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The Colour Variations of the Budgerygah (*Melopsittacus undulatus*); their Origins and Genetic Relationships (with Chart).

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The Budgerygah in its natural state varied but slightly in appearance, and must be regarded as remarkably uniform when we take into consideration its great numbers and the immense area of its habitat. Although ornithologists have divided them into two distinct sub-species, there is a strong general resemblance in all of them, and it has never been suggested that the differences that existed in the colours of the wild birds were in any way responsible for the many colour variations now existing amongst the aviary bred birds, or indeed, for any of them. They were exported in great numbers to England and Europe as cage birds, and, breeding freely in captivity, became very popular. Later on, when new and beautiful colour varieties were produced, they became a formidable rival all over the world of the Canary as exhibition, cage, and aviary birds.

The first notable colour variation was the appearance of yellow Budgerygahs in Holland about the year 1870. It was a variation that appeared quite unexpectedly and without any known cause, being in the nature of a sport or mutation affecting only the colour factors of the bird. This factor proved to be hereditarily transmissible, but recessive to the natural green colouring.

The second new colour produced was the blue. This, too, was the result of an unexpected mutation which appeared suddenly, and was not intentionally evolved by any system of selective mating or other means. However, it provided the means of producing a fourth colour class. Blues, when mated with yellows, produced greens, but these greens, although similar in appearance to the original greens, differed from them genetically. Mated *inter se* they produced not only greens, yellows, and blues, but also another new colour variety, the silvers, or so-called whites. Thus, from the original greens with the aid of only two mutations were produced these four colour classes, which stand to-day as the four main or fundamental divisions of Budgerygahs. Nature, in her subsequent revelations, appears to have always recognized one or more of these four classes as a foundation as it were. Note that these four colour classes, greens, blues, yellows, and silvers, are entirely separate and distinct, and that the colour classes of Budgerygahs are not complete if any one of them is left out. On the other hand, all other colour classes are but variations of one or other of these four classes.

The original greens and the first yellows, blues, and silvers, were all light coloured birds. Then a third mutation appeared in the form of a darker coloured bird. There does not appear to be any record of the first discovery of this mutation, probably because its importance was not at first realized. Whether it was the darkest of the three different degrees of darkness or the middle one, it brought with it the possibility, with the assistance of the existing light colour factor, of producing a third degree of darkness, for there are three separate degrees of darkness, each one distinct from the other two, and each one faithfully following the Mendelian laws in its hereditary transmission regardless of which colour factors it is associated with. Therefore, this third mutation increased the number of colour classes of Budgerygahs to twelve.

These twelve classes were named as follows:—Light green, dark green, olive green, skyblue, cobalt, mauve, light yellow, dark yellow, olive yellow, white blue, white cobalt and white mauve, or, as the last three named are known in Australia, blue silver, cobalt silver, and mauve silver. Thus, in a comparatively short space of time, eleven new and beautiful colour varieties appeared in Budgerygahs. It was not generally known that they were the direct result of *only three mutations*, and that those three mutations were totally incapable of producing other colours. Consequently, many persons got the impression that these birds would produce endless colour variations. There was a widespread desire to be the first to produce a new colour, and a boom in Budgerygahs took place, such as has never occurred in connection with any other species of bird. In the meantime German scientists discovered that the various colour classes were reproduced hereditarily with strict fidelity, and Dr. Hans Duncker and Herr Konsul Cremer made a careful study of the subject, and published a number of treatises. To those two scientists the world is indebted for a correct scientific classification of the species, and for clear and simple explanations of the hereditary factors involved in the production of the various colour classes. Careful observation of the breeding of many hundreds of Budgerygahs of all the colours mentioned has convinced me that their theories of expectations of breeding results from the various matings are absolutely reliable, and, further, that the Budgerygah is the most marvellous medium in the world for the study and demonstration of the systems under which the laws of heredity operate. According to their explanation, the foregoing twelve colour classes are produced by three separate colour factors only, designated F, or fat colour (yellow), O, or oxydase (blue), and B (brown), or darkness factor. Each of these three colour factors may be absent or may be present in either of two degrees or quantities, and such absences or quantities present decide the visible colours and also the hidden genetic colour factors.

