

CRESTS – TOWARDS A BETTER UNDERSTANDING

by George Clarke Western Australia

Part 1 – The PE Theory for the Crested Budgerigar

The understanding of the Crest variety has always been frustrated by the lack of an accurate genetic theory.

The theory currently adopted by the Crested Budgerigar Club, the **Initiator Theory**, was first proposed in 1970 by Dr J.E.Fox (Refs 1 & 9). While the theory has for many years remained the best available, it has been proven to have serious inaccuracies which can cause confusion for breeders. An attempt to correct these inaccuracies via the introduction of “linkage” (Ref 9) has, on the whole, proved unsuccessful in eliminating the anomalies.

It is found in practice that the theory generally overestimates the number of visual crest progeny from various matings. In some cases the prediction is grossly overstated, (eg Crest x Normal pairing, 56% v 13% actual).

The Initiator theory precludes some breeding outcomes which are known to have actually occurred in practice and makes quite erroneous predictions for some pairings, eg Full Circular x Normal pairings produce all three types of crest, but the theory predicts only tufted progeny. (Refer examples in Annex 1)

Based on analysis of breeding results comprising 1,759 progeny including 570 visuals, an alternative theory is proposed, which is shown to be far more accurate than the Initiator theory. The theory, which the author has named the “**PE Theory**”, is based on the genetic concepts of **Penetrance** and **Expressivity**.

The concepts of Penetrance and Expressivity

Simple Mendelian genetics do not always explain the range of phenotypes produced by a particular genetic combination. The concepts of **penetrance** and **expressivity** are sometimes used to account for the observed phenotypic variability.

“Differences in environmental conditions or in genetic backgrounds may cause individuals that are genetically identical at a particular locus to exhibit different phenotypes. The percentage of individuals with a particular gene combination that exhibit the corresponding character to any degree represents the penetrance of the trait.

Eg One type of polydactyly (extra fingers and/or toes) in humans can be produced by a dominant gene (P). The wild-type condition with five digits on each limb is produced by the recessive genotype (pp). However, some heterozygous individuals (Pp) are not polydactylous. If 20% of Pp individuals do not show polydactyly (i.e. are wild-type), the gene has a penetrance of 80%.

A trait, although penetrant, may be quite variable in its level of expression. The degree of effect produced by a penetrant genotype is termed expressivity.

Eg. The polydactylous condition may be penetrant in the left hand (six digits) and not in the right (five digits), or it may be penetrant in the feet but not in the hands.” (Ref 7)

Penetrance and Expressivity in Crests

Applying these concepts to the Crest mutation in the Budgerigar, **Penetrance** determines whether the crest characteristic will be exhibited, while **Expressivity** determines the location and form of the crest characteristics.

Summary of the PE Theory

In essence the PE Theory postulates that the presence of a crest is due to the crest gene “Cr”, while the actual form of the crest is due to a group of secondary modifiers or expressivity genes, (E genes). The crest gene is an autosomal dominant with low penetrance and highly variable expressivity. The exact number of E genes and the nature of their action is unknown. Crest phenotypes comprise a continuous spectrum ranging from a single feather to multiple crests.

Definitions of the PE Theory

It is necessary to define some terms as they apply to the PE Theory. Some of these definitions may, as a consequence of the theory, differ slightly from those adopted previously by other writers. In particular readers should erase from their minds any remaining memories from the Initiator theory. The concept is very different.

Symbols. The crest gene is given the symbol “Cr”, while the symbol for the wild type allele is “cr”

Crest. A Crest is a bird which exhibits a crest phenotype and carries at least one Crest gene. The definition includes birds which exhibit crest characteristics temporarily as nestlings but do not do so as adults.

There are two basic genetic forms of the Crest,
 Single Factor (SF) Crests, having one crest gene and one wild type gene, (Cr,cr)
 Double Factor (DF) Crests, having two crest genes, (Cr,Cr)
 These two genetic forms are thought to be visually indistinguishable.

Crestbred. A Crestbred is a bird having at least one Crest or Crestbred parent but at no time exhibiting any permanent or temporary visible crest characteristics. Crestbreds exhibit a Normal phenotype but carry either one or zero crest genes. A Crestbred cannot carry two crest genes because all DF’s are visual crests.

