S gene into the Crested model not only addresses the separation of swirl genes from locus genes but also substantially removes the flaw of overestimation of the quantity of visual Cresteds in the Initiator Theory.

Time Shifting

If the population breakup idea is correct then this adds extra vagueness to a theoretical Crested mating table as the breakup proportions are unknown (but you could make an educated guesstimate by working backwards from real breeding statistics). However, since the breakup is influenced by man and his fickle fads then this breakup may vary over time

In the last fifty years the Crested variety has gradually become more popular. Crested breeders tend to produce a lot of excess Crestbred stock which are sold to the general bird population and the majority of these birds and their descendants will inevitably be used as if they were Normals. In short, as the Crested variety gets more popular the frequency of the S₁, S₂ and L_S genes in the “Normal” population is likely to increase. Thus when Crested breeders purchase outcross “Normals” the chance increases of actually buying in Crestbreds (carrying any of the S₁, S₂ or L_S genes) and/or Normals carrying the L_S gene without knowing. This means it is likely that the number of visual Cresteds from matings involving apparent “Normal” parents will increase significantly over time until some maximum limit is reached. Any Crestbred progeny from those same matings are also more likely to carry more S₁, S₂ and L_S genes and hence a downstream spin off of this is that when they eventually breed they may cause a minor increase in the proportion of visual Cresteds in their matings also over time. With an increased frequency of S₁ and S₂ genes also comes a minor increase in higher order Cresteds versus lower order Cresteds from matings over time. Table 2 below shows the time shift data based on a study of 3825 records over 50 years from my archive. (The definitions of “Normal” and “Crestbred” used in Table 2 are not strictly genotype based but based on older more practical definitions.)

Table 2 - Percentage of Visual Crested Progeny Over Time

Mating Summary	UK 1960s % Visual	UK 1980s % Visual	Aust Pre-2002 % Visual	Aust Post-2002 % Visual
Visual x Visual	62%	69%	58%	55%
Visual x “Crestbred”*	30%	39%	29%	30%
Visual x “Normal”**	14%	29%	15.5%	16.5%

* “Crestbred” = Non-visual with at least one visual Crested parent.

** “Normal” = Non-visual with no visual Crested parents

Reviewing the UK data, as expected, there is an obvious increase in the percentage of visual crests from all matings over time. My personal Australian crest data does not show the increases of the UK birds because I have a highly inbred family of Cresteds which rarely uses outcrosses and hence I am not injecting any new stray unknown S_1 , S_2 or L_S genes into my stock from outcross "Normals". The increase in the UK Visual x Visual matings seems a little high to me so this hints to another additional mechanism in play, probably affecting not only this category but all three categories.

Modifiers

Experienced breeders will be familiar with the term "modifier" and in particular "modifier genes". Modifier genes are genes whose action influence or modify the action of other genes. They have long been cited as causing lots of subtle "natural variation" in otherwise stable budgerigar varieties.

Genetic science has progressed and discovered lots of other ways in which the action of genes can be modified. These include, but are not limited to, duplicated genes, tandem repeat DNA, junk DNA (all of which change the DNA code) and gene regulators and other biological processes (which do not change the DNA code). As far as budgerigar varieties are concerned it appears that the number of true modifier genes is less than we first thought and most of the natural variation we see is caused by these other mechanisms. The details of all these mechanisms are beyond the layman so I will cover them all with the one umbrella term of "modifiers" since it is a term that budgerigar breeders are already familiar with.

These modifiers can increase, decrease, start or stop the action of a gene. In his writings on this subject Don Burke uses the apt analogy of modifiers being akin to "volume controls" for a gene's action. The tricky part of these modifiers is that some can be inherited and some cannot, and some can be affected by external factors from the environment.

In Crested genetics we can look at the potential effects of modifiers on the S_1 and S_2 genes as increasing or decreasing the number of swirled feathers. So now the number of feathers in a swirl can be determined both by the number of S_1 and S_2 genes AND additionally the modified "strength" of each S_1 and S_2 gene. There may also be a threshold effect where below a particular strength swirls may not be visible despite having all the required genes.

Since we as breeders are more likely to select for birds with stronger swirls, then over time we will inadvertently be selecting for those inheritable modifiers which strengthen our feather swirls. The result is all our visual Cresteds will be stronger now than they were in the past. It also means that some of those birds which previously only had one stray feather or a disappearing crest which many breeders completely did not see at all, will now have more swirled feathers and be more obvious and permanent. Thus we will actually have a small practical increase in the number of visual Cresteds from our matings (particularly the lower order matings). This forms another piece in the puzzle and helps further explain why in Table 2 above we see an increase in the % visuals over time in all categories.

