White feathers in black birds

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Blackbird *Turdus merula* with progressive greying

Abstract The most common plumage abnormalities in birds involve some form of white feathering, ranging from birds with just a few white feathers to individuals that are completely white. The causes of aberrant white feathers are diverse and, in many cases, unknown. Some are heritable, based on simple, genetically determined changes in the pigmentation process. More commonly, the causes are less clear-cut and can include environmental conditions (particularly in relation to food availability), and the physical condition and/or age of the bird. In this paper, white feathering is explored in three common species: Carrion Crow *Corvus corone*, Hooded Crow *C. cornix* and Blackbird *Turdus merula*. Results from the BTO Abnormal Plumage Survey are summarised, and data from a museum-based study of Blackbirds with plumage abnormalities are reported. In all three species, partly white plumage is recorded regularly and is often referred to incorrectly as albinism or leucism.

Introduction

Aberrant white feathers in birds have always intrigued people, resulting in many published records in the ornithological literature. In these publications, a variety of names are used to identify and classify the pigment abnormalities. The terminology used is, however, often conflicting, confusing and incorrect. Most commonly, the terms albino, partial albino or leucistic are used for almost all different forms of aberrant white feathering, yet in only a tiny proportion of cases are they used correctly (Mahabal *et al.* 2016). A 'partial albino' is simply impossible, since albinos cannot produce melanin pigment at all. The true albino aberration is encountered far less often than is generally supposed. In fact, aberrant white feathers are hardly ever

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caused by albinism; typically, they are either a form of leucism or, more commonly, 'progressive greying'. Non-heritable causes, such as dietary imbalance, can also be responsible. This paper explores two of these abnormalities – progressive greying and dietary imbalance – on the basis of their occurrence in three common species: Carrion Crow *Corvus corone,* Hooded Crow *C. cornix* and Blackbird *Turdus merula.*

As a source of data on the occurrence of different plumage abnormalities, the results of the BTO's Abnormal Plumage Survey are reported. This survey began in December 2011, in conjunction with the familiar Garden BirdWatch (GBW) survey, in which several thousand volunteers across the UK record weekly lists of the birds in their garden, throughout the year; www.bto.org/volunteer-surveys/gbw). The Abnormal Plumage Survey aimed to find out more about the plumage abnormalities being seen by GBW participants.

For recording birds with aberrant white feathers, participants could select from three different types of aberration: melanism, leucism and albinism. Since many aberrations can be difficult to distinguish from each other without some experience, the BTO used 'Leucism' as an umbrella term to encompass a range of plumage irregularities involving lighter, white, or partially white plumage. Importantly, however, the 'Description' section of each record – a free text field in which the participant is asked to describe the bird's appearance in detail – turned out to be extremely helpful and it was by analysing these descriptions that (most of) the aberrations could be distinguished and categorised more accurately.

The records used for this paper spanned a period of five years, from December 2011 to November 2016. By November 2016, about 4,350 records, involving over 70 species, had been received. Easily the most commonly reported species was Blackbird, with over 1,550 records, followed by House Sparrow *Passer domesticus*, Jackdaw *Coloeus monedula* and Carrion Crow. More than 30% of respondents have been watching birds in their garden for over 20 years, showing that many records are coming from areas that are routinely observed, and over 90% of gardens were classed as suburban or rural.

For Carrion Crow, the survey received 198 records, but ten of these lacked further description so the data from 188 records were used. For Blackbird, the data from 1,516 records (1,588 in total minus 72 without further description) were used. For most records, a more accurate definition for each aberration could be assigned, since many descriptions gave sufficient clues to make a positive identification possible. Many records were accompanied by a photograph, which made identification easier and more accurate.

Hans-Martin Berg, NMW

171. Juvenile Blackbird *Turdus merula* showing leucism in its typical form: the face, primaries, belly and feet lack pigment (specimen at Natural History Museum Vienna, NMW 13424). Note that the white feathering is already present in the bird's first (juvenile) plumage, and this pattern will not change during later life.