There are two basic genetic forms of the Crestbred,
 Single Factor (SF) Crestbred, having one crest gene and one wild type gene, (Cr,cr)
 Zero Factor (ZF) Crestbred, having two wild type genes, (cr,cr)
 These two genetic forms are visually indistinguishable.

Table 1 Summary of Crest Phenotypes and Genotypes

Description	Phenotype	Genotypes		
		DF	SF	ZF
Crest	Crest	Cr,Cr	Cr,cr	
Crestbred	Normal		Cr,cr	cr,cr
Normal	Normal			cr,cr

Predictions of the PE Theory

According to the proposed PE theory, the crest gene is an autosomal dominant with low **penetrance** and highly variable **expressivity**.

While it has been possible to calculate a reasonably accurate estimate of penetrance and consequently produce reliable predictions for the percentage of visual crests from various pairings, it **is not** possible with any degree of accuracy to define or quantify the crest forms to be expected. However it **is** possible to make some broad generalisations regarding the expected forms of crest.

Penetrance

The **penetrance** of the crest gene determines the percentage of birds, carrying the crest gene, which will at some stage exhibit visual crest characteristics.

When the Crest gene is present as a double factor (DF), Penetrance (Pdf) is 100% (all DF's are visual crests) and when present as a single factor (SF), Penetrance (Psf) is approximately 15%-20%. (Calculated by the author from available published breeding data).

The percentage of visual SF crests is determined by the formula,

$$\% \text{ of Visual Crests (SF)} = [\% \text{ of (Cr,cr) genotype}] \times \text{Psf}$$

Theoretical expectations for all possible Crest, Crestbred, and Normal pairing combinations are summarised together with their derivations in **Table 2**

Table 2 PE Theory – Theoretical Breeding Expectations

Parents			Progeny								
Mating	Pairing		Genotype			Visual Crests			Crestbreds		
			Cr,Cr	Cr,cr	cr,cr	Total	DF	SF	Total	SF	ZF
Crest x Crest	DF Crest	DF Crest	100%			100%	100%	0%	0%	0%	0%
	DF Crest	SF Crest	50%	50%		59%	50%	9%	42%	42%	0%
	SF Crest	DF Crest	50%	50%		59%	50%	9%	42%	42%	0%
	SF Crest	SF Crest	25%	50%	25%	34%	25%	9%	67%	42%	25%
	Average					63%	56%	6%	37%	31%	6%
Crest x Crest- bred	DF Crest	SF CB	50%	50%		59%	50%	9%	42%	42%	0%
	SF Crest	SF CB	25%	50%	25%	34%	25%	9%	67%	42%	25%
	DF Crest	ZF CB		100%		17%	0%	17%	83%	83%	0%
	SF Crest	ZF CB		50%	50%	9%	0%	9%	92%	42%	50%
	Average					29%	19%	11%	71%	52%	19%
Crest x Normal	DF Crest	Normal		100%		17%	0%	17%	83%	83%	0%
	SF Crest	Normal		50%	50%	9%	0%	9%	92%	42%	50%
	Average					13%	0%	13%	87%	62%	25%
Crest- bred x Crest- bred	SF CB	SF CB	25%	50%	25%	34%	25%	9%	67%	42%	25%
	SF CB	ZF CB		50%	50%	9%	0%	9%	92%	42%	50%
	ZF CB	SF CB		50%	50%	9%	0%	9%	92%	42%	50%
	ZF CB	ZF CB			100%	0%	0%	0%	100%	0%	100%
	Average					13%	6%	6%	87%	31%	56%
Crest- bred x Normal	SF CB	Normal		50%	50%	9%	0%	9%	92%	42%	50%
	ZF CB	Normal			100%	0%	0%	0%	100%	0%	100%
	Average					4%	0%	4%	96%	21%	75%

[**Note.** Table 2 is based on a Penetrance value (Psf) = 17%

As always these theoretical expectations are average expectations over a large number of matings and are not necessarily accurate for individual nests. See Note to Table 4 and Part 2 for discussion of averages]

Expressivity

Expressivity determines the type of crest which will be exhibited.

Any bird penetrant for the Crest gene will exhibit one of the many crest forms, depending upon the modifying expressivity genes (E genes) present.

Any pairing in which at least one parent carries a crest gene, expressed or not, may produce any form of visual crest depending upon the E genes present. The frequency of occurrence of some forms may be low.

