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WHAT COLOUR IS THAT SPARROW? A CASE STUDY: COLOUR ABERRATIONS IN THE HOUSE SPARROW *PASSER DOMESTICUS*

"...far too well-known to need any description of its appearance or habits, …."
Alfred Newton. 1896,
A Dictionary of Birds, volume 4.

ABSTRACT

In this paper 16 distinct, heritable colour aberrations (mutations) in the House Sparrow are described, based on specimens found in museum collections, records of individuals seen in the wild and from bird breeders keeping aberrant coloured sparrows in captivity. Based on the frequency found in the museum specimens Brown is the most common mutation in the House Sparrow, followed by Ino and Albino. Besides the mutations there is also a, presumably, non-heritable aberration called Progressive Greying described. Progressive Greying is in fact by far the most common colour aberration found in the species but was, in the past, always assigned as 'Partial Albino' without its real nature being understood. This paper will give some insight in the nature of Progressive Greying.

Keywords: House Sparrow, Colour aberrations, Albino, Brown, Progressive Greying.

INTRODUCTION

Colour aberrations in the House Sparrow have been known for a long time although historically they were not recognised as such. Brisson named in his Ornithologia (1760) a white House Sparrow as *Passer candidus* (Latin for 'shining white') and referred also to *Passer albus* described by Aldrovandi (1599). According to Brisson this 'species' has white plumage, yellow bill and feet and dark eyes. Brisson also mentioned that specimens which are partly white and partly coloured do occur as well.

The specimen on which Brisson had based his description was kept in 'Du Cabinet de M. de Reaumur' of which Brisson was the curator. De Reaumur was a French scientist and his bird collection was one of the richest in his time.

Sparrman, a Swedish explorer and a student of Linnaeus, in 1786 also described a white sparrow kept in the Museum of Gustavus Carlson, Secretary of State to his

Swedish Majesty. He used the species name given by Brisson but placed the sparrows in the genus *Fringilla* just as his teacher had done. The Gentlemen's Society in London mentioned in their review of Sparrman's work (The Critical review or Annals of Literature, Vol. 67, 1789) that a similar specimen of *Fringilla candida* was also present in Link's Museum in Leipzig. So white and pied sparrows were not that uncommon then and white plumage still seems to be a common aberration in the House Sparrow.

Besides white feathers many more colour aberrations are known in the House Sparrow. However, naming aberrations correctly was always a reason for confusion (van Grouw 2013). A variety of names are (still) used, seemingly randomly, to identify the mutations. Most commonly and most often wrongly, applied is the name albino or partial albino (Rollin 1964; Buckley 1982, 1987; van Grouw 2006, 2010). Albino is widely used for all sorts of different colour aberrations, but in only a tiny proportion of cases is it used correctly. Partial albino as a term is wrong, as albinos cannot produce pigment at all and therefore being partial albino is simply impossible.

The confusion is mostly caused by the desire of ornithologists, now and in the past, to use names which describe the actual appearance of a particular aberrant coloured bird. However, the appearance of mutations may differ radically between species, sexes and the age of the bird; all depending on the original pigmentation.

For example, the appearance of the mutation Brown in a Rook *Corvus frugilegus* is nothing like Brown in a House Sparrow as both species are completely different in plumage colour in the first place. The same, of course, can apply when there is a difference in colour between sexes, as in the House Sparrow. And because the pigment distribution and/or concentration are often different between juveniles and adults, certain mutations correspondingly appear different according to the age of the bird. So the appearance of mutations also differs between plumage stages within the same species.

Finally, aberrant pigmentation due to mutations often is very light sensitive and will bleach rapidly, so in old plumage a bird can look quite different from its fresh plumage (see fig. 2 and 3).

All of this, plus the fact that the bird in the field might be too far away or is moving too quickly, makes it hard to distinguish the different mutations without breeding tests. And that is why there is still a lack of clarity in the ornithological world about the correct naming of them. However, if we keep the original colouration of the House Sparrow in mind while examining an aberrant specimen, and noticing the actual changes in the pigmentation, one will notice that these changes are all based on only a few basic principles. And being aware of these principles makes distinguishing the different aberrations easier.

Pigmentation

The main pigments that determine plumage colour are melanins. Melanins can be distinguished in two forms, eumelanin and phaeomelanin, and both forms are present in

the House Sparrow. 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.

The colour of the eyes is due to eumelanin only, while the bare parts contain eumelanin and carotenoids. Carotenoids are pigments responsible for pale yellow to scarlet red in birds and they have a vegetable origin. Carotenoids cannot be synthesised by birds and therefore they must be acquired from food. The yellowish colour in the beak and feet (and body fat and egg yolk) of the House Sparrow is due to carotenoids called xanthophylls. Although normally not visible in the plumage colour, House Sparrows seem to be able to form carotenoid-based colours in their plumage as well. Whether this is only in particular individuals, or that it only shows because of an 'unnatural' diet is unclear but the fact is that specimens with clearly visible yellowish tones in their plumage are found from time to time (see fig. 5). This yellow pigment is also xanthophyll. However, mutations affecting the carotenoid coloration are rare and, given that this coloration is not standard in the House Sparrow, only the melanin aberrations will be discussed further in this paper.

Melanins are produced in pigment cells (melanocytes) in the skin which add the pigment to the feather cells as the feathers grow. The addition of melanin does not always occur at a constant rate. In the House Sparrow, for example, 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. Any disturbance or aberration in the 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 six most common heritable colour aberrations found in birds are: **Albinism, Leucism, Brown, Dilution, Ino** and **Melanism** (for a detailed description of these aberrations see van Grouw 2013). This paper will examine the occurrence of these aberrations in the House Sparrow.

Leucism, Dilution and Melanism can be caused by several different mutations but all with a comparable effect while Albino, Brown and Ino are all caused by a single genetic mutation (van Grouw 2013).

The mutations in the House Sparrow

The information presented below is based on the examination of 362 aberrant coloured specimens found in 22 Museum bird collections (see acknowledgements) by the author.