White feathers

Leucism, from the Greek *leukos* (for white), can be defined as the lack of melanin from all or parts of the plumage and skin. Leucism thus occurs in different forms: all-white and pied. In cases of all-white plumage, no pigment cells at all are present in the skin to provide the growing feathers with melanin pigment. In cases of Partial leucism, the pigment cells are absent from only parts of the skin, leaving only these areas without pigmentation. Owing to the way the early pigment cells (melanoblasts) migrate from their embryonic origin into the rest of the body (see van Grouw 2013), the white pattern caused by Partial leucism is normally patchy and bilaterally symmetrical – typical examples include a few white outer flight feathers on both wings and/or some white feathers in the face. In more extreme cases, the entire face, all the primaries, the belly and the feet lack pigment (plate 171). Fully white birds may cause confusion with an albino, but eye colour is the most obvious difference: in albino the eyes are red, in leucism eye colour is unaffected. The underlying causes of the two aberrations are completely different. An albino has pigment cells but lacks the necessary enzyme (tyrosinase) to start melanin synthesis, whereas a leucistic bird lacks pigment cells altogether and is thus unable to provide its feathers with melanin (see van Grouw 2014). Leucism is congenital (present from birth) and heritable.

Anne Riley

172. Adult male Blackbird, Yorkshire, April 2011. Progressive greying is a progressive loss of melanin pigment with each successive moult. In the early stages the affected feathers are often spread randomly over any part of the plumage, but finally the bird can become entirely white (plate 173).

Tim Heathfield

173. Blackbirds that become (almost) entirely white often also lose the melanin from their bare parts (bill and feet). One or two remaining pigmented feathers in these birds are evidence that their white plumage is the result of progressive greying in its final stages. Owing to the loss of melanin pigment in the skin, the bill colour in both sexes is yellow.

A far more common cause of white feathers is 'progressive

greying' (van Grouw 2012b, 2013), which is the progressive loss of melanin pigment with each successive moult. The loss of pigment can be the result of a gradual reduction of tyrosinase activity in the pigment cells, but also of the pigment cells dying off. In the early stages of progressive greying, the affected feathers are usually spread randomly all over the bird (plate 172), but finally the entire plumage can become white (plate 173). Different forms of progressive greying occur and, for many, the causes are still unknown. In some cases, the cause may be simple Mendelian (straightforward) inheritance (van Grouw & Hume 2016), but these cases seem to be rare. More commonly, the condition may be linked with factors such as environmental conditions or age, while the progressive loss of pigment cells may also be due to heritable disorders such as vitiligo (pigment disease).

Austin Brady

174. Carrion Crow *Corvus corone*, after its partial post-juvenile moult, UK, March 2016. The tail feathers and larger wing feathers are still juvenile feathers, and these clearly show a lack of pigment, as a result of dietary imbalance.

External, non-heritable factors such as illness or dietary imbalance can also result in pigment loss (plate 174). In such cases, the bird is unable to extract the necessary nutrients from its food, which affects melanin synthesis. The bird's pigmentation will return to normal as soon as the external causes are removed. Progressive greying was initially thought to be related to diet (Rollin 1964), but whereas a dietary deficiency causes wide white bars in the feathers and also often poor feather structure, in progressive greying the feathers are completely white and their structure is unaffected. Dietary imbalance is generally rare in wild birds, but one exception seems to be Carrion and Hooded Crows, since individuals with pigment loss resulting from dietary deficiency are not uncommon.

Why are these crows particularly affected? Many other groups of birds include species that are habitual scavengers, including wildfowl, gulls, some raptors (such as kites *Milvus*) and passerines (such as sparrows). Plumage aberrations seem markedly less common in many of these groups than in the crows. Perhaps one reason for this is that these other species are in reality more omnivorous than the crows, which may require much more animal protein to grow healthy feathers. This distinction may operate even within the corvid family. From personal experience, I know that hand-reared juvenile Carrion Crows do not thrive on a diet that juvenile Jackdaws and Rooks *C. frugilegus* develop very well on. Carrion and Hooded Crows are perhaps far less omnivorous than often assumed and thus more prone to developmental problems (including loss of pigment) owing to diet imbalances.

Harry Taylor, NHM

175. The degree of white feathering depends on the stage of progressive greying and can be divided into four categories: clockwise from top left, <25% of the total plumage, 25–50%, 50–75% and 75–100% (specimens at the Natural History Museum, Tring, respectively NHMUK 1987.24.315, NHMUK 1987.24.318, NHMUK 1996.42.2330, NHMUK 2014.73.139).