The expressivity of the Crest is a polygenic characteristic and cannot be predicted theoretically for individuals.

While it is possible to speculate on factors which are expected to influence expressivity, (location of locus, number of loci, number of feathers involved, proximity of boundaries such as cere and eyes, etc), the number of genes involved is unknown, as is the nature of their interaction, (dominant, recessive, partially dominant, over-dominant, linked, etc). In the face of these unknowns and this degree of complexity, it would appear futile at this time to attempt to produce a model which would aim to predict theoretically the resultant expressivity of individuals from any particular pairing.

It is possible, by selective breeding, to influence the frequency and variability of expected Crest phenotypes. Expressivity is discussed in further detail in Part 2 of this article in the Commentary section and in Annex 2.

Empirical rules for making approximate predictions of expressivity can be developed by analysing a sufficiently large number of breeding results.

The author has analysed a sample of breeding results comprising 1,411 progeny including 403 visual crests. Visual progeny in the sample included approximately 23% Full Circular Crest (FC), 10% Half Circular Crest (HC), and 67% Tufteds (T).

This sample is not large enough to make expressivity predictions for all Crest forms over a wide variety of matings. However by grouping results some broad indicators of expressivity inheritance patterns can be produced.

The visual crest forms found in the sample progeny have been divided into two groups.

Group T. Tufts and Weak Tufts including single feathers,

Group C. Half Circular Crests, Full Circular Crests and Multiple Crests.

Table 3 shows how visual crest progeny were split between these groups for various Matings in the sample.

Table 3 Expressivity Results

Mating	Group T (Tufts)	Group C (FC/HC)	No of Crest Progeny
Crest x Normal	85%	15%	111
Tuft x Tuft	72%	28%	137
Crest x Crestbred	63%	37%	46
Crest x Crest	59%	41%	246
Crest x FC or HC	43%	57%	109

Table 3 may be used as a rough guide to the expected split between Group T and Group C Crest forms for the Matings listed. Many more results are needed to improve the accuracy of the table and to permit a further breakdown of the groups into all the individual Crest forms, and to include all Mating combinations.

Use of the PE Theory to improve breeding results

A new and more accurate theory is all very well but can it help breeders to make better pairing decisions and faster, and more certain, progress?

Table 2 allows breeders to predict the % of visual Crests and Crestbreds expected from any mating and Table 3 to predict the % split of Crest forms expected within those visuals.

There are really only three matings to adopt when upgrading crests. Crest x Crest, Crest x Crestbred or Crest x Normal. (Crestbred x Crestbred and Crestbred x Normal produce too few Crests to be useful.)

Crest x Crest will usually be slow to improve general exhibition characteristics and may even diminish them, but needs to be used to strengthen Crest characteristics and maximise production of DF crests.

Crest x Normal produce too few visuals to provide a good selection for the next generation, but this mating is the vehicle by which good non-crest exhibition characteristics can be introduced.

Crest x Crestbred is the optimum mating to make steady progress on both fronts.

From Table 2, the best Crest x Crestbred pairing is DF Crest x SF Crestbred, producing 59% visuals. The best pairing to produce SF Crestbreds is DF Crest x Normal. This produces 83% Crestbreds and all are SF. Are DF Crests identifiable? Intuitively it seems that the birds with the more extreme crest characteristics, the full circular and multi-crested, would be the DF Crests. The PE theory does not imply any such direct relationship (But see Commentary), different genes being responsible for the presence of the crest, and its crest expression. Since Crest x Crest matings (Table 2), produce on average 56% DF, and only 6% SF visuals, identification becomes a less critical issue for crest breeders when this mating is used to produce DF crests.

The optimum breeding program is therefore to firstly mate Crest to Crest to produce DF Crests, and next to mate these DF Crests to high quality Normals, and finally to mate the best of the Crest or Crestbred offspring (all SF) from this mating, back to the DF Crests to produce visual crests (59%).

The author claims no particular originality for this breeding program. However the PE theory provides a sound rationale for the program, and a guide to its implementation and breeding expectations. Breeders can now proceed with greater confidence, avoiding pitfalls and optimising results through having a better understanding of the underlying genetics.