Records of live aberrant coloured Sparrows seen in the wild and the practical breeding experiences gathered from bird breeders are also included in this review.

Given that aberrantly coloured birds have always intrigued people, these specimens were often especially targeted for (museum) collections. Therefore the number of aberrant coloured specimens in proportion to normal coloured birds in collections is much higher and does not represent the true ratio occurring in the wild. However, we can assume that the ratio between the different aberrations is quite representative, as any unusual bird was collected regardless of its actual colour.

For every mutation the general description will be given followed a discussion of its occurrence in the House Sparrow. Potential differences typical in the House Sparrow will be given as well as the inheritance of the aberration in this species, if known.

Albinism

Albinism, from the Latin *albus*, meaning white, is defined as a *total lack 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 usually is 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. Due to the absence of tyrosinase in an Albino, no melanins can be produced, thus, as mentioned above, there is no such thing as a 'partial albino'.

Albino sparrows are rarely seen 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, with a poor depth of vision. It is mainly their poor eyesight, rather than white plumage that makes albinos vulnerable, and most die soon after fledging.

The inheritance of Albino is recessive and therefore the number of birds that are carrier of the gene is probably far higher than expected. An individual must receive the gene for Albino from both parents (carriers) to be afflicted with the absence of tyrosinase. However, for every Albino that is hatched, two carriers are also hatched on average. And half of the offspring of a carrier mated with a non-carrier will also be carriers on average.

A rare mutation related to Albino, called Acromelanism, is also known in the House Sparrow. It is not found in the sample of museum specimens but the mutation does occur in captive populations (based on an individual caught from the wild). Acromelanism, from the Greek *akro*, meaning top or point, can be defined as *a melanin deposit in the body extremities mainly*. Due to the mutation the tyrosinase in the pigment cells is temperature dependent and at normal body temperature no melanin synthesis will take place. Melanin is only formed in parts that are lower than the normal, average body temperature. Therefore only the body extremities, as they are colder, are pigmented.

Acromelanism is well known in mammals and is, for example, responsible for the colour markings in Siamese cats and Himalayan rabbits. In all mammals Acromelanism is an allele of the albino gene (Robinson 1973, Searle 1968 and 1990) (alleles, from Greek meaning 'each other', are variant forms of a gene). In birds the author has found Acromelanism in several crow species, the Song Trush *Turdus philomelos*, Eurasian Blackbird *Turdus merula*, European Starling *Sturnus vulgaris*, Tree sparrow *Passer montanus* and the domesticated Ringneck Dove *Streptopelia roseogrisea*. Breeding tests have proven that in the latter species Albino and Acromelanism are allelic, with Acromelanism dominant over Albino but recessive to Wild-type (van Grouw 1997). Therefore it is reasonable to assume that in the House Sparrow Acromelanism also is an allele of Albino.

Melanins, as stated above, are mainly formed in the extremities e.g. beak/face and feet/claws as these are the coldest parts of the body. However, melanin production also depends on the environment temperature during moult and, during colder periods, melanin will also be produced sporadically in other parts of the plumage. As male House Sparrows have a higher melanin concentration than females the expression of Acromelanism shows clearer in males. The female's plumage is mainly white with only a light-brown face.

The inheritance of Acromelanism in the House Sparrow seems to be dominant.

Leucism

Leucism, from the Greek *leukos* (for white), can be defined as *the lack of both melanins from all or parts of the plumage (and skin)*. The lack of melanin is a result of the congenital and heritable failure of the pigment-producing cells called melanoblasts to migrate to the skin during embryonic development. Pigment cells are therefore absent from some or all of the skin areas where they would normally provide the growing feather with colour. The extent of white feathering can vary, from just a few white feathers (partially leucistic) to the plumage being completely white (100% leucistic); the skin is colourless for individuals in the latter category. Partially leucistic birds may have a normal coloured bill and feet, depending on where the colourless patches occur, but all leucistic birds have normal coloured eyes. The white pattern in leucistic birds is often patchy and bilaterally symmetrical; most commonly the head, the wingtips, the feet and the belly are affected. The white pattern occurs in juvenile plumage and the amount of white feathering does not change with age. In the House Sparrow completely white individuals are found from time to time but Partial Leucism seems to be extremely rare.

White feathers in sparrows are however very common but the absence of pigment in the feathers is almost always caused by Progressive Greying. 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 and in many birds the entire plumage becomes white eventually. 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 (pigment disease). Progressive Greying is the most common cause of white feathers in House Sparrows.

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 a few white outer primaries on both sides and/or some white feathers in the face are typical. Progressive Greying in its early stages shows white feathers spread randomly while the skin (bill and feet) is often unaffected. Most forms of Progressive Greying finally results in the entire plumage being white.

Besides this random way of Progressive Greying, two other, distinct forms occur in the House Sparrow. In the first case the Progressive Greying starts in the flights and tail feathers while the rest of the plumage is hardly affected. In the second case the flights and tail feathers are the last feathers to be affected. These remarkable patterns may be simply due to the way House Sparrows moult in relation to the onset of Progressive Greying, but further research is necessary to either confirm or deny this.

External, non-heritable factors such as illness or food deficiency can also be the cause of pigment loss (these are not included in the sample). In such cases, the bird is unable to extract sufficient quantities of tyrosine from its food, which results in 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 and also often a poor feather structure, in Progressive Greying the feathers are entirely white and their structure is unchanged.

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 normally black pigment remains dark brown. The phaeomelanin is unaffected.

Eumelanin that is not fully oxidised is part of the original plumage colour in the House Sparrow, for example the dark-brown remiges and rectrices. So in these cases, the mutation Brown will turn the original dark brown feathers light brown (since the eumelanin will be less oxidised than normal). Aberrations due to incompletely oxidised eumelanin are very sensitive to sunlight and will bleach quickly. Consequently, older plumage becomes almost white and is hard to distinguish in the field (see fig. 2). For a correct identification, try to examine parts of the 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 (see fig. 3). The colour of the eyes is not visibly affected by Brown but the feet and bill are slightly paler than those of normally-coloured birds.