We will deal first with the F and O factors, which follow a system of hereditary transmission peculiar to themselves, and quite distinct from a second system followed by the three darkness factors, with which they in no way interfere. Both of these hereditary systems are distinct from a third system followed by the cinnamon and albino factors, introduced later on, which faithfully adhere to their own system of hereditary transmission, which alone is sex-linked. The F (yellow) and O (blue) factors may be designated the normal colour factors. Their different combinations or their absence cause the division of the species into the four main fundamental colour classes. Every recognized variety of Budgerygah possesses one or other of these four combinations of factors, constituting the bird a green, a blue, a yellow, or a silver genetically, regardless of its appearance. *Additional* factors, independently operating, are responsible for further variations in colour. Green is indicated by the presence of both F and O. Whenever these two factors are present in a normal bird, the colour of the bird is green. Green is hereditarily dominant over all the other colours. The presence of O and the absence of F constitutes the blue. Blue, whilst recessive to green, is dominant over silver (so-called whites). The presence of F and absence of O produce the yellow. Yellow, though recessive to green, is also dominant over silver. Blue and yellow are neither dominant nor recessive in relation to each other, but when mated together they produce greens, though such greens are not genetically pure greens, but greens split to the blue, the yellow, and the silver factors. The silver, or so-called white, is recessive to each of the other foregoing factors.

More than one of these factors, or combinations of factors, may be present in one bird. In such cases the dominant colour factor or combination decides the actual colour of the bird; and the other factors are carried as hidden genetic factors, which enable the bird, when mated with a similar bird, to produce birds of the recessive colour or colours, in addition to birds of its own dominant colour. Such birds are described as being split to the recessive factors, the simplest explanation of the meaning of the word "split" being "capable of producing." Birds of any dominant colour may be split to any colour recessive to it. Thus, green coloured birds can be split to blue only, to yellow only, or to blue, yellow, and silver, though they cannot be split to silver without being at the same time split to blue and to yellow. Blues can be split to silver only, and yellows can be split to silver only.

It is remarkable that each of these hidden genetic factors operates as a separate factor of equal potency. Therefore, the mating of a green split blue yellow silver to a green split blue yellow silver results in the production of progeny in the same colours and proportions thereof as would be produced by mating a green to a green, a green to a blue, a green to a yellow, and a green to a silver; a blue to a green, a blue to a blue, a blue to a yellow, and a blue to a silver; a yellow to a green, a yellow to a blue, a yellow to a yellow, and a yellow to a silver; and a silver to a green, a silver to a blue, a silver to a yellow, and a silver to a silver. The average production from the mating of a green split blue yellow silver to a green split blue yellow silver is one pure green, two green split blues, two green split yellows, four green split silvers, one pure blue, two blue split silvers, one pure yellow, two yellow split silvers, and one silver out of every sixteen. It is not to be expected that small numbers of such matings will average as above, but the results from large numbers of such matings will approximate this average.

The Darkness Factor.

Genetically the three distinct degrees of darkness retain their separate identities, and each strictly adheres to the Mendelian laws. They are transmitted independently of the other colour factors, and their genetic possibilities are as follows:—Light mated with light produce all light; light mated with medium produce light and medium; and light mated with dark produce all medium. Medium mated with medium produce one-quarter light, one-half medium, and one-quarter dark; medium mated with dark produce medium and dark; and dark mated with dark produce all dark. These results are obtained quite irrespective of the other colour factors in the combination, while the other colour factors independently faithfully follow a different genetic system. Thus we see that the original greens with the aid of *only three mutations,* the yellow, the blue, and the darkness factors, produced twelve distinct colour classes, while the distinct genetic classes they produced numbered thirty. These thirty genetic classes provide 465 separate matings, no two of which will produce similar birds in the same proportions.

The Greywing Factor.

The fourth valuable mutation produced the birds known as greywings. A Madam Weiss, in Austria, noticed some birds in her aviary whose wing-markings were grey in colour and of only about one-half the colour value of the black wing-markings of the normal birds. The body colour also was of about one-half the depth or intensity of that of the normal birds. These were proved to breed true to type, and it appears to have been from these birds and their progeny that the world gained its first knowledge of this valuable mutation, although a German scientist has since claimed that he produced greywing blues about the same time. Dr. Duncker states that the greywing factor is a modification of the Oxydase factor O. This makes it impossible for the factor to operate in the case of yellows or silvers, which do not possess the O factor. Therefore, there are not, and cannot be, any greywing yellows or greywing silvers. This factor increased the number of colour classes from twelve to eighteen, and the genetic classes from thirty to fifty-four. Dr. Duncker next discovered that there are two distinct types of each of the following classes producing different genetic results, namely, dark green split blue, dark green split silver, dark yellow split silver, greywing dark green split blue, greywing dark green split silver, and dark green split blue split greywing. Owing to the existence of a linkage between the factors F and B, these birds are divided into two classes, which produce different genetic results. These, then, increased the number of genetic classes from fifty-four to sixty. These sixty distinct genetic classes provide 1,830 separate matings all different in the classes of progeny and the proportions thereof that they will produce. *And these far-reaching effects on the species were produced by only four mutations.*

The Cinnamon Factor.