As far as the **expressivity** of the crest is concerned, apart from the guidance of Table 3, the only proven tools available to the breeder seeking to improve the quality of the crest, or to introduce more complex forms of crest, are the same simple breeding strategies he would use when dealing with other polygenic traits (size, type, etc). These strategies, aimed at gradually concentrating desirable genes by selective breeding, are well documented and understood by experienced budgerigar breeders and will therefore not be discussed further here.

One point to be considered by breeders, and central to later discussion in Annex 2, is that it is probable that when the Crest mutation appeared the modifying expressivity genes were already existing in the normal population in both heterozygous and homozygous forms. It is highly improbable that the expressivity genes came into existence as new mutations at the same time as the Crest gene. This means that while "Normals" have no active crest genes they should not be regarded as being free of the active forms of the expressivity genes (E genes). The expressivity genes simply do not act to determine a crest form until an active (penetrant) crest gene is present. The author believes this to be the reason that it is possible, contrary to the predictions of the Initiator theory, to produce Half circular and the occasional Circular from Tuft x Normal pairings. (e.g. Ref 9 reports Tuft x Normal matings producing 247 Normal, 29 Tuft, 8 Half circular, and one Circular progeny).

Similarly it is reported in Ref 9 that FC x Normal can produce all forms of crest, but any one particular pairing may only be able to produce one or two types of crest, while another pair produce different types. This variability in results from identical pairings is probably due to different concentrations of E genes in the individual normals used in the pairings. The normals of course show no indication of their E gene content.

A tentative expressivity model, (still at a very early stage of development), which may assist the understanding of breeders is included at Annex 2 in Part 2 of this article.

Accuracy of the PE Theory

A comparison of the theoretically expectations with published breeding results is summarised in **Table 4**. Examination of Table 4 shows very clearly the over-estimation of visual crested progeny by the Initiator Theory compared to the relatively accurate predictions of the PE Theory.

Table 4 Comparison of Theoretical and Actual Results

		Percentage of Visual Crested Progeny					
		Group 1 Crest x Crest	Group 1A Tuft x Tuft	Group 2 Crest x Crestbred	Group 3 Crest x Normal	Group 3A Half Circ x Normal	Group 3B Tuft x Normal
Theoretical Expectations	Initiator Theory	57-100%	57%	25-100%	25-100%	50%	25%
		Avg 88%		Avg 68%	Avg 56%		
	PE Theory	34-100%	34-100%	9-59%	9-17%	9-17%	9-17%
		Avg 63%	Avg 63%	Avg 29%	Avg 13%	Avg 13%	Avg 13%
Published Breeding Results	Ref 1					15%	
	Ref 2	58%		28%	10-16%		
	Ref 9		43%	40%	10-12%	15%	10-13%

Notes to Table 4. The theoretically predicted results depend upon the genetic composition of the parents in each pairing. Each group comprises several different possible pairings, producing a range of predicted results. The average for each group, is calculated on the basis of the group comprising equal numbers of all possible pairings. Reported actual breeding results are similarly dependent on the particular mix of pairings involved and one should expect variability between reported percentages for any group. (See Part 2 for discussion of averages). Differences in classification of temporary crests is another source of variability in reported results.

Annex 1 Significant Anomalies in the Predictions of the Initiator Theory

1 Percentage of visual Crests

- 1.1 Half circular x Normal. Predicted by Initiator theory to produce 50% Tufted & 50% Normal, in fact produces only 15% Tufted & 85% Normal. (Refs 1, & 9)
- 1.2 Crest x Normal. Predicted by Initiator theory to produce 25%-100%, (avg 56%), Visual crests, in fact produces only 10-12% visuals. (Refs 2, & 9)
- 1.3 Tuft x Normal. Predicted to produce 25% Tufted, in fact produces only 13% Tufted. (Ref 9).

2 Form of visual Crest

- 2.1 Crestbred x Normal. Predicted by Initiator theory to produce no crests, but reported to produce occasional crested, nearly always Tufted. (Ref 9)
- 2.2 Full Circular x Normal. Predicted by Initiator theory to produce only Tufts, but reported to produce all three crest forms (Ref 9)
- 2.3 Tuft x Normal. Predicted to produce Tufts only. However Ghalib Al Nasser reports his winning Circular Grey Green cock (1987-1990) was bred from a Tufted to a Normal. (Ref 6)

Note. All the above anomalies are resolved using the PE Theory.