The mutation Brown is widespread amongst House Sparrows and, after Progressive Greying, is the most frequently encountered colour aberration in this species.

Given that Brown is the result of only one recessive mutation, the occurrence of so many Brown House Sparrows is remarkable. But perhaps the fact that Brown is also sex-linked explains why it is not that uncommon. Sex-linked means that the gene is located at the X-chromosome (remember that in birds males have 2 X-chromosomes and females have an X and Y). The gene for Brown is symbolised as b and the unchanged form of this gene (= normal-coloured) is therefore B. Given that the males have two X-chromosomes they can have therefore three different genotypes for Brown; BB (normal-coloured), Bb (normal-coloured but heterozygous for Brown) or bb (Brown). Females are either normal (B-) or Brown (b-) but can't be heterozygous for Brown. When a male which is heterozygous for Brown but normal coloured, breeds with a normal female, half of his daughters (= 25% of his total offspring) will be Brown. And besides half of the daughters being Brown, half of the male offspring from a heterozygous father will also be heterozygous for Brown. By comparison, for recessive mutations which are not sex-linked you need both parents to be heterozygous to get 25% aberrant offspring.

This also explains why only Brown females are seen in the wild, as females need only one gene for Brown to express the mutation. To get a Brown male you need a heterozygous father and a Brown mother. The likelihood of this occurring in the wild is very minute but not impossible, of course. In many species Brown females successfully breeding in the wild have been recorded (Carrion Crow *Corvus corone*, Eurasian Jackdaw *Corvus monedula*, Common Magpie *Pica pica*, European Starling and House Sparrow).

Dilution

Dilution, from the Latin *dilutior* (paler or weaker), can be defined as *a quantitative reduction of melanins* – 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 are perceived as black, while fewer black dots in a same-sized area 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 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 counterpart, and are termed Pastel (derived from 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 stays reddish or yellow-brown. This form of Dilution is called Isabel (from the Latin *Isabellinus* meaning greyish-yellow). The phaeomelanin often seems to be even brighter in colour due to the reduction of the overlying eumelanin. In some mutations the reduction of eumelanin is almost complete and the parts of the plumage that were originally black appear virtually white. The absence of one melanin pigment while the other is still present and unaffected is often called Schizochroism (Greek, meaning colour dividing). However, mutations causing this are very rare; in most cases the affected melanin is not completely eliminated in the plumage while the skin may be even less affected, resulting in the bill and feet still being coloured. Therefore, nowadays, I recognise mutations formerly called Schizochroism as a distinct form within the dilution mutations, as the total lack of one melanin being nothing more than the most extreme degree of dilution.

In the first form, the pastel-group (a reduction of both melanins) many different mutations occur in the House Sparrow. Some are easy to recognise while others have very similar pigment reductions and are hard to distinguish from each other. The first mutation in this group and easily distinguished, causes a strong but equal reduction of both melanins. The general appearance is silvery-grey all over, but the original pattern is still visible (see fig.19). This mutation is recessive in inheritance.

The second mutation in the pastel group reduces the eumelanin heavily while the phaeomelanin seems to be lacking almost completely. The general impression is a 'whitish' bird with clearly visible darker patterns (see fig. 20). This mutation is also recessive in inheritance.

The most common mutation in this group is very variable in expression and between individuals the reduction in the juvenile plumage can be from 50% to almost 100% (see fig. 21). The almost white youngsters will finally show a dilution of about 50% in adult plumages, while the darker juveniles appear barely affected adults. In this mutation the deep-black eumelanin seems to be less affected than the phaeomelanin and brown eumelanin.

Several other pastel mutations are recorded in the House Sparrow. All of them causing their own specific degree of melanin reduction and resulting in their own specific diluted appearance. However they all fall within the range of melanin reduction (and appearance) exhibited by the above mentioned variable pastel-mutation. Without breeding tests this makes them hard to distinguish from each other and therefore they are not separated in the sample of museum specimens. The variable pastel-mutation is recessive in inheritance and so are most of the others. However, at least one pastel-mutation is known for being recessive and sex-linked and this mutation affects the eumelanin more than the phaeomelanin.

Within the isabel group (a reduction of eumelanin only while the phaeomelanin is unaffected) two distinct mutations are found in the House Sparrow. The most common causes a eumelanin reduction of about 50% resulting in all the originally black parts appearing as solid grey. The second isabel mutation is variable in expression but on average the eumelanin is almost completely removed. Any remaining eumelanin is not uniformly deposited, resulting in patchy grey feathers, which distinguishes it from the first isabel mutation. The first isabel mutation is recessive in inheritance while the second is dominant.

Ino

Ino is defined as *a strong qualitative reduction of both melanins*. In Ino the melanin synthesis is incomplete, resulting in barely visible phaeomelanin and pale-brown eumelanin. The relevant gene also appears to mutate easily, as different mutations (alleles) from that gene occurring in many species (e.g. domesticated pigeon, 'Ringneck Dove', Japanese Quail, *Coturnix japanensis*, Zebra Finch *Taeniopygia guttata* and Bengalese Finch *Lonchura domestica*).

In the House Sparrow, also at least two different Ino-alleles are known. Depending on the relevant allele, the degree of melanin oxidation differs. However, the reddish-brown phaeomelanin is always very pale or even hardly visible in Ino, while the black eumelanin can vary from dark to very pale brown. In the dark form the incompletely oxidised eumelanin may show as a comparable colour as in the mutation Brown, but Ino can be distinguished from Brown in that the phaeomelanin is also reduced.