The Crested variety basically started to gain popularity in the UK from the 1960s. In Australia that similar movement did not start until the 1980s, so the UK has a 20 year head start on the Australians with regard to the time shifted, modified and improved quality of the feather swirls. In my 2002 article I mentioned the history of my own Australian Cresteds and related how one branch of my family of pure Australian Cresteds had an outcross to a single bird likely containing UK crested genes. I remarked at the time that this branch of the family tended to produce Cresteds that were of a higher order than they should have been, and that I suspected that the UK Crested variety might be more "potent" than, or slightly different to the Australian Crested, albeit that the overall genetic rules seemed identical. The above 20 year

head start on “improvement” of the UK crests explains my previous observation perfectly. For better or worse, the vast majority of Crested stock in Australia (excluding my own) is now based on UK bloodlines since importation of UK Cresteds in the 1990s.

Multiple Crests

The effect of modifiers on the L_S gene has the potential to affect the number of loci and the position of loci. These modifiers could move the locus to slightly different areas on the skull e.g. forward, back, left or right. (These variations can however also be explained simply by variation in embryonic growth.) Early Crested breeders were of the opinion that at least two separate strains existed, Continental with a more forward locus and American with a more rearward locus. If this is true, this can be explained by modifiers acting on the L_S gene or even a second very similar multiple allele of L_S .

The most obvious expression of modifiers acting on L_S is a change in the number of loci. If you ramp up the L_S gene you get multiple loci on the skull, i.e. Multi-Crests. If you ramp up the L_S gene in Crestbred no.s 10-13 (which have S_1 , S_2 and only one L_S gene) then it is possible to ramp up from no locus to one locus, hence one reason why some (originally about 20%) of these particular Crestbreds can show a swirl. This observed 20% value is an approximation and will vary from family to family and likely be more prevalent in families that have Multi-Crests, and the value will likely vary over time.

If you ramp down the L_S gene you have the potential to reduce the number of loci from one to none, hence no visual swirl on a bird which is otherwise genotypically Crested. These examples may also be another piece in the puzzle as to why the Initiator Theory has poor estimates of the percentage of visual Cresteds in many matings.

Since the number of feathers in a swirl is determined by the S_1 and S_2 genes and its modifiers, then it is now possible to have Multi Low Crests, Multi Medium Crests and Multi High Crests. This is exactly what we see in our real breeding results.

Frills

Feather swirls (and hence their loci) can also appear on the chest, back and wings. All these birds were called Frills or Frilled, although other names have come into vogue. Feather swirls in these areas will never be as strong as they are on the skull because every budgerigar has a higher density of feathers on the skull than on other body areas. The common theme of all Frill variations is that they have a locus that is generally level with the shoulder area and almost all also has a skull locus. The position of the shoulder locus is generally central (on the mantle) but can be left or right (onto the wings or around to the upper chest) or up (to the neck) or down (on the back).

I confess that I have never bred a single Frill out of my approximately 800 Crested related progeny. This suggests that a separate gene is involved which I do not have in my Crested family. The variety is only seriously encouraged in Asia and the Middle East and is actively discouraged in most other countries. As a result the amount of serious genetic study on Frills is virtually zero. My hypothesis below is based on observation and discussion with a handful of Frill breeders and some extremely limited published breeding statistics.

Taking a very broad view at the possibilities, Frills might be caused by:-

- i. Genes unrelated to Cresteds, or
- ii. Modifiers acting on the S_1 , S_2 and/or L_S genes, or
- iii. Genes similar to, or multiple alleles of the S_1 , S_2 and/or L_S genes.

Option i) is unlikely and will not be explored here. Option ii) requires modifiers to extremely ramp up the L_S gene and either or both of the S_1 and S_2 genes, essentially becoming the “super” form of a Multi-Crest and would breed with the same genotypes as Table 1A (however based on limited actual breeding data there are some possible anomalies with this option that require further future study, but I do not rule this option out). Option iii) will be explored below.

I am proposing a new rare recessive allele L_F (“L” for “Locus” and subscript “F” for “Frill”). L_F is a multiple allele of L_S and L_+ . An order of dominance exists with L_+ being dominant over L_S which in turn is dominant over L_F . L_F creates TWO loci zones, one on the skull AND one near the shoulders. This Frill hypothesis does fit all examined breeding records to date but the amount of data is so small that I fully expect that modifications to this hypothesis may occur in the future. It may still be possible that L_F is not a multiple allele but only a similar acting gene to L_S at a different gene location, but early data suggests not.