Blackbirds and progressive greying with age

Although we know about feather pigmentation and how mutations can change a bird's colour, there are still aberrations for which the cause remains unclear. One of these is progressive greying: the occurrence of a seemingly random spattering of white feathers, giving the bird a pied or variegated appearance. At least 1,371 of the 1,516 aberrant Blackbirds (90%) recorded in the BTO survey were birds with some form of progressive greying. The sex ratio within this subset is unknown as birds that are more white than coloured are often difficult to sex reliably in the field.

During many years of personal research to identify and record the many aberrantly plumaged bird specimens in museums all over Europe (and in America), I noticed that most specimens with white feathers were at odds with any of the known forms of heritable leucism found in domesticated birds like pigeons, budgerigars, canaries and zebra finches. Almost all of the aberrant museum specimens had white feathers randomly scattered throughout their plumage. Some had only a few white feathers, others had more, while others were almost completely white (plate 175). None of them seemed to follow the normally patchy and bilaterally symmetrical pattern of leucism. Furthermore, I found no juvenile pied birds, even though the white pattern caused by partial leucism is already apparent in juvenile plumage, and does not change with age. However, the diversity in the degree of white plumage found in the specimens, from hardly any to almost totally white, seemed to suggest that in this aberration the numbers of white feathers increases with age.

Given that aberrantly coloured birds were often targeted by collectors in the past, it seems likely that at least some young birds would

have become study skins before reaching adulthood. So, the absence of juvenile birds with white feathers among museum samples supports the theory that this loss of pigment occurs in later life. However, museum specimens obviously show only one plumage, and do not provide data on how the condition alters through successive moults in individual birds. The BTO survey provides some useful evidence in this regard, charting the changes in resident individual Blackbirds. A typical comment reported was: 'the resident Blackbird with white feathers becomes whiter every year', proving that a progressive loss of pigment over time is more than just conjecture (plates 176 & 177). Further evidence was already available from ringers. In the late 1950s, Band (1956) reported that a 'normal' adult male Blackbird trapped in Lancashire on 24th November 1950 was retrapped on 4th December 1955 when 'there were considerable patches of white over most of its plumage'. In response to Band's observation, several other ringers also reported cases of 'albinism related to age' in the Blackbird (Foott 1956; Spencer 1956; Wigzell 1956). Spencer (1956) had noticed that the birds became whiter over successive years and called it 'progressive albinism'. Rankin (1954) had also reported an increase of white feathers over time.

Bill Barnett

Bill Barnett

176 & 177. Male Blackbird photographed in September 2012 (176) and September 2013 (177) showing a significant increase of white feathers during the intervening year due to progressive greying. Note, however, that the bare parts (the legs and feet) are not (yet?) affected.

Museum data on Blackbirds

The information regarding museum specimens presented below is based on my examination of 221 aberrant Blackbird specimens in several museum collections (see Acknowledgments). Although aberrant birds were often targeted by collectors, and the number of such specimens compared with normally plumaged birds in collections does not represent the ratio in the wild, we can assume that the ratio *between* the different aberrations is quite representative; any unusual bird tended to be collected, regardless of its colour.

Progressive greying was the most common colour aberration found in the sample (147 specimens, or 66.5%; table 1). The other 74 specimens were assigned as follows: brown (8.6%), ino (6.8%), dilution (6.3%), grizzle (3.6%), melanism (3.2%), albinism (2.7%) and leucism (2.3%). Given that most forms of progressive greying are probably not heritable, Brown was therefore the most common heritable aberration found in this sample of Blackbirds.

Since the degree of white feathering depends on the stage of progressive greying, the 147 specimens were categorised into four groups: up to 25% of the total plumage, up to 50%, up to 75% and up to 100% (plate 175). The majority, 89 specimens (61%) were

Table 1. Colour aberrations found in the Blackbird *Turdus merula*, based on a sample of 221 museum specimens.