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Continued in Part 2 - Commentary & Validation of the PE theory

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Part 2- Commentary and Validation of the PE Theory for Crested Budgerigars

Lethality and Low percentage of visual Crest progeny

In the past it was suggested that the crest gene may be lethal (as in the case of the canary) and it was thought this could be the explanation for the observed low percentage of visual crest progeny. Ref 3 reported evidence of a lethal factor, but subsequent studies by Ken Yorke in Australia (Ref 2), and Hans Classen in Germany (Ref 4) showed no evidence of a lethal factor associated with the Crest gene and it is assumed that the earlier study related to a very inbred strain of crests and that it was this inbreeding that caused the lethality problems noted in the earlier study. Ref 9 also refutes the suggestion of the lethality of the gene.

The PE Theory now provides a satisfactory explanation for the observed low percentage of visual crest progeny without the need to invoke lethality as a cause.

Variability in breeding results

Along with general comments on variability of results it is frequently reported that some breeders seem to be able to produce high numbers of visual crests compared to other breeders.

An examination of Table 2 reveals the reasons behind these observations.

Firstly there is a large difference in the average number of visuals produced by each of the following matings; Crest x Crest (63%), Crest x Crestbred (29%), Crest x Normal (13%).

Secondly within each of these mating combinations there is a wide range of results depending upon the genetic make-up of the parents. Crest x Crest (34%-100%), Crest x Crestbred (9%-59%), Crest x Normal (9%-17%).

Care and luck is needed when selecting pairings. Eg when upgrading using the Crest x Crestbred pairing it makes a big difference if the pairing involves a DF Crest x SF Crestbred (59% visual progeny) compared to a SF Crest x ZF Crestbred (9% visual progeny). The difficulty is that visually we cannot reliably differentiate between a DF and SF Crest, or between a SF and ZF Crestbred. Fortunately for a breeder armed with the PE theory and Table 2, there are breeding strategies (described in Part 1) which can minimise this problem.

Temporary crests

There is a particular phenotype, the temporary crest, which is only identifiable in the nest. Some authors classify them as crestbreds, but in the PE theory they are classified genetically as crests; the temporary crest confirming the presence of the crest gene. (Ken Yorke's breeding results also show birds with very weak feather distortions demonstrate greater similarity in breeding behaviour to the Tufts than to crestbreds. (Ref 2)). Breeders need to take great care to identify Crests while in the nest. Differences in classification and failure to identify temporary Crests may account for some variability in reported breeding results and calculated Psf values.

Phenotypic Variability of the Crest

Crests have been standardised in three ideal forms, Tuft, Half Circular, and Circular. In reality these are but three forms in a spectrum ranging from very weak crests (single feather and temporary crests) through to multiple crest forms. Ref 8 recognises twelve different forms within this crest spectrum, while Ref 3 reports involvement of from one to 160 feathers. The wide variability found in the forms of crest expressed in the crest phenotype indicates that the **expressivity** of the crest is a **polygenic** characteristic,

dependent on the action of several, (possibly many), genes, (as are other familiar polygenic characteristics such as “Size” and “Type”).

In considering the genetics of expressivity it is necessary to decide whether the population of crest phenotypes should be viewed as exhibiting continuous or discontinuous variability. In the case of discontinuous variability very few genes are involved and phenotypes can be easily classified into distinct categories. In the case of continuous variability many genes are involved and phenotypes fail to fit easily into distinct categories, but instead form a spectrum of phenotypes that blend imperceptibly from one type to another.

The Initiator theory opted for discontinuous variability, involving just three crest phenotypes, and attempted to represent the crest population using all the nine possible combinations of two genes, (initiator and determiner genes), and their wild type alleles. The Initiator theory has been found in practice to be too simplistic to adequately represent the real world.

It may be possible to improve the accuracy of the Initiator theory and perhaps to accommodate all the observed phenotypes by introducing additional genes and considerable additional complexity, but the current Initiator theory is already too complex for most breeders. The development of a more complex Initiator theory would also be impractical at this time due to the paucity of published breeding data.

The author believes that for any theory to have practical usefulness to breeders it must meet two tests.

- (1) It should be consistent with actual breeding results,
- (2) It should be relatively simple to apply.

The author has therefore chosen to proceed on the basis of a crest population exhibiting continuous variability, with a view to meeting these tests. The author does not exclude the possibility that future analysis of further data may point to a lesser number of E genes than has been assumed in this article.