If the dark form of Ino may look like Brown; the light form seems to resemble Albino. In these birds the phaeomelanin has almost disappeared and there is also hardly any oxidation of eumelanin, so originally black patterns will turn very pale brown. In fresh plumage, the House Sparrow's colour and pattern remains just visible, but worn plumage however will be heavily bleached and thus almost white. In Ino the eyes are reddish due to the reduction of melanin, but the eyesight of an Ino sparrow is much better than that of an Albino. Any adult wild bird with 'white' plumage and reddish eyes is an Ino and not an Albino. The inheritance of Ino, either the dark or the light form, is recessive and sex-linked, so only females will be found in the wild (see also under Brown for sex-linkage).

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 altered distribution; the 'abnormal deposit' of the same amount of melanin.

In general, the appearance of a melanistic bird is dark; mostly but not always blackish. There are three ways in which melanism can affect birds' plumage:

1. Dark markings are bolder and noticeably 'overrun' their typical boundaries (the rest of the plumage is often somewhat darker as well).
2. The entire plumage is darkened and appears dark brown or black.
3. Normal pattern and/or pigment distribution is changed but plumage is not darker.

The first category of melanism is not found amongst the 362 museum specimens examined but nevertheless has been observed in House Sparrow populations in the Netherlands and the UK.

So far only adult males and juvenile birds have been seen by the author. The overall appearance of the juvenile plumage is darker and there is also a noticeable darkening of the beak and feet. In the adult males the black bib extends all over the under parts. In winter plumage the dark under parts are less obviously as all feathers have a light coloured tip, just as the bib feathers in normal coloured males (see fig 32B.), These tips become worn down during winter, as usual, so in summer plumage the deep black under parts show best. Besides the increase of eumelanin in the under parts, in the upper parts also an increase of phaeomelanin is noticeable (see fig 32A and 33.). Remarkably the grey cap seems to be unaffected.

The second category seems to be the most common form. However, the overall 'blackish' plumage often found in sparrows is, in fact, due to artificial discoloration. It is often wrongly referred to as 'Industrial Melanism' but this form of darkening is not hereditary and is therefore not true melanism (Harrison 1963, Johnston 1963, Rollin 1964). The dark aspect is uniformly distributed over the whole plumage and is the result of dust-bathing in industrial areas polluted with cinder dust, ash and soot.

To confirm the statements above the author has examined at least 60 of these 'sooty' specimens (not included in the sample). No dark specimens were found with fresh, new plumage and the darkest birds had the oldest, most worn plumage. This agrees with an accumulation of soot in the feathers during a year. Also the scaling on the feet was very pronounced in these specimens as a result of dirt (soot) underneath the scale rims; the scales themselves were not remarkably darker.

Another case of probable artificial discolouration was found and described in Poland. In early 1900 Dybowski heard about a population of dark coloured House Sparrows in a village close to Jaroslaw in Poland. He acquired a few specimens and named the variety *Passer domesticus* var. *Scheffneri*, after P. Scheffner, Dybowski's student, who drew his attention to these sparrows (Dybowski 1916). According to the description all birds were more or less solid chestnut brown coloured with hardly any pattern noticeable. Unfortunately the specimens from Dybowski's collection seem to be lost so the real identity of this aberration cannot be revealed.

A further case of undisputed artificial discolouration was recently found in Rossshire, Scotland. Many 'pinkish-red' House Sparrows occur in the local population and the cause of this aberration was for a while unclear. However, it turned out that a salmon farm was based in the area and that House Sparrows ate the salmon's food pellets. The salmon food is enriched with carotenoids (from prawns) to give their flesh

the required pink colour. As House Sparrows are able to form carotenoid based colour in their plumage the red carotenoid from the salmon's food seems to be the obvious cause for the reddish colouration. Carotenoids can only be taken up by the feather cells during feather growth. However birds are able to store an excess of carotenoids in their liver to be available for colouration of the feathers whenever required. So even when the sparrows take in carotenoids for only a few weeks during the winter, the effect will show the following summer during moult.

Although 'artificial discolouration' seems to be responsible for most of the cases of melanism within the second category, a true form of melanism *is* found in the House Sparrow. This true mutation causes a strong increase of eumelanin in the plumage, hiding the original pattern almost completely, with an almost solid black bird as a result. The bare parts, bill and feet, are not affected. The inheritance of this mutation is not yet known.

Within the third category different aberrations occur. The most common form is the distribution of reddish-brown in the normally black bib of male House Sparrows (not included in the sample). This aberration 'heeft de gemoederen van de ornithologen altijd bezig gehouden'. Bonaparte (1850) named the variety as a distinct species, *Passer rufipectus,* while Studer and Von Burg (1916) noting its commonness in a region of the Jura mountains, Switzerland, described it as a local race of the House Sparrow *Passer domesticus rufescens*.

A minimal amount of phaeomelanin, resulting in brownish feathers in this part of the plumage is not unusual. Van Heurn (2003) found in a sample of 515 adult male House Sparrows, all from the same place in the Netherlands, 122 (24%) specimens with some phaeomelanin in their bib. However in almost all cases the reddish-brown was restricted to only one or a few feathers partly brown and not visible without close examination of the feather bases. Counting only the specimens with clearly visible reddish brown in their bib, without moving feathers, the same sample yields 15 specimens (3%). In a sample of 557 adult male specimens Selander and Johnston (1967) found a comparable percentage, 25.5%, with some brown in their bib, varying from 1 partly brown feather to more than half the bib being brown. However, only 1.6% had clearly visible reddish-brown in the bib. Piechocky (1954) found 211 specimens (3.5%) clearly showing brown in their bib within a sample of 5992 male specimens.

As one can expect the rate of birds with brown bibs among museum specimens is slightly higher, as the obvious cases were probably especially targeted. Calhoun (1947) found 79 specimens (8.1%) with a brown tinged bib among 974 adult male specimens from the US kept in several American museums. In a sample of 460 adult male specimens from the UK kept in three different British collections (NMS, NHM and HZM) 25 specimens (5.4%) with a brownish bib were found.

