What Colour is that bird? The causes and recognition of common colour aberrations in birds

Article in British Birds - February 2013

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The causes and recognition of common colour aberrations in birds

Hein van Grouw

Abstract The naming of colour aberrations in birds still causes widespread difficulty and confusion. This paper introduces a uniform system of nomenclature and provides a simple identification key for the most common plumage aberrations. Six main aberrant plumage types are grouped and named by their pigment reductions (gene actions). Identifying colour mutations in the field can be extremely difficult but this paper should make it possible to name many mutations correctly.

As might be imagined, correct identification of these various effects is difficult, and the literature abounds with errors. (P. A. Buckley, 1987, Avian Genetics)

In earlier times, when little or nothing was known about plumage pigmentation and mutations, aberrantly coloured wild birds were often regarded as new species or subspecies and several were formally named. Perhaps the oldest example of a colour aberration named as a distinct species is the ‘Mountain Partridge’ Perdix montana (Brisson, 1760). In Brisson’s time this ‘species’ was known only from the mountains of the French region of Lorraine, which resulted in it being named P. montana (‘of the mountains’). However, it was subsequently revealed to be simply a melanistic form of the Grey Partridge P. perdix. Sabine’s Snipe Scolopax sabinii (Vigors, 1825) is another example – this dark-coloured snipe is actually a melanistic form of the Common Snipe Gallinago gallinago.

Aberrant plumage colour is not uncommon in birds. Indeed, in some species it is sufficiently common that the aberrant forms represent a fairly large proportion of the whole population and are thus considered to be a colour morph within the species. In such cases the term ‘polymorphism’ is often used instead of aberration. Melanism is the most common polymorphism represented in birds (Mundy 2006). Pomarine Stercorarius pomarinus and Arctic Skuas S. parasiticus are examples of species in which a dark (melanistic) morph is a standard colour feature.

Genetic studies of domesticated animals, in particular mice and chickens, furnished us with a greater knowledge of pigmentation and mutations. At an early stage, it became obvious that different mammal species had a similar series of heritable coat-colour variants. Similar mutations were soon allocated the same name in all species. The similarity was based on the relevant gene action on the pigmentation process and not necessarily on the appearance of the final coat colour, as this can differ among species. Despite the comparable nature of the pigmentation process in birds and mammals, establishing some uniformity in the nomenclature of genes (loci) between mammals and birds has so far been neglected. Consequently, the naming of colour aberrations still causes problems in the ornithological world.

A variety of names are still used seemingly randomly to identify the mutations. Most commonly misapplied is the name ‘albino’ or ‘partial albino’ (Rollin 1964; Buckley 1982, 1987; van Grouw 2006, 2010). The term ‘albino’ is widely used for all sorts of different colour aberrations, but in only a tiny proportion of cases is it used correctly. Albinism is actually far less common than was previously
thought by most ornithologists; in fact, aberrant white feathers are hardly ever caused by albinism and are usually due either to a form of leucism or (more commonly) to a non-heritable cause such as disease, food deficiency or trauma. Probably the most common mutation in birds is ‘brown’ (van Grouw 2010), yet this mutation is given many different names in the literature – albino, partial albino, cinnamon, leucistic, isabella, fawn, pale morph, non-eumelanic form, flavistic, erythristic or schizochroistic (to name just a few).

This paper aims to introduce a uniform system of naming colour aberrations. The six most common heritable colour aberrations in birds are defined, grouped and named by their pigment reductions (gene actions), and discussed in simple terms. At the end of the paper, a basic identification key for the most common aberrations should make it easier for birders to name the mutation correctly.

**Melanins and plumage coloration**

The most common pigments in both birds and mammals are melanins (Fox & Vevers 1960) and the pigmentation process in mammal hair is identical to that in bird feathers (Lubnow 1963). The many mutations that cause a change in the melanin pigmentation, and thus an aberration in an animal’s colour, are also directly comparable between mammals and birds.