MUTATION (definitions based on van Grouw 2013)	EFFECT ON COLOUR	NO.	%
ALBINISM Complete lack of melanin in feathers, eyes and skin due to the heritable absence of the enzyme tyrosinase in the pigment cells.	All-white plumage, red eyes, yellowish bill and pink feet.	**6**	**2.7**
LEUCISM		**5**	**2.3**
Complete leucism Lack of melanin from all parts of the plumage and skin owing to the heritable absence of pigment cells from all of the skin areas.	All-white plumage, yellow bill, pink feet, normally coloured eyes.	0	0
Partial leucism Lack of both melanins from parts of the plumage and skin owing to the heritable absence of pigment cells from some areas of skin.	All-white feathers adjacent to normally coloured ones. White pattern bilaterally symmetrical. Yellow bill and pink feet **or** normally coloured bill and feet; normally coloured eyes.	5	0.8
PROGRESSIVE GREYING Lack of melanin in parts of the plumage owing to progressive loss of pigment with age. Most forms seem to be non-heritable.	All-white plumage **or** all-white feathers mixed randomly with normally coloured ones. Yellow bill and pink feet **or** normal coloured bill and feet; normally coloured eyes.	**147**	**66.5**
	<25% white feathers.	89	40.3
	25–50% white feathers.	26	11.8
	50–75% white feathers.	12	5.4
	75–100% white feathers.	20	9.0
BROWN Qualitative reduction of eumelanin owing to incomplete synthesis (oxidation) of eumelanin. Phaeomelanin unaffected. Mutation is sex-linked and therefore only female birds in the sample.	Black becomes brown and brown becomes light-brown; reddish-/yellowish-brown is unaffected.	**19**	**8.6**
DILUTION Quantitative reduction of one or both melanins. Since male Blackbirds have eumelanin only, certain forms of dilution, e.g. pastel and isabel, cannot be separated without breeding tests. However, at least three different forms are present in the sample.	Black and brown (eumelanin) becomes silvery grey; reddish-/yellowish-brown (phaeomelanin) may or may not be affected.	**14**	**6.3**
INO		**15**	**6.8**
Ino – light Strong qualitative reduction of both melanins due to incomplete synthesis (oxidation) of both melanins. Mutation is sex-linked and therefore only female birds in the sample.	Black and brown becomes pale cream; reddish-/yellowish-brown becomes hardly visible. Yellow feet and bill; eyes pinkish.	10	4.5
Ino – dark Qualitative reduction of both melanins due to incomplete synthesis (oxidation) of both melanins. Mutation is sex-linked and therefore only female birds in the sample.	Black and brown becomes pale brown; reddish-/yellowish-brown becomes hardly visible. Yellowish feet and bill; eyes dark pinkish.	5	2.3
MELANISM Abnormal deposit of melanin.	Increase of black and/or reddish-brown.	**7**	**3.2**
GRIZZLE Lack of both melanins in part of the feather barbs in each feather.	Grizzled-white plumage. Pink feet, yellow bill and normally coloured eyes.	**8**	**3.6**
Total number aberrant specimens		**221**	**100**

in the first category, up to 25%; 26 birds (17.7%) had between 25% and 50% white feathers; 12 (8.2 %) were more than half white and 20 (13.6%) had 75% or more of their plumage white.

The large percentage of birds in the early stage is easy to explain. A bird affected by progressive greying has to moult several times before becoming entirely white, but any aberrant Blackbird with a few odd white feathers would have been desirable for collectors. Furthermore, it can be assumed that relatively few birds become old enough to reach the final stages. Annual mortality of adult Blackbirds varies between 34% and 69%, depending on habitat and year (Simms 1978), but it may be higher in urban than rural areas (Snow 1988). All specimens examined were in adult plumage, and about three-quarters were males (109 males, 35 females and three unknown). For the fourth category, up to 100% white feathers, the sex ratio is less clear as the three unidentified specimens belonged in this category (15 males, 2 females and 3 unknown) but it can be assumed to be similar to other categories.