According to the above the deposit of phaeomelanin in parts of the plumage that normally contain only eumelanin is quite common in the House Sparrow, and is very

likely hereditary. The same mutation is found in the Zebra Finch and is called 'orange-breasted'. In this species the inheritance is recessive so therefore we can assume that orange-breasted in the House-Sparrow is also based on a recessive mutation.

As this mutation affects mainly the black markings, the effect is not visible in the female House Sparrow. In many male specimens the abnormal phaeomelanin distribution in the bib goes together with an increased phaeomelanin deposit in the plumage of the neck and back. Some even have scattered brown feathers on the head and/or rump.

A mutation that causes the opposite effect: the deposit of eumelanin in parts of the plumage that normally contain phaeomelanin only, also occurs. In the Zebra Finch this mutation is known as 'black cheek' and the inheritance is recessive. In the House Sparrow one adult male specimen was found in the sample. The author is not familiar with other records of this mutation occurring in the wild or kept in captivity. The normally deep reddish-brown parts (lesser wing coverts and supercilium/neck plumage) are changed into black while the phaeomelanin in the rest of the plumage is reduced. Given the fact that in female House Sparrows no plumage parts with deep reddish-brown phaeomelanin are present, we can expect that this mutation does not clearly express itself in females.

RESULTS

The results presented in table 1 are based exclusively on the sample of 362 museum specimens. Not all of the above described aberrations are found in the sample (e.g. Acromelanism and Melanism Category 1). Also the artificial discolorations and the aberrant brown in the bib are deliberately not included in the sample. Mutations in the Dilution group, especially the pastel-group, are often difficult to distinguish from each other in museum specimens and therefore they are not further separated into distinct mutations.

It is impossible to make the distinction between Albino and 100% Leucism in museum specimens when the eye colour is not mentioned on the label. Fledgling birds were deemed to be Albino. However, any totally white bird in a later life stage and with no eye colour mentioned on the label was assigned to Leucism, as an Albino would not have survived long after fledging. Therefore it is unlikely that any Albino is counted for Leucism. The proportion designates as Albino however may be slightly exaggerated as there may be a few leucistic fledglings among them.

Likewise, an occasional specimen in the final stage of Progressive Greying, and therefore completely white, might be wrongly identified as 100% Leucism. Usually the two can be distinguished, as House Sparrows with Progressive Greying normally don't lose the pigments in their bare parts. However, the pale bill colour of females outside the breeding season is sometimes difficult to distinguish from a unpigmented bill of a leucistic bird in museum specimens.

Although the percentages are presumably not entirely accurate, on average it gives a good idea of the ratio between the different aberrations.

With 34.5% (125 specimens) Progressive Greying is the most common colour aberration found in the sample, and Brown is the second-most common (93 specimens = 25.7%). Given that most forms of Progressive Greying are probably not heritable, Brown is therefore the most common heritable aberration (mutation) found in the House Sparrow.

Dilution (56 specimens = 15.5%) seems to be quite common too but one has to keep in mind that many different distinct mutations occur that all cause a form of quantitative melanin reduction. Individually, these different mutations are all fairly rare. Within the pastel-group (42 specimens), 12 birds (3.3%) had the mutation causing a strong but equal reduction of both melanins with the general appearance being silvery-grey as a result (see fig. 19). Only four 'whitish' birds with clearly visible darker patterns (1.1%) were found whose plumage colour was due to the mutation that strongly reduces eumelanin and almost completely reduces phaeomelanin (see fig. 20). The remaining 26 specimens (7.2%) were not clearly distinguishable as distinct mutations but the majority probably belong to the variable pastel-mutation earlier described.

Within the isabel-group (14 specimens = 3.9%), 10 birds (2.8%) belonged to the recessive, eumelanin-reducing mutation, and four specimens (1.1%) were afflicted with the dominant form. Although mutations in the pastel-group are more common than in the isabel-group, the distinctive mutations in both groups are all quite rare. The Ino-mutation therefore appears to be the second-most common mutation (38 specimens = 10.5%). Although there are two distinguishable forms, a light and a dark, we consider them as a whole because the same gene is involved.

The commonness of this mutation is probably due to the fact that the gene is located on the sex chromosome and therefore females need only one gene to express the mutation (see under Brown for further explanation). Records of Ino-dark females breeding in the wild are known and therefore one would expect to have found a higher number of these in the sample. On the other hand the dark form of Ino is not very obviously different from normal-coloured and therefore might well be less targeted by collectors than other colour aberrations.

Albino is clearly different from normal-coloured and one can assume that most specimens noticed in the past would have been targeted. Because of their short life-span after fledging however, few Albinos live long enough to fall prey to the collector. Nevertheless 17 Albino specimens (4.7%) were found in the sample.

Leucism (the heritable absence of pigment cells) is rare in the House Sparrow and only 12 specimens (3.3%) were encountered. Three of them (0.8%) were Partial Leucistic. The others (2.5%) were all 100% Leucistic.

Besides the abnormal phaeomelanin deposition in the bib, heritable Melanism (an abnormal deposit of melanin) in the House Sparrow is rather rare. 11 specimens (3%)

were found with an increase of eumelanin all over (Category 2) and only one specimen (0.3%) with the phaeomelanin replaced with eumelanin.

Finally, nine specimens could not be assigned to any of the above described mutations. Five of these specimens showed an aberration known among bird keepers as Grizzle 9 see fig. 40). In Grizzle each feather is an intermixture of white, as some barbs are white and others are normal-coloured. Comparable mutations are found in the Domesticated Pigeon, the Domesticated Canary *Serinus canaria* and the Zebra Finch. In these species, with age, after every moult, the number of white barbs increases until finally the bird will become almost completely white (or yellow in the case of the Canary). In that respect Grizzle seems to be a form of Progressive Greying. However, Grizzle is already evident in the juvenile plumage and therefore differs from Progressive Greying. As Grizzle is heritable in the species mentioned above, it can also be assumed to be heritable in the House Sparrow. The other four unknown aberrations were probably all caused by non-heritable factors as they all show features of different aberrations combined in each bird. Two of them show an incomplete melanin synthesis in combination with an abnormal deposit of melanin (specimens in the American Museum of Natural history). One specimen has distinguishing marks of a complete eumelanin reduction but also some normal-coloured feathers (specimen in National Museums of Scotland, see fig. 41). The last bird is mainly white (or yellowish because of carotenoid colouration) with some diluted feathers and some full coloured feathers (specimen in the Natural History Museum, Tring, see fig. 42).