Carotenoids are the second most common pigments in birds (Fox & Vevers 1960) and vary in colour from pale yellow to scarlet red. Changes in carotenoid-based pigments caused by mutations are rare and are therefore not discussed further in this paper. Carotenoid pigmentation is usually not affected by melanin mutations and therefore yellow or red remains clearly present in the otherwise aberrant plumage (and similarly in the eyes, bill and feet).

There are two forms of melanin: eumelanin and phaeomelanin (Lubnow 1963). Depending on concentration and distribution within the feather, eumelanin is responsible for black, grey and/or dark brown colours, whereas phaeomelanin is responsible for warm reddish-brown to pale buff. Both melanins together can give a wide range of greyish-brown colours.

In some groups of birds, the colour of the adult plumage is caused by eumelanin only, for example in most oystercatchers (Haematopodidae), gulls and terns (Laridae), auks (Alcidae), woodpeckers (Picidae), crows (Corvidae), tits (Paridae) and the male Blackbird *Turdus merula*. However, in most birds both types of melanin are present. There are no species in which only phaeomelanin occurs. In feathers that contain both forms of melanin, the eumelanin is found mainly in the central part of the feather while the phaeomelanin occurs at the feather edges.

Melanin is produced by cells called melanocytes, which are found mainly in the skin and the feather follicles. The melanocytes develop from melanoblasts, which are formed at an early embryonic stage in the ‘neural crest’ – derived from the embryonic spinal cord. As a result of genetic processes, the melanoblasts migrate from the neural crest to the skin and feather follicles, where they develop into melanocytes and are then able to produce melanin to add to the feather cells as the feathers grow.

The addition of melanin does not always occur at a constant rate. In most species, the feathers have certain patterns and/or colour differences caused by the type, amount and distribution of melanin. During feather growth, sudden changes from the production of eumelanin to phaeomelanin may occur, giving rise to these different patterns. The development of melanin is the result of a chemical process called melanin synthesis, in which the amino acid tyrosine (released from nutrients in the food) and the enzyme tyrosinase (present in the melanocytes) are necessary to start the synthesis. Every disturbance or aberration in the melanoblast migration or melanin synthesis can influence the final plumage pigmentation. The aberration can be caused by a temporary, external factor or may have a heritable cause (mutation).

The mutation names used for birds in this paper are based mainly on the names used for Feral Pigeons *Columba livia*. Where this is inappropriate, genetic nomenclature of the House Mouse *Mus musculus* is used.

**The mutations**

There are many genetic mutations that cause colour aberrations in birds. In domestic
pigeons, for example, more than 50 different colour mutations (genes) are known, which cause about ten distinguishable colour aberrations (van Grouw & de Jong 2009). The six most common heritable colour aberrations in birds will be discussed here: albinism, leucism, brown, dilution, ino and melanism. Some of these aberrations can be caused by several mutations with a comparable effect (van Grouw 2006).

Both albinism and brown are caused by a single genetic mutation, which is the same in every species. Albinism is a recessive mutation and the responsible gene is symbolised as ‘c’, while brown is symbolised as ‘b’. Brown is ‘sex-linked’ recessive, which means that a brown individual with normal-coloured parents is always female. An albino can be of either sex. There are strong indications that ino is based on a single, sex-linked gene in all species, too.

For leucism, dilution and melanism, several genetic mutations can be responsible for more or less the same aberration. In domestic pigeons at least 16 dilution mutations are known, more than ten for leucism, and six for melanism (van Grouw & de Jong 2009). However, these different mutations all cause comparable effects in the pigmentation and therefore they can all be distinguished as being ‘dilution’, ‘leucism’ or ‘melanism’.

Albinism
Albinism, from the Latin albus, meaning ‘white’, is defined as an absence of both melanins in feathers, eyes and skin. The lack of melanin results from the (hereditary) absence of the enzyme tyrosinase in the pigment cells. The result is usually a completely colourless bird. The red or pinkish hue that can be seen in the eyes and skin is caused by blood that is visible through the colourless tissue. Thus, as mentioned above, there is in fact no such thing as a ‘partial albino’.

The forming of carotenoid pigments is
Albino birds are rarely found in the wild, although the mutation is not uncommon and occurs quite frequently in most populations. The reason for their apparent scarcity is that the absence of melanin in the eyes makes them highly sensitive to light, and gives them a poor depth of vision. It is mainly their poor eyesight, rather than their white plumage, that makes albinos vulnerable, and most die soon after fledging.