Crows and loss of pigment as a result of diet

The occurrence of abnormal white feathering in the crows typically shows as whitish transverse bars in the flight feathers (plate 178); in more extreme cases, the wing-coverts and tail feathers are also affected. The first records of 'white wing-barring' in the Carrion Crow in Britain are from the early 1950s (Sage 1954, 1956a,b; Harrison 1957a,b). Both authors assumed the white wing-barring to be genetic in origin and J. M. Harrison believed it was a symptom of an 'ancestral' plumage in the Corvidae. However, C. J. O. Harrison (1963) considered the loss of pigment in Carrion Crows to be diet-related, stating that the species 'seems particularly prone to such defect, especially in urban or suburban areas where the principal feeding places are often rubbish tips, and the diet is likely to be abnormal or deficient.' Sage (1964) disagreed, but the evidence gathered subsequently suggests that C. J. O. Harrison was correct.

Slagsvold *et al.* (1988) investigated the causes of white wing-barring in Hooded Crows in Norway. They concluded that the condition (which they misleadingly labelled 'partial albinism') was primarily related to food availability during the nestling stage rather than to any genetic factors. Dietary imbalance was also found to be the cause of white wing-barring in Carrion Crows in the Netherlands, Germany and France (Terluin 1996, 1998, 2009; Malher 2003; Bosch 2004).

The effects of dietary imbalance

The white wing-bars in crows are often compared with fault-bars, but in fact fault-bars are a subset of the wider category of white wing-barring. Fault-bars are defined as interruptions in feather growth caused by a temporary lack of the required nutrients. As a result, the structure of the feather is incompletely developed in the corresponding areas, appearing as an almost transparent line or lines right across the feather. Fault-bars weaken the feather considerably, owing to the incomplete development of the shaft and barbs. Although fault-bars can be accompanied by narrow lines where pigment is lacking, the feathers of the crows being discussed here often lack

Harry Taylor, NHM

178. Carrion Crow wing showing the effects of moderate dietary imbalance in juvenile plumage (specimen at Natural History Museum, Tring, NHMUK 2016.28.1). Since the juvenile feathers grow simultaneously, the loss of pigment will show in the same part of each feather and form the continuous white bars in the open wing.

Harry Taylor, NHM

179. Carrion Crow wing, showing a more severe effect of dietary imbalance in its juvenile feathers adjacent to newly moulted and unaffected adult-type inner primaries (specimen at Natural History Museum, Tring, NHMUK 2016.28.4).

pigment over more than half of their length. Close examination reveals the presence of fault-bars, but also that the loss of pigment extends over a much larger part of the feather.

The amino acids necessary for growth in general, and melanin development in particular, are tyrosine and lysine, and these need to be processed directly or indirectly from food. A lack of essential nutrients over an extended period during feather growth not only causes a loss of pigment, but the affected birds are also smaller than unaffected birds (Slagsvold *et al.* 1988; Terluin 2009). The most severely affected birds rarely survive their first year because of stunted growth and poor overall physical condition, while the poor quality of their feathers often reduces their capability to fly. Research has shown that affected birds also have smaller thyroid glands and that those which die early are nearly all females (Terluin 2009). Crows that survive their first year usually grow healthy and fully pigmented feathers during their first complete moult (plate 179).

Since the feathers of a nestling all grow at the same time, the loss of pigment will show in the same part of each feather to form the continuous white bars in the open wing (plate 178). Consequently, 'white wing-barring' as a result of dietary deficiency is found mainly in juvenile crows. Crows undergo only a partial post-juvenile moult in their first year of life, replacing their body plumage and some wing-coverts only and retaining their juvenile flight feathers (plate 174). Most records of 'adult' crows with white wing-barring are in fact birds early in their second calendar-year, before the first moult of the flight feathers in May or June.

Olivier Poncin

180. Adult Carrion Crow, Brussels, Belgium, April 2010, showing the result of dietary imbalance during part of the bird's last wing moult. The innermost primaries (P1–P3) were unaffected and show normal pigmentation. P4 shows the first signs of dietary deficiency and P5–P7 are strongly affected, being extensively white but also slightly shorter, as are the two outermost secondaries (S1–S2), which grew at the same time. The bird's feeding habits must subsequently have improved, since P8–P10 and the remaining secondaries are only weakly affected.