True breeding forms

It would be helpful if it were possible to develop strains of crests to produce only the three ideal forms. According to Ken Yorke Ref 2 this has not proven possible in his long experience. There is nothing in the PE theory either, which suggests this should be possible. The best that can be done is to continue to select individuals closest to the desired crest ideal in the hope that selective breeding techniques will gradually concentrate favourable gene combinations in a strain, just as we do with many other characteristics of the exhibition budgerigar. Breeders should be aware that every outcross to a normal (having unknown hidden E genes) is likely to disrupt this process through dilution of the favourable E gene content.

Double Factor / Higher Crest form Relationship

In Part 1 it was stated that there is no direct relationship between DF's and higher forms of Crest.

However there is an important indirect relationship. The production of higher forms of Crest requires the concentration of favourable “E” genes. This is best achieved by mating Crest x Crest. Coincidentally this is also a mating which produces a high proportion of DF's. Hence DF's and the higher crest forms can frequently, but not always, be found together in the one bird.

It is usually found that matings involving the higher forms of Crest produce slightly higher percentages of Crest progeny. The author believes these higher percentages are due, not to the presence of the higher form of Crest itself, but to the fact that these birds are more likely to be DF's.

Different Mutations

Whether there are two or more different crest mutations and how they might interact remains an open question. Ref 2 suggests there may be some difference between the Australian mutation and imports from UK.

Penetrance Value

The penetrance value Psf, for the SF crest has been based on analysis of the limited breeding results available to the author. The penetrance value needs to be confirmed by analysis of additional data. The validation exercise carried out by the author (see below) suggests that the figure of 17% adopted in Table 2 is fairly accurate.

Validation of the PE Theory

A number of breeding results have been kindly provided by the following experienced Crest breeders; Ken Yorke. Breeding results published in Ref 2 included 387 progeny over 20years; plus Ken also provided unpublished records over the last 3 years comprising 23 pairings and 116 progeny. Rob Hugo provided unpublished records comprising 163 pairings over 24 years including 725 progeny.

These records have been analysed. Where possible raw data has been cross-checked and inconsistencies corrected. Table 5 below compares the summarised results to the predictions of the PE Theory tabulated earlier in Table 2. (Refer Part 1 of this article).

Also included in Table 5 are two summary results for Tufts & HC's published in the Crest Handbook (Ref 9).

Table 5 Validation of PE Theory

Breeder		Crest x Crest			Crest x Crestbred			Crest x Normal		
		Total Progeny	Visual Crests	% Crests	Total Progeny	Visual Crests	% Crests	Total Progeny	Visual Crests	% Crests
K Yorke Ref 2.		225	130	58%	112	31	28%	50	8	16%
K Yorke		67	42	63%	42	9	21%	4*	0	0%
R Hugo		285	144	51%	91	37	41%	334	50	15%
Crest Handbook HC's								100	15	15%
Crest Handbook Tufts		138	60	43%				285	38	13.3%
All Results		715	376	53%	245	77	31%	773	111	14.4%
PE Theory	Average	63%			29%			13%		
	Range	34-100%			9-59%			9-17%		

Individual results for % crests are generally well within the predicted ranges, (except for small sized samples*).

A comparison between the % Crests for All Results, and the PE Theory Average shows good agreement.

Averages- What do they mean?

When calculating predicted average results, or when averaging actual results, for a particular Mating it is necessary to consider the probable composition of the pairings included in the Mating. The unusual genetics of the crest, in particular the fact that only approximately one in six SF crests are visual, can cause strong bias in the averages. The other major factor causing bias is the actual breeding strategy being followed by the breeder.

Crest x Crest Matings. If a breeder continually breeds Crest x Crest in successive generations, the low % of visual SF progeny will mean that very quickly the breeder will reach the situation where all matings

and all progeny will be DF's. His average progeny from Crest x Crest matings will be close to 100% visuals.

If on the other hand a breeder uses only Crests from Crest x Normal matings in his Crest x Crest matings his pairings will always be SF Crest x SF Crest and as such his average progeny will be only 34% visuals. A breeder following the more popular strategy of using Crests from Crest x Normal matings paired to DF Crests from Crest x Crest matings, will produce an average of 59% visuals.

Predicted average results, and actual average results, will therefore both depend upon the actual mix of pairings used and the breeding strategy being followed.