In summary, Brown is the most common heritable colour aberration in the House Sparrow, followed by Ino and Albino. Although Dilution (a quantitative reduction of melanins) as an aberration is more common than Ino or Albino, the distinct, single mutations causing a diluted phenotype are all less common.

Brown, Ino and Albino are all mutations that cause a defect in the melanin synthesis while other mutations affect the melanin transfer: from the pigment cells into the feather cells (Dilution), the distribution between eu- and phaeomelanin in the plumage (Melanism), or the absence of melanin cells (Leucism).

Normal melanin syntheses is dependent on the enzyme tyrosinase and evidently genes affecting tyrosinase mutate easily in the House Sparrow.

As Progressive Greying seems to be non-heritable and probably caused by external factors, it is worth discussing in more detail. First, as the amount of white feathers is progressive, there is a huge difference in the amount between the specimens. Therefore the 125 specimens were categorised into four groups: up to 25% white feathers, up to 50%, up to 75% and up to 100%. Most birds were found, as one can expect, in the category up to 25% white feathers (44 specimens = 35% of all birds affected by Progressive Greying). Thirty-eight birds (30.5%) had between 25 and 50% white feathers, and 23 specimens (18.5 %) were more than half white. Finally 20 sparrows (16%) had almost reached the final stage of Progressive Greying and had therefore three quarters or more of their plumage white.

No remarkable sexual difference in frequency was found although slightly more females appeared to be affected. All birds, without exception, had an adult plumage (House Sparrows have a complete post-juvenile moult and cannot be aged reliably beyond 'adult'), and juvenile plumage was not found in specimens affected by Progressive Greying. This also proves that the loss of pigment begins only after a certain age.

Lastly, only 63 birds (17.4%) within the sample could be defined as fledglings or juvenile. So 82.6% of the birds passed beyond these critical life stages in spite their aberrant colour. Common belief that birds with colour aberrations do not survive for long in the wild due to being targeted by predators might be proven wrong with these results (humans are not taken into account as being predators).

DISCUSSION

Several studies on House Sparrow populations in the past have also recorded the frequency of colour aberrations. Unfortunately the different aberrations were never properly defined in these studies. However, given that, according to the results above Progressive Greying is the most common aberration, one can assume that the majority of the aberrations named White, Albino or Partial Albino in these studies were in fact a form of Progressive Greying. Selander and Johnston (1967) reported that only 'partial albinism' was found in their sample of 2,271 specimens from Europe and North America, "varying in extent from a single feather to a condition in which approximately one-third of the plumage is white". In this sample 1.89% of the birds had one or more flights or tail feathers white, or two or more contour feathers white. Ilyenko (1960) found in a sample of 3,605 specimens from Moscow and the rural area of Chashnikov that 1.8% was 'partial albino'. The same percentage, 1.83%, of birds with white feathers was found by Holyoak (1974) in a sample of 2,616 birds seen in and around London. All of Ilyenko's birds with white feathers were found in urban Moscow and none in the rural area. Also Holyoak found the highest frequency of birds with white feathers in urban London (2.6%). In suburban areas he found a percentage of 1.1%, while in rural areas only 0.2% had some white feathers.

Lastly Ilyenko reported that white feathers were more than twice as frequent in females than in males. In the sample of Selander and Johnston there was no significant sexual difference in frequency although the amount of white feathers was more extensive in females. None of the authors found white feathers in juvenile birds.

The results from the studies mentioned above agree with the results found in our study: Progressive Greying is quite common, it occurs only in adults and it seems to be more common in females. Except in Holyoak's sample no other aberrations were found by the other authors. Among his 2,616 House Sparrows Holyoaks recorded four birds he named 'Diluted' without defining the term. One can assume they were actually Brown, but the real identity of these four aberrant coloured birds is unknown.

Progressive Greying does seem to be non-heritable or, at least, it is not simply

based on one changed gene, while the other aberrations are all caused by a single gene-mutation and therefore are heritable. It is fair to conclude that the mutations are far less common than Progressive Greying. Given the fact that it is common, non-heritable and mainly found in urban areas, the cause of Progressive Greying appears to be an external factor related to human activity. It might be indirectly related to the diet or perhaps the pollution in the air? Further research is necessary to discover the nature of the true cause of Progressive Greying, especially as it is also common in several other species living in urban areas like the Eurasian Blackbird and the Eurasian Jackdaw.

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Table 1. Colour aberrations found in the House Sparrow based on a sample of 362 museum specimens

MUTATION	EFFECT ON COLOUR	NUMBER	PERCENTAGE
ALBINO = Total lack of both melanins in feathers, eyes and skin due to the heritable absence of the enzyme tyrosinase in the pigment cells.	All-white plumage all over, red eyes and yellow feet and bill.	17	4.7
Leucism		12	3.3
Leucism 100% = the lack of both melanins from all parts of the plumage and skin due to the heritable absence of pigment cells from all of the skin areas	All-white plumage all over, yellow bill and feet and normal coloured eyes.	9	2.5
Partial Leucism = the lack of both melanins from parts of the plumage and skin due to the heritable absence of pigment cells from some of the skin areas	All-white feathers next to normal-coloured ones. White pattern bilaterally symmetrical. Yellow bill and feet **or** normal coloured bill and feet and normal-coloured eyes.	3	0.8
PROGRESSIVE GREYING = the lack of both melanins with age in parts of the plumage due to progressive loss of pigment cells in the skin. Most forms seem to be non-heritable.	All-white plumage all over **or** all-white feathers mixed randomly with normal-coloured ones. Normal-coloured bill, feet and eyes	125	34.5
	Upto 25% white feathers.	44	12
	Between 25 and 50% white feathers.	38	10.5
	Between 50 and 75% white feathers.	23	6.5
	Between 75 and 100% white feathers.	20	5.5
BROWN = Qualitative reduction of eumelanin due to incomplete synthesis (oxidation) of eumelanin. Phaeomelanin unaffected.	Black becomes brown and brown becomes light-brown while reddish/ yellowish brown stays unaffected.	93	25.7
Dilution		56	15.5
Dilution – pastel = Quantitative reduction of both melanins. Multiple mutations are known to cause comparable phenotypes.	Black and brown becomes silvery grey and reddish/yellowish brown becomes buff/cream	42	11.6
Dilution – isabel = Quantitative reduction of eumelanin only. Two mutations are known for causing comparable phenotypes	Black and brown becomes silvery grey while reddish/ yellowish brown stays unaffected.	14	3.9