The following genotypes are possible:-

- L_FL_F POTENTIALLY creates a Frill with a skull locus and a shoulder locus;
- $L_S L_F$ POTENTIALLY creates a Crested with a skull locus and is split for Frill;
- $L_F L_+$ wild type split for Frill (no visible loci in most cases);

A visible swirl on the skull and the shoulder requires two recessive L_F genes AND at least one each of the dominant S_1 and S_2 genes. Allowing for the above L_F allele then the previous Table 1A can now be extended to include Table 1B below:-

Table 1B - List of Frill Related Genotypes

Type Name	Genotype	Phenotype
28. High ₁₁₂₂ Frill	$S_1 S_1 S_2 S_2 L_F L_F$	Skull and shoulder swirls with high number of feathers
29. Medium ₁₁₂₂ Frill	$S_1 S_1 + S_2 S_2 L_F L_F$	Skull and shoulder swirls with medium number of feathers
30. Medium ₁₁₂ Frill	$S_1 S_1 S_2 S_2 + L_F L_F$	Skull and shoulder swirls with medium number of feathers
31. Low ₁₂ Frill	$S_1 S_1 + S_2 S_2 + L_F L_F$	Skull and shoulder swirls with low number of feathers
32. Frillbred _{11FF}	$S_1 S_1 S_2 + S_2 + L_F L_F$	Normal
33. Frillbred _{1FF}	$S_1 S_1 + S_2 + S_2 + L_F L_F$	Normal
34. Frillbred _{22FF}	$S_1 + S_1 + S_2 S_2 L_F L_F$	Normal
35. Frillbred _{2FF}	$S_1 + S_1 + S_2 S_2 + L_F L_F$	Normal
36. Normal _{FF}	$S_1 + S_1 + S_2 + S_2 + L_F L_F$	Normal
37. High ₁₁₂₂ Crest / Frill	$S_1 S_1 S_2 S_2 L_S L_F$	Skull swirl with high number of feathers
38. Medium ₁₁₂₂ Crest / Frill	$S_1 S_1 + S_2 S_2 L_S L_F$	Skull swirl with medium number of feathers
39. Medium ₁₁₂ Crest / Frill	$S_1 S_1 S_2 S_2 + L_S L_F$	Skull swirl with medium number of feathers
40. Low ₁₂ Crest / Frill	$S_1 S_1 + S_2 S_2 + L_S L_F$	Skull swirl with low number of feathers
41. Crestbred _{11S} / Frill	$S_1 S_1 S_2 + S_2 + L_S L_F$	Normal
42. Crestbred _{1S} / Frill	$S_1 S_1 + S_2 + S_2 + L_S L_F$	Normal
43. Crestbred _{22S} / Frill	$S_1 + S_1 + S_2 S_2 L_S L_F$	Normal
44. Crestbred _{2S} / Frill	$S_1 + S_1 + S_2 S_2 + L_S L_F$	Normal
45. Normal _S / Frill	$S_1 + S_1 + S_2 + S_2 + L_S L_F$	Normal
46. Frillbred _{1122F}	$S_1 S_1 S_2 S_2 L_F L_+$	Normal (small % may have swirls)
47. Frillbred _{122F}	$S_1 S_1 + S_2 S_2 L_F L_+$	Normal (small % may have swirls)
48. Frillbred _{112F}	$S_1 S_1 S_2 S_2 + L_F L_+$	Normal (small % may have swirls)
49. Frillbred _{12F}	$S_1 S_1 + S_2 S_2 + L_F L_+$	Normal (small % may have swirls)
50. Frillbred _{11F}	$S_1 S_1 S_2 + S_2 + L_F L_+$	Normal
51. Frillbred _{1F}	$S_1 S_1 + S_2 + S_2 + L_F L_+$	Normal
52. Frillbred _{22F}	$S_1 + S_1 + S_2 S_2 L_F L_+$	Normal
53. Frillbred _{2F}	$S_1 + S_1 + S_2 S_2 + L_F L_+$	Normal
54. Normal _F	$S_1 + S_1 + S_2 + S_2 + L_F L_+$	Normal

As with Cresteds, the number of feathers affected by swirls (on both skull and shoulder of a Frill) is proportional to the number of S_1 and S_2 genes (hence Low₁₂Frills, Medium₁₁₂Frills,

Medium₁₂₂Frills and High₁₁₂₂Frills) and their respective modifiers. The lower order Frills tend to be called BackFrills (or chest Frills). The higher order Frills tend to be called Helicopter or Japanese. It is also possible that a small percentage of modified Frillbred no.s 46-49 (which have S₁, S₂ and only one L_F gene) may in fact show a swirl or disappearing swirl for the same reasons as modified Crestbred no.s 10-13 mentioned above.