The predicted averages shown in Tables 2, 4, and 5, are based on the assumption of equal numbers of all possible pairings in a Mating and as such must be viewed only as "indicative" values when considering any Mating. To make an accurate prediction of "average" the composition of the pairings in the group must be known.

In the Crest x Crest mating discussed above, the average of actual results provided by breeders can be expected to be closer to the 59% value than either of the other extremes of 34% or 100%. This expectation is confirmed in the results shown in Table 5. The 43% result in Table 5 is quoted in the Crest Handbook for Tuft x Tuft matings and probably reflects the inclusion of an unusually high number of SF x SF pairings in that result.

Crest x Normal Matings. The low % of available visual SF's would be expected to bias the average of this mating towards the DF Crest x Normal prediction of 17% rather than the "indicative" predicted average of 13% of Table 2. The actual average of results in Table 5 shows 14.4%, consistent with this expectation.

Crest x Crestbred Matings. It is not possible to mount convincing arguments for bias one way or another in this mating. There are too many conflicting possibilities. Table 5 results reflect a slight upward bias in the average, 31% versus the "indicative" average of 28%. In addition the Crest Handbook quotes an average of 40% for this mating but no supporting details are given.

Specific Pairings. Comparisons with specific pairings in Table 2 are difficult to perform due to uncertainties as to the number of Crest factors present. However SF Crests can sometimes be identified given details of their parents.

SF Crest x Normal Pairings. An examination of Rob Hugo's data has identified 13 Crest x Normal pairings where the Crest is confirmed to be SF. (through having Crest x Normal parents). Of the 70 progeny from these 13 pairs, 8 were Tufts. This gives a % Crest progeny of 11% which approximates the 9% predicted in Table 2 for this pairing, and is further validation of the PE Theory. A larger sample is needed to confirm this result.

The only prediction in Table 2 that is a little surprising is in the case of the pairing SF Crestbred x SF Crestbred where 34% visual crests are predicted. There appears to be very little data available, but Crestbred x Crestbred matings are generally reputed to produce few visuals. Closer examination of Table 2 shows that the other three possible pairings in the Crestbred x Crestbred matings are predicted to produce only 0-9% visuals. Low visual percentages make Crestbred x Crestbred matings unpopular with breeders hence the scant reports. This unpopularity could also be due to uncertainty as to whether a particular Crestbred carries **any** Crest genes; uncertainty as to the quality of crest hidden within the Crestbred; strong preference for matings containing at least one visual Crest; the low probability (25%) that both Crestbreds will carry the Crest gene; or fear that the low % of visuals will be accompanied by poor quality of crest.

Again examination of Rob Hugo's data has identified only two CB x CB pairings in his extensive records. These produced a total of 15 progeny, 4 of which were Tufts, equating to 27% Crested from these two pairings. This is far too small a number of pairings from which to draw any firm conclusions, but the results do suggest that the "surprising" prediction of Table 2 for this pairing is credible.

Annex 2 A Tentative Expressivity Model

The following discussion is included as an aid to understanding expressivity in Crests. At this time it is largely speculative and is therefore presented as an Annex rather than as part of the main discussion. Many more breeding results are required to develop and refine these ideas and to improve our understanding of expressivity.

As a starting point in attempting to understand how expressivity might operate let us, in the absence of other evidence, postulate a simple model. Assume expressivity to be a polygenic trait in which the active expressivity genes (E1,E2,E3...etc) contribute additively to the phenotypic expression, and assume as discussed earlier in Part 1, that these genes exist in the Normal (non-crested) population.

Assume that the concentration of active E genes in the population is distributed according to the conventional "Bell curve" (ie. A few individuals will have very low or very high concentrations, while most individuals will have concentrations somewhere in between, with the greatest concentration being midway between low and high). A frequency distribution can be drawn for the population showing the percentage of individuals which carry particular percentages of active E genes. This distribution is shown as a full line in Fig 1.

If crests were allowed to breed naturally, without any selective breeding, the distribution of E genes in the crest population would be similar to that in the normal population breeding naturally.

Assume that increasing the concentration of active expressivity genes, (E genes), increases the complexity of the crest form; i.e. from Very Weak Tuft, to Tuft, to Half Circular, to Full Circular to Multi. (This assumption is supported in general by breeding results and is also basic to the Initiator Theory.)