Some three or four years ago a fifth mutation appeared in an aviary belonging to Mrs. Kerncke, of College Park, South Australia. It probably produced the first cinnamon Budgerygah in the world. Mrs. Kerncke bred at least two generations of them before reports appeared in English newspapers announcing the discovery of a new colour variety in England described as cinnamon-wings. According to the reports all were young birds in nestling plumage only. A stuffed skin of one of the South Australian cinnamons sent to England was stated by an expert there to be exactly similar to the English cinnamon-wings. Having the good fortune to obtain possession of four cocks and five hens of this new variety (probably all then surviving in Australia) provided the opportunity of testing this factor genetically. The breeding in controlled aviaries of over 130 cinnamons of eight different colour classes, together with an approximately equal number of normal birds split to the cinnamon factor has provided ample opportunity for studying the new mutation. The cinnamon factor is of an albinistic nature. It has on rare occasions been noted amongst wild birds, being generally known as the isabelline, cinnamon, or semi-albino form. The young birds of this variety have pink eyes when hatched, but they gradually darken, and in a few days become quite normal in appearance. The colour of wild birds of this description has been noticed to vary over a wide range. This has given the impression that the factor is inconstant and variable. A careful study of the cinnamon factor in Budgerygahs has, however, revealed the fact that it is a very uniform and constant factor. It is noticeable that there is a wide variation of the characteristic brown colouration in the cinnamon Budgerygahs also, but the variation is the result of the other colour factors of the bird, and not of the cinnamon factor. When the other colour factors were such as would produce birds of uniform colour, the cinnamons produced have been very uniform also. The cinnamon factor, although a colour factor in so far as it exercises a considerable control over colours, is entirely different and distinct from the other colour factors previously dealt with. It does not displace any of the normal colour factors, nor does it in any way interfere with their hereditary transmission, being neither dominant over nor recessive to any one of them. A cinnamon light green, for instance, possesses an exactly similar set of colour factors to that of the ordinary light green, but carries an additional cinnamon factor which modifies the visible effects of the normal factors by the partial inhibition of the production of melanin. The cinnamon factor introduced a third distinct genetic system, which operates entirely independently of the other two. Thus, we frequently find in the one bird three distinct factors or groups of hereditary colour factors, each faithfully following its own entirely different system of transmission without in any way interfering with each other. The partial inhibition of the production of melanin alters the black markings on the wings, back, etc., to a dark cinnamon brown in the case of such birds as possess the colour-factors that would normally produce black markings. The dark grey markings of the greywings are proportionately altered by the cinnamon factor, resulting in light cinnamon brown markings, indicating clearly that the variation is the direct result of the other colour factors and not of any variation of the cinnamon factor. In the case of silvers and of yellows there is not sufficient melanin present in the wing-markings to show any visible brown markings. Nevertheless, the cinnamon silvers and cinnamon yellows are cinnamons in exactly the same way and to the same degree as are the cinnamon greens and cinnamon blues with their pronounced brown wing-markings, and all transmit the factor in accordance with the same genetic system. The direct cause of the colour alteration effected by the cinnamon factor will be dealt with more fully later in connection with the full albino factor, where the degree of alteration is much greater, and consequently more easily understood. An important distinguishing characteristic of the genetic system in accordance with which the cinnamon factor is hereditarily transmitted is a definite and strong sex-linkage which is entirely absent from either of the two previously-mentioned groups. It is not necessary to explain how this linkage is caused, but the results of the principal matings will serve to show the essential difference between this sex-linked system and the other two. The cinnamon male mated with the cinnamon female produce all cinnamons. The cinnamon male mated with normal female produce all males normals split cinnamon and all females cinnamons. The cinnamon female mated with normal male produce all males normals split cinnamon and all females pure normals. The normal male split cinnamon mated with cinnamon female produce males, one-half of progeny normals split cinnamon and one-half cinnamons; females, one-half cinnamons and one-half pure normals. The normal male split cinnamon mated with normal female produce males, one-half normals split cinnamon and remainder pure normals; females, one-half cinnamons and remainder pure normals. Though the males can be cinnamons, normals split cinnamon, or pure normals, the females are all either cinnamons or pure normals.