The number of Frill loci is affected by modifiers acting on the L_F gene. Increases cause multiple loci on both the skull and the shoulder area and/or migration of the loci to nearby areas. The multiple loci on the shoulder can spread to each wing, these being called various names including Japanese, Helicopter, Pharaoh etc based on visual differences (the Pharaoh type having some loci further out toward the extremities of the wing). Decreases in the number of loci could remove the shoulder locus (making the bird look like a conventional Crested), or remove the skull locus and leave the shoulder locus (apparently a moderately rare occurrence), or potentially removing both skull and shoulder locus looking like a Normal (there is no hard evidence of the latter yet). It should be noted that many lower order Frills and/or those with ramped down S₁ or S₂ genes may have a “disappearing” shoulder swirl but still retain some skull swirl as the head has a higher density of feathers. Such birds may look like lower order Cresteds despite being genotypically Frill. This is probably why very few obvious visual Frills have low order head swirls but instead have medium or high order head swirls.

Again as with Cresteds, selective breeding for these modifiers will time shift the percentage of visual Frills from various matings, as will changes in the frequency of the currently very rare L_F allele in the wider outcross “Normal” population.

The avid Frill breeder could draw up a 54 x 54 square matrix to work out all the theoretical progeny involving Frills, Crests etc but this a daunting task and as I will show below, such tables are only of modest use for budgerigar varieties as complex as Crests and Frills.

Practical Breeding Rules

If you know the exact genotype of the parents Table 1A will give exact genotypes for the progeny and the exact percentages of each. (Frill progeny can be worked out using Table 1B with some manual calculations). Due to the action of modifiers on the S₁, S₂ genes there will be some plus and minus tolerance on the physical appearance for each progeny type and thus an apparent tolerance on the percentages of each visual type. Due to the action of modifiers on the L_S and L_F genes there may be multi-swirls or absent swirls of each visual type which again apply a tolerance on the physical appearance. All these tolerances can vary over time. It's like trying to predict a moving target. The approximate maximum percentage of progeny with visible swirls quoted in Table 1A matings will be reduced by those modifiers causing absent swirls.

Table 3A is an attempt to diagrammatically show how the old nice neat categories are now more vague when the effects of the S₁, S₂, L_S and L_F genes and their modifiers are factored in. Table 3B is the Frill equivalent, however as the category names for Frills (or even the name “Frill” itself for the whole group) has not been standardised, and we have not necessarily yet seen all the possible types, then Table 3B cannot be classed as completely accurate yet.

The real difficulty however, is that it is virtually impossible to be certain of the true genotype of the parents. For example, if you purchase a “Normal” looking outcross it could be any one of 42 different genotypes. Likewise a bird with a visual swirl could have 8 genotypes (20 if you include Frills). You are then left with making an average of all the possible matings (preferably using some guesstimate of population genetics to give some more likely matings

Some relevant points:-

- **True visual Crested x pure Normal (no.27) matings produce a small percentage of progeny with visual swirls.** This small percentage are actually modified Crestbred genotypes showing visual swirls. The majority of the above pairs that do appear to produce visual Cresteds actually contain a Normal_S (no. 18) or Normal_{SS} (no.9) or Crestbred (no.s 5-8, 10-17) in the pair, not a pure Normal (no.27).
- **The higher the order of crest, the more S₁ and S₂ genes it has and on average, is likely to produce higher order Crested progeny and in greater percentages.**
- Breeders can **select for** (but not necessarily completely control) the S₁ and S₂ **enhancing modifiers and gradually increase the strength of visual swirls** over time.
- Breeders can **select for the multi-swirl trait** but not necessarily completely control it.
- The above points apply equally to Cresteds and Frills.
- As accurate genotypes are hard to identify we are forced to use population wide average or summarised matings to give approximate predictions. Table 2 can be used in this regard and takes into account modifiers, time shifting etc.

I do not expect this theory to be the end of discussion on Crested or Frill genetics, but hope that it can be used as a springboard to make further refinements or alternatives. Frills in particular need more study. The research into pigeons offers some further potential advancement as does the recent DNA sequencing of the budgerigar genome. Unfortunately, even if all the theory in this article is completely correct, the very complexity of it and particularly the inability to accurately identify the parent genotypes means that a nice simple table of matings that precisely mirror the real world results will never be achieved.

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