The relationship between Crest form and percentage of E genes can then be shown indicatively on Fig 1. The boundaries between forms are not clear cut. There is a gradual blending from one form to the next.

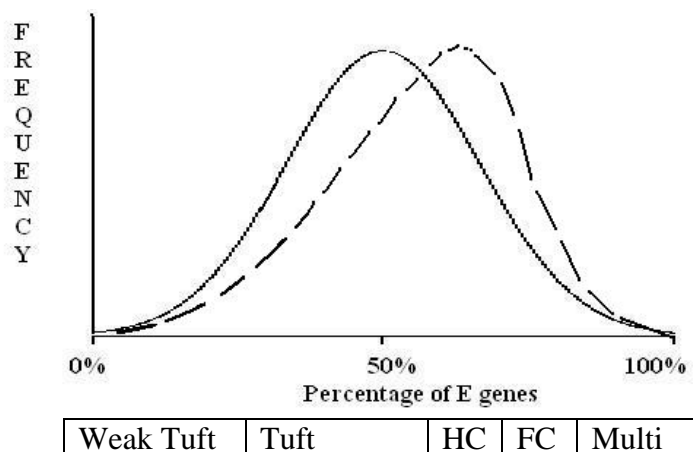


Fig 1

Fig 1 can be used to examine the effects of various selective matings. If for example FC's, (which will carry a relatively high percentage of E genes), are mated to other FC's, the average percentage of E genes in the progeny will be greater than the average in the parent population. The frequency distribution of the E genes in the progeny will be skewed to the right as shown by the broken line in Fig 1. There may still be a range of progeny from weak to multi crests but the percentages of each form will be changed to reflect a greater percentage of the more complex crest forms. Analysis of breeding records (Table 3) confirms this shift to the right.

In the above example it is possible to have a broadly predictable outcome because the visual form of the parents indicates their E gene content. However when using a crested (or normal) parent there is no visual indicator to show whether these contain a high or low percentage of E genes, so the resultant frequency distribution in the progeny can be quite variable and perhaps “unexpected”. Better control of the mean crest form and the distribution of crest forms in the progeny is possible when mating two visuals together.

Additionally, Fig 1 demonstrates how any mating involving a crest gene is potentially capable of producing any of the crest forms, although some forms may have a very low frequency of occurrence depending upon the expressivity genes carried by the parents.

The foregoing discussion relates primarily to progeny which are DF for the crest gene. In the case of SF progeny, only approximately 15%-20% of these will express the crest. It would appear that this is not simply a case of exclusion of the Crest forms with the lower percentage of E genes, because Crest x Normal produce only SF progeny and all crest forms are found to be exhibited. In the case of SF's the relationship shown in Fig 1 between Crest form and Percentage of E genes, may require modification or may still apply except that the resulting percentages of progeny of all forms is reduced uniformly by 80-85%.

The nature of the interaction between the SF crest gene and the E genes is unclear. One hypothesis considered by the author is that there are some specific E genes which must be present to enable the SF crest gene to overcome the influence of its wild type allele and express the crest. Eg If we assume this involves three of the E genes, two semi-dominant present in homozygous or heterozygous form, and one homozygous recessive, the probability of occurrence of this combination would be $\frac{3}{4} \times \frac{3}{4} \times \frac{1}{4} = \frac{9}{64} = 14\%$. This is seen to approximate the calculated 15%-20% value for Psf.

When crossing out to a Normal, the breeder can be sure of two things. The % of visual crests will be low, and all visual crest progeny will be SF. The quality of the crest however will depend upon the hidden E genes present in the Normal parent just as much as the visible E genes present in the Crest parent. Fig 1 shows why it is even possible to produce from this mating a higher order crest than that of the crest parent. Refer Para 2.3 in Annex 1 for an example.

The above discussion focuses on genetic influences on Expressivity. In addition there are probably some non-genetic (environmental) influences operating. eg.(reported changes in the crest with age including the disappearing crest and changes in the form of crest following a major moult etc, also physical constraints such as boundaries formed by cere, eye, adjacent feathers etc.).

Additional Data

The author would welcome the contribution of breeding results by experienced crest breeders to enable the PE Theory to be further refined. Forms for reporting of breeding results may be obtained from the author at the following address, 2 Redgum Lane, Denmark, Western Australia 6333 (Email address, agamclarke@optusnet.com.au).

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