Leucism
Leucism, from the Greek *leukos* (for ‘white’), can be defined as *the partial or total lack of both melanins in feathers (and skin)*. The lack of melanin is a result of the congenital and heritable failure of the pigment-producing melanoblasts to migrate to some or all areas of the skin. Pigment cells are therefore absent from some or all of the skin areas where they would normally provide the growing feather with pigment. The extent of white feathering can vary, from just a few white feathers (partially leucistic) to the plumage being completely white; the skin is colourless for individuals in the latter category. Partially leucistic birds may have a normally coloured bill and feet, depending on where the colourless patches occur, but all leucistic birds have normally coloured eyes. (The embryonic origin of eye pigments is different from that in the rest of the body. Eye pigments originate mainly from cells in the outer layer of the optic cup, while the pigment cells for the rest of the body originate from the neural crest; since leucism affects the migration of...
melanoblasts from the neural crest only, it has no influence on eye colour.)

The white pattern in leucistic birds is often patchy and bilaterally symmetrical, owing to the way the melanoblasts migrate from their embryonic origin into the rest of the body, leaving certain areas without pigmentation. The white pattern occurs in juvenile plumage and the amount of white feathering does not change with age. Leucism most commonly affects the body parts farthest from the neural crest: the head, the wing-tips, the feet and the belly.

There are, however, other causes for an absence of pigment in feathers which are much more common than leucism. For example, ‘progressive greying’ arises after a bird reaches a certain age and is defined as the progressive loss of pigment cells with age. From the onset of the condition, the bird will gain an increasing number of white feathers after every moult: finally the entire plumage becomes white. Progressive greying may or may not be heritable; some forms may be related solely to age while in others the progressive loss of pigment cells may be due to disorders such as vitiligo. Progressive greying is common in Blackbirds, House Sparrows Passer domesticus and Jackdaws Corvus monedula. White feathers in these species are hardly ever due to leucism.

External, non-heritable factors such as illness or food deficiency can also be the cause of pigment loss. In such cases, the bird is unable to extract sufficient quantities of tyrosine from its food, which results in a disturbed melanin synthesis. The pigmentation will return to normal as soon as the external causes are removed. Progressive greying was initially thought to be caused by a form of food deficiency (Rollin 1964), but whereas a dietary deficiency causes wide, white bars in the feathers, in progressive greying the feathers are entirely white.

Leucism and progressive greying are hard to distinguish in the field, especially when the latter has reached an advanced stage. The white pattern caused by leucism is normally patchy and bilaterally symmetrical, so the presence of a few white outer primaries on both sides and/or some white feathers in the face is typical for leucism. Progressive greying in an early stage shows white feathers spread randomly, often on the head, back and flanks at first, though the skin (bill and feet) is often unaffected.

In both leucism and progressive greying, aberrant feathers are pure white because melanin production in these parts is impossible. Partly coloured individual feathers are very unusual. In both cases any pigmented feathers and skin will be normally coloured. Heavily bleached plumage is often attributed to leucism but this is the result of other mutations, of which brown is the most common (Buckley 1982; van Grouw 2010).

Brown
This mutation is defined as a qualitative reduction of eumelanin. The number of eumelanin pigment granules remains unchanged but the appearance of the pigment is altered (the eumelanin synthesis is incomplete as the eumelanin is not fully oxidised) and thus pigment that is normally black remains dark brown. The phaeomelanin is unaffected.

Formerly, it was thought that the mutation brown was caused by an absence of black pigment (eumelanin) while the brown
pigment (phaeomelanin) remained unchanged (Rollin 1962, 1964; Harrison 1963a,b). In that case, however, a Rook *Corvus frugilegus* with this mutation would be white, since phaeomelanin is not present in corvids. In reality, a brown Rook has dark brown plumage because the eumelanin is incompletely oxidised.