INO		38	10.5
Ino – light = Strong qualitative reduction of both melanins due to incomplete synthesis (oxidation) of both melanins.	Black and brown becomes pale cream and reddish/yellowish brown becomes hardly visible. Eyes pinkish; yellow feet and bill.	22	6.0
Ino – dark = Qualitative reduction of both melanins due to incomplete synthesis (oxidation) of both melanins.	Black and brown becomes pale brown and reddish/yellowish brown becomes hardly visible. Eyes dark-pinkish; yellowish feet and bill.	16	4.5
MELANISM = Abnormal deposit of melanin	Increase of black and/or reddish brown	12	3.3
GRIZZLE = lack of both melanins in parts of the feather barbs in each feather.	Grizzled-white plumage all over. Normal-coloured bill, feet and eyes.	5	1.4
Coloured differently		4	1.1
TOTAL NUMBER ABERRANT COLOURED SPECIMENS		362	100.0

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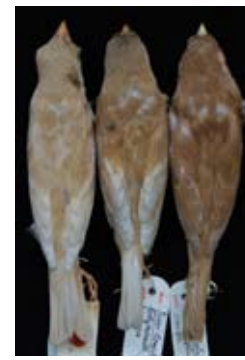
1. White sparrow *Fringilla candidans* in Sparrman, 1786, Museum Carlsonianum. Photo: Harry Taylor, The Natural History Museum.



2. Brown House Sparrows, three adult females. Aberrant coloured feathers are easily bleached by light. Old plumage (left) can be much lighter in colour than fresh plumage (right). Specimens in the collection of the Natural History Museum, Tring. Photo: Hein van Grouw.

3. An examination of plumage areas shielded from daylight eg. the inner webs of flight feathers, reveals the unaffected aberrant colour. Brown House Sparrows, females. Photo: Hein van Grouw.

4. House Sparrows, adult male, adult female and juvenile. Photos: Ryan Clark.

5. House Sparrows, two adult males collected at the same time of the year. The right bird clearly shows yellow carotenoid colouration. Specimens in the collection of the Natural History Museum, Tring. Photo: Hein van Grouw.

6. Juvenile House Sparrow, Albino, July 2009, Dirleton, Lothian, Scotland. Photos: William Edmond.

7. House Sparrow, adult female, Albino, hatched in the wild but kept in captivity. Photo: Rudy Driesmans.

8. House Sparrow, adult males, Acromelanistic. Bred and kept in captivity. **A**: Melanin production mainly in the body extremeties. **B:** bird moulted during a cold period resulting in sporadic production of melanin in other parts of the plumage. Photos: Pieter van den Hooven.

9. House Sparrow, adult female, March 2011, Diksmuide, Belgium. White feathers caused by Progressive Greying (about 25% white feathers). Photo: Rudi Debruyne.

10. House Sparrow, adult male, April 2010, Garlieston, Wigtown, Scotland. White feathers caused by Progressive Greying (about 50% white feathers). Photo: Gavin Chambers.

11. House Sparrow, adult female. White feathers caused by Progressive Greying. Typical pattern in which the body plumage is affected first. Specimen in the Natural History Museum, Tring. Photo: Harry Taylor BMNH.

12. House Sparrow, adult female, hatched in the wild but kept in captivety. White feathers caused by Progressive Greying. Typical pattern in which the flight feathers are affected first. Photo: Pieter van den Hooven.

13. House Sparrows, five adult females showing progressive Greying in different degrees. Specimens in the American Museum of Natural History. Photo: Hein van Grouw

14. Juvenile House Sparrow, May 2011, Zwolle, The Netherlands. Loss of pigment as a result of physical disorders. Photo: Jan van Dijk.

15. Brown House Sparrow, adult female, 11 May 2010, Germany. Old plumage and therefore strongly bleached by the light. Photo: Aat Bender.

16. Brown House Sparrow, adult female, bred and kept in captivety. Fresh plumage. Photo: Pieter van den Hooven.

17. Juvenile House Sparrow, Brown, 24 July 2010, St. Mary's, Isles of Scilly, England. Photo: Martin Goodey.

18. Brown House Sparrow, adult male, bred and kept in captivity. Because Brown is recessive in inheritance and the gene is located at the X-chromosoom, males are not likely to be found in the wild. Photo: Pieter van den Hooven.

19. House Sparrow, adult male, Dilution – pastel, one of the distinct forms in the pastel-group; a strong but equal reduction of both melanins. January 2011, Maarn, The Netherlands. Photo: Erwin van Laar.

20. House Sparrow, adult male and female, Dilution – pastel, one of the distinct forms in the pastel-group; strong reduction of eumelanin while the phaeomelanin is almost lacking completely. Bred and kept in captivity. Photos: Pieter van den Hooven.

21. House Sparrows, three juveniles and an adult female, 29 June 2011, Ooijpolder, Nijmegen, The Netherlands. Two juveniles, from the same nest, showing the variable expression of melanin reduction within this pastel-mutation. Photo: Harvey van Diek.