The cinnamon factor has a far-reaching effect on the colour variations of the species. It produces six new and beautiful colour varieties with dark cinnamon brown wing-markings, etc.—cinnamon light green, cinnamon dark green, cinnamon olive, cinnamon skyblue, cinnamon cobalt, and cinnamon mauve—and six with light cinnamon brown wing-markings, etc.—cinnamon greywing light green, cinnamon greywing dark green, cinnamon greywing olive, cinnamon greywing blue, cinnamon greywing cobalt, and cinnamon greywing mauve. It also clears and purifies in a remarkable degree the colours of the yellows and the silvers. The cinnamon factor is semi-albino in nature, and its effect on colours differs only in degree from that of the full albino factor. The eyes of newly-hatched cinnamons are pink in colour, but gradually darken, and in a couple of weeks or so are indistinguishable from the eyes of the normal bird. The fact that the cinnamon factor is a separate factor acting independently of the other colour factors indicates that there will be a cinnamon form and a split cinnamon form (males only) of each and every one of the normal genetic classes. Therefore, this factor increases the number of distinct genetic varieties from sixty to 180. Thus, we see that the original green with the assistance of *only five mutations* produced 180 distinct genetic varieties, and 16,290 distinct matings.

The Albino Factor.

A sixth mutation, the full albino factor, was reported in England about two years ago in the form of a white albino, but only normal birds have been produced from it so far as the writer has been able to ascertain. Reports indicate that a number of albinos and lutinos have been bred in Germany, but particulars are not available. The word lutino is freely used in England, and also in this country, to indicate the pure yellow bird with red eyes, yet a diligent search in dictionaries and encyclopaedias has failed to discover it. The word albino is usually understood to mean abnormal absence of colour. The Encyclopaedia Britannica contains this definition of albinism:—"An albino is an individual whose tissues lack the power to elaborate either the ferments or the colour bases. Pigmentation depends upon the presence and interaction in the tissues of colour bases, chromogens, colourless in themselves, and ferments or enzymes which, acting upon the colour bases, yield coloured products. If either of these ingredients of pigmentation is absent from the constitution of an individual it must perforce remain pigmentless."

This represents the popular conception of albinism, together with the idea that all albinos are sterile, or at least that the factor is not hereditarily transmissible. My investigations clearly indicate that the factor is consistently hereditary and sex-linked in exactly the same way as is the cinnamon factor, and further, that the only pigment affected by albinism is the melanin, the production of which is totally inhibited. Its visible effect on birds of various species is the complete elimination of black, brown, grey, blue, and green. Red and yellow are not affected in any degree and are present in the albino form to exactly the same extent as they are in the normal form of the species. The black appearance of the markings on the feathers of the Budgerygah is due to the pigment melanin, which, in dense masses, absorbs so much of the light rays that it appears black. Blue is a structural colour produced by the structure of the cells reflecting the blue rays of light. But this effect can be produced only if there is a background of melanin to absorb the other light rays. Green is produced by a combination of the yellow pigment with the blue structural colour. It necessarily follows that the total inhibition of the formation of melanin by the albino factor results in the complete elimination of black, blue, and green. If all of the black and all of the blue are removed from the colouration of skyblues, cobalts, mauves, blue silvers, cobalt silvers, or mauve silvers their appearance will be snow-white. If all of the black and all of the blue portion of the green are removed from the light greens, dark greens, olives, light yellows, dark yellows, or olive yellows, only a clear canary yellow will be left. This shows that the albino factor and the lutino factor are one and the same. The albino factor is genetically similar in all respects to the cinnamon factor, following as does that factor the sex-linked third definite system of hereditary transmission without in any way interfering with the normal colour factors or the darkness factors in their faithful adherence to their own particular genetic systems. Therefore, there will be an albino form and a split albino form (males only) of every genetic class of normal Budgerygahs. The word normal here indicates birds with the F, O, and B factors, but without the additional factors for cinnamonism or albinism. Albinism, however, produces only two new colour classes, a clear canary yellow with red eyes and whitish main tail-feathers and wing-primaries, and a snow-white with red eyes, for these are the only two colour classes not dependent on the presence of melanin.

The Austral, or Royal, Factor.

Australia has had the good fortune to produce another new mutation which provides twelve more colour classes, several of which are strikingly beautiful. It was a great misfortune that this mutation was not produced or first discovered by an aviculturist able and willing to test out the factor genetically before releasing it to the public. The unfortunate result has been that they have been variously designated as jades, royals, yellow-wings, white-wings, and australs, though they are all of the one variety. The body-colours of these new colour classes are deep and intense, in some cases as deep as those of the corresponding normal birds, but quite distinct in colour, and some are very beautiful. Probably the two most attractive are those with jade green body colour and wings similar to wings of the yellows and those with royal blue bodies and wings similar to wings of silvers. The greywing austral greens are also entirely different in appearance from the true greywing greens, as they have intense body-colours of similar tones to those of the other birds belonging to this factor. This mutation belongs to the normal group following the first-mentioned genetic system of hereditary transmission.