In many species, eumelanin that is not fully oxidised is also part of the normal plumage colour – for example, the dark brown remiges and rectrices of the House Sparrow. In such cases, the mutation brown will turn normally dark brown feathers light brown (since the eumelanin will be less oxidised than normal). Plumage aberrations that result from incompletely oxidised eumelanin are very sensitive to sunlight and will bleach quickly. Older plumage thus becomes almost white, making this type of aberration difficult to distinguish in the field since the original coloration is lost. For a correct identification, try to see parts of the plumage that are not usually exposed to sunlight.

19. Brown Jackdaw *Corvus monedula*, a first-summer female, Friesland, the Netherlands, April 2008. This bird’s feathers are heavily bleached by the light.

20. Aberrant feathers are very prone to bleaching by exposure to light. Old feathers can be much lighter in colour than fresh ones (left), but when the plumage is checked in places not normally affected by light, such as the inner webs of the flight feathers, the original aberrant colour is visible. Brown Jackdaw *Corvus monedula*, specimen in the collection of the Natural History Museum, Tring.
plumage that should be less affected by sunlight, such as the inner webs of flight feathers when the bird is wing-stretching. This should determine whether the plumage has been bleached differentially by the light. The colour of the eyes is not visibly affected by the mutation brown but the feet and bill are slightly paler than those of normally coloured birds.

The mutation brown is widespread among all species and, after progressive greying, is the most frequently encountered colour aberration in birds. The brown gene is located on the sex chromosome. In birds, the male has two sex chromosomes and the female only one, which explains why most wild birds with the mutation brown are females – since females need only one gene for brown to express the mutation. One species in which brown males are more frequent is the Mute Swan Cygnus olor – although the only difference in appearance between a brown adult Mute Swan and a normal one is the paler feet of the former. The juvenile plumage, however, is rather different: the cygnets are white instead of grey and the first-year plumage is also white instead of brown. In 1838, Yarrell described this aberration as a new species, the Polish Swan, and he named it Cygnus immutabilis (‘unchangeable’) since the colour of the birds did not change. Munro et al. (1968) showed that the Polish Swan’s colour was recessive and
sex-linked in inheritance. Close observation of the down colour of the hatchlings and the first-year plumage of the juveniles shows a light creamy coloration instead of pure white, indicating that the mutation brown is responsible for Yarrell’s mistake.

Dilution
Dilution, from the Latin dilutior (‘paler’ or ‘weaker’), can be defined as a quantitative reduction of melanos—the number of pigment granules is reduced but the pigment itself is not changed. The lower concentration of granules forms a weaker (or diluted) colour as a result. This is analogous to a photograph in a newspaper: a high concentration of black ink dots close together is perceived as black, while fewer black dots in an area of the same size appears grey. Although many different mutations are known for reducing pigmentation, and therefore have the effect of diluting the colours, dilution can be separated into two main forms.

The most common form is a reduction of both eumelanin and phaeomelanin. Black feathers will turn grey, and reddish- or yellow-brown feathers will turn buff or cream-brown. The degree of dilution varies both between individuals and within a single mutation but most mutations cause a melanin reduction of about 50%. All birds with this form of dilution look like a pale version of their normal counterparts, and are termed ‘pastel’ (from the Latin pastellus,
‘a pale, delicate colour’).

The second form is a reduction of eumelanin only, with phaeomelanin unaffected. Black feathers will turn grey, but reddish- or yellow-brown feathers are unaffected. This form of dilution is called ‘isabel’ (from the Latin *isabellinus*, or greyish-yellow). In species with only eumelanin in their plumage, such as crows, it is impossible to distinguish a dilution mutation as either isabel or pastel. In species with both melanins, such as sparrows, the phaeomelanin often seems to be even brighter in colour owing to the reduction of the overlying eumelanin. In some mutations the reduction of eumelanin is almost complete and the originally black parts of the plumage appear virtually white. The absence of one melanin pigment while the other is still present and unaffected is often called ‘schizochroism’ (meaning ‘colour dividing’). However, because schizochroic mutations often do not reduce the affected melanin completely in the plumage, schizochroism is recognised as a form of isabel.