22. House Sparrow, adult male and female, Dilution – pastel, exhibiting the average degree of melanin reduction within this variable pastel-mutation. In this mutation the black eumelanin is proportionally less affected than the phaeomelanin and brown eumelanin. Bred and kept in capetivity. Photo: Pieter van den Hooven.

23. House Sparrow, female (post-juvenile moult almost completed), Oslo, Norway, September 2009. Dilution – pastel, exhibiting a stronger degree of melanin reduction within this variable pastel-mutation. Photo: Chris van Rijswijk.

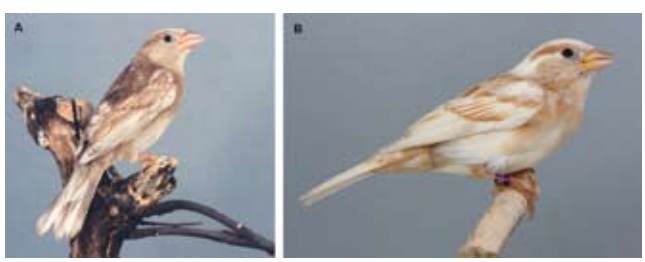
24. House Sparrows, adult female and adult male, both Diluted – pastel, and likely another distinct mutation within the pastel-group. Male in old and bleached plumage. Some new feathers show the true colour of this mutation. Specimens in the American Museum of Natural History (female) and the Natural History Museum, Tring (male). Photo: Hein van Grouw.

25. House Sparrow, adult male and female, Diluted – pastel. Another distinct form within the pastel-group. The eumelanin is affected more than the phaeomelanin. Specimens in the American Museum of Natural History. Photo: Hein van Grouw.

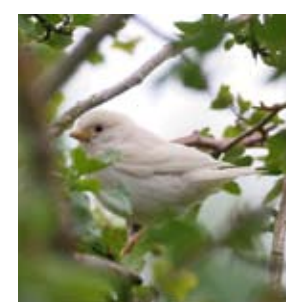
26. House Sparrows, adult female, juvenile male and adult male, Diluted – isabel. In this distinct form the degree of eumelanin reduction is always the same. Specimens in the American Museum of Natural History (female) and the Natural History Museum, Tring (males). Photo: Hein van Grouw.

27. House Sparrow, adult males, Diluted – isabel, bred and kept in captivity. This distinct mutation in the isabel-group can express a variable degree of eumelanin reduction between individuals but the reduction is always strong to almost complete. **A:** This bird still has some visible eumelanin left. **B:** This is genetically the same mutation as the bird in Figure 27A. However, in this individual the reduction of eumelanin is almost complete and therefore it can been termed as schizochroism. Note that eumelanin is still present in the eyes, beak and feet. Photo: Pieter van den Hooven.

29. House Sparrow, adult female, Ino – light form, bred and kept in captivity. Photo: Pieter van den Hooven.



28. House Sparrow, adult females, Diluted – isabel, bred and kept in captivity. This is genetically the same mutation as the birds in Figure 27. **A:** In this bird is still a fair amount of eumelanin left. **B:** In this bird the visible eumelanin is completely reduced from the plumage. Note that eumelanin is still present in the eyes, beak and feet. Photo: Pieter van den Hooven.



30. Juvenile House Sparrow, Ino – light form, July 2007, Lolland, Denmark. Photo: Mogens Hansen.

31. House Sparrow, adult female, Ino – dark form, bred and kept in captivity. Photo: Pieter van den Hooven.

32. **A**: House Sparrow, adult male, Melanism Category 1 in partially worn breeding plumage, June 2012, Mitcham, Surrey, England. **B:** House Sparrow, male, Melanism Category 1 in fresh plumage with buff fringes, August 2012, Mitcham, Surrey UK. Photos: Paul Davis

33. House Sparrow, adult male, Melanism Category 1 in partially worn breeding plumage, June 2011, Andijk, The Netherlands. Photos: Stichting Witte Mus.

34. House Sparrow, adult male, December 2011, Ross-shire, Scotland. Pink colour due to carotenoids in the food. Photo: Ian Collier.

35. *Passer domesticus* var. *Scheffneri*, a dark coloured House Sparrow specimen thought by Dybowski to be a distinct variety. Plate from Dybowsk 1915.

36. House Sparrow, adult female, Melanism Category 2, January 2006, Longecourt en Plaine, France. Photo: Michel Bailly.

37. House Sparrow, adult male, Melanism category 3 with a clear reddish-brown bib due to an abnormal deposit of phaeomelanin. Specimen part of van Heurn's collection and now in NCB Naturalis, Leiden. Photo: Eelco Kruidenier.

38. House Sparrows, adult males. Melanism category 3 (brown bib) on the left and normal-coloured on the right. Notice that the increase of phaeomelanin is not only in the bib but also in the neck and mantle plumage. Speciemens in the collection of the Natural History Museum, Tring. Photos: Hein van Grouw.

39. House Sparrow, adult male, Melanism category 3. Another distinct form in this category; in this case the phaeomelanin is replaced with eumelanin. Specimen in the Niedersächsisches Landesmuseum, Hannover. Photo: Niedersächsisches Landesmuseum.

40. House Sparrow, adult male. Grizzle. The whitish appearance is due to the an intermixture in each feather of white barbs and normal coloured barbs. Specimen in the collection of the Museu di Storia Naturale, Florence. Photo: Fausto Barbagli.

41. House Sparrow, adult male. Aberrant colour probably due to a non-heritable factor. Plumage has distinguishing marks of a complete eumelanin reduction while a few primaries are normal coloured. Specimen in the National Museums of Scotland, Edinburgh. Photo: Hein van Grouw.

42. House Sparrow, adult male. Aberrant colour probably due to a non-heritable factor. Plumage has distinguishing marks of a complete melanin reduction, Diltion, and also some normal-coloured feathers on the chin. Specimen in the Natural History Museum, Tring. Photo: Hein van Grouw.