The Fallows.

Another distinct variety, first produced in Germany and there named the fallows, has been recently introduced into England, but very little information concerning it is as yet available.

Freaks and Slight Variations.

Although the different colour classes are capable of reproducing themselves and each other with marvellous fidelity, freak colours appear occasionally, in addition to numbers of birds that vary considerably from the standard colours of their genetic class. Among the former are bi-coloured birds with one-half of the body differing in colour from the other half, and particoloured birds with patches of various colours. The latter have been considerably increased by attempts to evolve new colours by mating birds that are farthest from the correct standard. In England these birds have been regarded as bad specimens of their class, but in Australia in many instances they have been given names such as greywing yellows, greywing olive yellows, satinettes, golden olives, etc., and classes have even been provided at shows for such faulty specimens.

TERRILL—Colour Variations of the Budgerygah.

This becomes a serious matter when its effect on the species is considered. The faculty of the Budgerygah of reproducing its colours in strict conformity with certain genetic systems can be preserved for future generations only by consistent effort to maintain the standards of the different genetic varieties and by correct scientific classification and nomenclature. If through ignorance or neglect this faculty is destroyed, the world will lose its most valuable medium for the study of genetic problems of vast importance to the human race, a science as yet in its infancy.

			Albino	Cinnamon	Greywing	Austral
Greens	Light	L i g h	t G	r e	e	n
	Medium	D a r	k G	r e	e	n
	Dark	O l i v	e G	r e	e	n
Blues	Light	Sky	B	l	u	e
	Medium	Cobalt	B	l	u	e
	Dark	Mauve	B	l	u	e
Yellow	Light	Light	Y	e	l l	o w
	Medium	Dark	Y	e	l l	o w
	Dark	Olive	Y	e	l l	o w
Silvers	Light	Blue	S	i l	v e	r
	Medium	Cobalt	S	i l	v e	r
	Dark	Mauve	S	i l	v e	r

This chart is intended to show the simplicity of Nature's method of multiplying the number of colour classes of the Budgerygah. The four fundamental colour classes were divided by the darkness factor each into light, medium, and dark, making twelve classes which have been named as shown on the chart. These classes, or some of them, as the case may be, were further subdivided by the various factors as indicated.

TERRILL—Colour Variations of the Budgerygah.

The Austral factor (covering first vertical section from the right) produces austral greens and austral blues. The greywing factor (covering first and second sections) produces greywing greens, greywing blues, greywing austral greens, and greywing austral blues. The cinnamon factor (covering first, second, and third sections) produces cinnamon greens, cinnamon blues, cinnamon yellows, cinnamon silvers, cinnamon greywing greens, cinnamon greywing blues, cinnamon greywing austral greens, cinnamon greywing austral blues, cinnamon austral greens, and cinnamon austral blues.

The albino factor (covering first, second, fourth, and probably the third, sections) will produce an albino form of each of the forementioned colour classes, with the possible exception of albino cinnamons. We are at present testing this point, and our results to date seem to indicate that there will be an albino form of each of the cinnamon classes, but consisting of males only, or alternatively, an albino split cinnamon form (males only) of each of the non-cinnamon classes. However, that remains to be proved.

[*The description of the species in the wild state is as follows (Editors)*:—

Gould, Handbook, Birds of Australia, Vol. 2, 81, 1865:—
The sexes are precisely alike in the colouring and marking of their plumage; but the female is somewhat smaller than the male, and has the colouring round the nostrils of a lighter tint.

The adults have the forehead and crown straw yellow; the remainder of the head, ear-coverts, nape, upper part of the back, scapularies and wing-coverts pale greenish yellow, each feather having a crescent-shaped mark of blackish brown near the extremity, these marks being numerous and minute on the head and neck; wings brown; the outer webs of the feathers deep green, margined with greenish yellow; face and throat yellow, ornamented on each cheek with a patch of rich blue, below which are three circular drops or spots of bluish black; rump, upper tail-coverts, and the under-surface bright green; two centre tail-feathers blue; the remaining tail-feathers green, crossed in the middle by an oblique band of yellow; irides straw white; nostrils bright blue in some, greenish blue and brown in others; legs pale bluish lead-colour.

The young are distinguished from the adults by the crown of the head, which is yellow in the adult, being crossed by numerous fine bars of brown, and by the absence of the deep blue spots on the throat.]