A third form of dilution is the reduction of phaeomelanin while eumelanin is unaffected. This is extremely rare and recorded in only a few species. The most well known is the so-called ‘silver’ – a dominant and sex-linked mutation in domesticated chickens.
Ino

Ino is defined as a strong qualitative reduction of both melanins. In contrast to dilution (where the chemical composition of the melanins is normal, but their quantity is deficient), for ino mutations both melanins are produced in normal quantities, but are incompletely oxidised, resulting in brown eumelanin and pale phaeomelanin. Ino seems to be connected to the same gene, located on the sex chromosomes, in all species. The relevant gene also appears to mutate easily, as different mutations (alleles) from that gene are known to occur in many species.

Depending on the relevant allele, the degree of melanin oxidation differs but the black eumelanin can vary from dark to very pale brown, while the reddish-brown phaeomelanin is always very pale or even hardly visible. In the darkest forms of ino the incompletely oxidised eumelanin may produce the same colour as the mutation brown; but ino can be distinguished from brown in that the phaeomelanin is also reduced. In species without phaeomelanin, ino can be distinguished from brown by the bill and feet, which are always pink because of the absence of melanins.

While the darkest forms of ino resemble brown, the lightest forms resemble albino. In the latter, the phaeomelanin has almost disappeared and there is also hardly any oxidation of eumelanin, so that black becomes a very pale brown. In fresh plumage, colour and pattern remain just visible, especially in the plumage parts that normally have the highest eumelanin concentration; but worn plumage is heavily bleached and thus almost white.

In ino the eyes are reddish due to
the reduction of melanin, but the eyesight of an ino bird is much better than that of an albino. Any adult bird in the wild with ‘white’ plumage and reddish eyes is thus an ino and not an albino. The inheritance of ino (both the light and the dark forms) is recessive and sex-linked so only females will be found in the wild.

Melanism

Melanism, from the Greek *melanos* (‘dark-coloured’), is an abnormal deposit of melanin in skin and/or feathers. Melanism is not necessarily an increase of pigment but may be the result of an altered distribution or ‘abnormal deposit’ of the same amount of melanin. For example, wild Rock Doves *Columba livia* are slate blue-grey above with a black tail-bar and two black bars on each wing. These two colours are the result of different arrangements of the same black melanin granules. In the grey parts, the granules are arranged in a clumped fashion and, due to the reflection of the light, what we see appears as blue-grey. In the black parts the granules are evenly spread and the colour appears black. In the domestic pigeon, a dominant mutation called ‘spread’ results in all the granules being distributed in the manner usually found only in the black wing-bars and tail-bar, resulting in uniformly black plumage.

In general, the appearance of a melanistic bird is dark, mostly but not always blackish. There are three ways in which melanism can affect plumage: (i) normally dark markings are bolder and noticeably ‘overrun’ their typical boundaries (the rest of the plumage is often somewhat darker as well); (ii) the entire plumage is darkened and appears dark brown or black; or (iii) normal pattern and/or pigment distribution is changed but plumage is not darker. In most cases it is only the eumelanin that is affected and as a result most melanistic birds look ‘blackish’. Abnormal deposits of phaeomelanin only is rare (but not unknown), and a phaeomelanistic bird will appear entirely reddish-brown.

Melanism is the only mutation in which there is no loss of pigment or change in the shape or size of the melanin granules. The plumage of a melanistic bird is therefore not obviously aberrant: the plumage looks ‘natural’ but is often completely different from that of any known species. The fact that melanistic birds were, in the past, mistaken for ‘new species’ is therefore entirely understandable.

Conclusion

Identifying colour mutations in the field can
be extremely difficult and is by no means always possible. The views of the bird may be less than ideal or the plumage may already be strongly bleached and no longer show the original coloration caused by the mutation. When trying to name a mutation correctly, it is important that you know exactly how the normal plumage colour of the relevant species should look! Then try to see parts of the feathering that should be less influenced by sunlight to determine whether the plumage appears to have been bleached differentially by the light. Having done that, and with the original coloration in mind, the summary in table 1 should make it easier to name the mutation correctly.

### Table 1. Identification key to aid recognition and naming of the most common colour aberrations in birds.

<table>
<thead>
<tr>
<th>Mutation</th>
<th>Gene action</th>
<th>Effect on colour</th>
</tr>
</thead>
<tbody>
<tr>
<td>Albinism</td>
<td>Total lack of both melanins in feathers, eyes and skin due to the heritable absence of the enzyme tyrosinase in the pigment cells.</td>
<td>All-white plumage, red eyes and pink feet and bill.</td>
</tr>
<tr>
<td>Leucism</td>
<td>Partial or total lack of both melanins in feathers (and skin) due to the heritable absence of pigment cells from some or all of the skin areas.</td>
<td>All-white plumage or all-white feathers mixed with normal-coloured ones. Pink bill and feet or normal-coloured bill and feet. Always normal-coloured eyes.</td>
</tr>
<tr>
<td>Progressive greying</td>
<td>Partial or total lack of both melanins in feathers (and skin) due to progressive loss of pigment cells in some or all of the skin areas with age.</td>
<td>All-white plumage or all-white feathers mixed with normal-coloured ones. Pink bill and feet or normal-coloured bill and feet. Always normal-coloured eyes.</td>
</tr>
<tr>
<td>Brown</td>
<td>Qualitative reduction of eumelanin due to incomplete synthesis (oxidation) of eumelanin.</td>
<td>Originally black is brown, originally reddish-/yellow-brown unaffected.</td>
</tr>
<tr>
<td>Dilution – pastel</td>
<td>Quantitative reduction of both melanins.</td>
<td>Originally black is silvery grey, originally reddish-/yellow-brown is buff/cream.</td>
</tr>
<tr>
<td>Dilution – isabel</td>
<td>Quantitative reduction of eumelanin only.</td>
<td>Originally black is silvery grey, originally reddish-/yellow-brown unaffected.</td>
</tr>
<tr>
<td>Ino – light</td>
<td>Strong qualitative reduction of both melanins due to incomplete synthesis (oxidation) of both melanins.</td>
<td>Originally black is very pale brown/cream, originally reddish-/yellow-brown hardly visible. Eyes pinkish, pink feet and bill.</td>
</tr>
<tr>
<td>Ino – dark</td>
<td>Qualitative reduction of both melanins due to incomplete synthesis (oxidation) of both melanins.</td>
<td>Originally black is light brown, originally reddish-/yellow-brown is buff/cream. Pink feet and bill.</td>
</tr>
<tr>
<td>Melanism</td>
<td>Abnormal deposit of melanin.</td>
<td>Increase of black and/or reddish-brown.</td>
</tr>
</tbody>
</table>

### Acknowledgments
I am very grateful to the various photographers who kindly supplied the images used in this paper and I would particularly like to thank my wife, Katrina van Grouw, for editing the text and improving my English.

### References
30. Brown juvenile Griffon Vulture *Gyps fulvus*, Tarifa, Spain, November 2012. This striking individual accompanied a large flock (c. 300) of conspecifics. Juvenile Griffons from throughout the Iberian Peninsula move south in autumn and large flocks of (mainly) juvenile birds are seen regularly along the northern shore of the Strait of Gibraltar, waiting for optimal conditions to cross into Africa. Such ‘brown’ juvenile Griffons have been observed in every autumn since 2008. Javier Elorriaga, who took this photograph, tells us that he has never been aware of adult birds with a similar colour aberration, so it may be that birds such as these rarely survive beyond their first winter. Such individuals are typically found on the margins of these large flocks and are often subdominant to Griffons with normal plumage.


Munro, R. E., Smith, L. T., & Kupa, J. J. 1968. The genetic basis of color differences observed in the Mute Swan (*Cygnus olor*). *Auk* 85: 504–505.


Hein van Grouw has been a Bird Curator since 1997, first at the National Museum of Natural History Naturalis, Leiden, the Netherlands, and now at the Natural History Museum in Tring. His main interest and ongoing research is into the occurrence and correct identification of colour aberrations, heritable and non-heritable, in European birds.

Within the scope of his research the author would like to hear about observations of aberrant coloured birds. The research is focused mainly on corvids and House Sparrows but any record of any species would be much appreciated.