Although pigment loss resulting from dietary imbalance appears to be largely restricted to juveniles fed on inappropriate food by the parents during the nestling stage, the problem can also occur in older birds, even if they were not previously affected (plate 180). Slagsvold *et al.* (1988) examined almost 3,500

birds and found that 5% of juveniles showed pigment loss as a result of dietary deficiency compared with only 1% of adults. More recent observations from a study of Carrion Crows in Belgium showed a higher proportion of affected adults (van Grouw 2012a). Around 7.2% of all crows sampled (855 individuals) had white feathers, which is a remarkably high percentage (Olivier Poncin pers. comm.). In juveniles (n=668), 5.5% had white feathers, while no less than 8.9% of the adults (n=180) were affected. Birds with white feathering were also smaller (both weight and wing length were on average around 3% less than for normal birds).

Eddy Vaes

181. Adult Carrion Crow, Belgium, October 2015. Dietary imbalance in adult plumage results in a more patchy appearance than in juvenile plumage, since each individual feather has regrown at a different time.

In adult plumage, the pattern is generally different from the more regular 'white wing-barring' in juveniles and is best referred to more simply as a 'lack of pigment' (plate 181). It seems very likely that the plumage abnormalities of these Belgian crows stem from the birds' diet, considering that all the birds were caught in urban areas or next to a rubbish dump. However, further research is still necessary to examine the precise way(s) in which poor diet results in lack of pigment in crows.

BTO survey data

The BTO survey results suggest that pigment loss due to dietary imbalance, as described above, is the most common colour aberration in Carrion Crows in the UK. Plumage descriptions indicated that in 168 of the 188 records the white feathering was due to dietary deficiency. The other 20 records could be assigned to brown (6), ino (3), 'all-white' (5), acromelanism (4) and unknown (2); see van Grouw (2013) for more information about other colour mutations.

Discussion

Based on both the museum specimens examined and data from the BTO Survey, it appears that the distribution of white feathers in Blackbirds showing progressive greying can be roughly divided into three types. In the first, which is the most common, progressive greying begins around the head (plate 182). The second form affects mainly the wings and body first (plate 183), and in the third type all of the plumage is affected equally (plate 184). In the first two types the colour change is progressive but the birds probably never obtain fully white plumage (plate 185). In the third type, however, the condition seems to progress more rapidly and birds with this type of progressive greying appear to be those that do become completely white (plate 173). Many of these fully white Blackbirds in the BTO survey were recorded in autumn, winter or early spring, which might suggest that they are winter migrants. In the case of many resident birds, however, survey participants were able to observe the transformation of individual birds, four of which were recorded as becoming fully white.

In the final stage of progressive greying, when almost the entire plumage is white, many Blackbirds also lose the melanin pigment in the bare parts (bill and feet) as well as the plumage, resulting in pink feet and a yellow bill in both sexes (plate 173). In Blackbirds, both sexes have a yellow bill, but in females the yellow pigment (carotenoid) is masked by the melanin; in the absence of melanin, the bill therefore appears yellow. Based on pigmentary defects in humans, the disappearance of melanin from the skin

John Oakley

182. Female Blackbird, UK, July 2010. It appears that progressive greying in the Blackbird occurs in broadly three different forms. In the most common form, the progressive whitening starts at the head, and although the extent of white does increase with each successive moult, most birds probably never become fully white (see plates 176 & 177).

David King

183. Male Blackbird, UK, November 2013. The rarest form of progressive greying affects mainly the wings and body first; while the extent of white increases with each successive moult, these birds also probably never become fully white (see plate 185).

seems to suggest a progressive loss of the pigment-producing cells rather than a gradual reduction of tyrosinase activity. Grey hair in elderly people, for example, is caused by a tyrosinase reduction; only the colour of the hair is affected and not that of the skin. In many bird species other than Blackbird, progressive greying does not appear to affect the melanin in the skin.

Progressive greying is clearly the most common colour aberration in the Blackbird, but the causes are often unknown (see above). Rollin (1953a,b, 1959, 1964, 1981) considered that the white feathering is non-hereditary and solely diet-related. Sage (1962), while recognising food deficiency as a possible cause for pigment loss, believed the white feathering in Blackbirds to be heritable and disagreed with Rollin over its relationship to diet: 'I know of no evidence that wild birds ever encounter conditions which compel them to exist on an unbalanced diet for any length of time.' Later research, summarised above, indicates that plumage abnormalities in wild Carrion and Hooded Crows are affected by diet. As far as Blackbirds are concerned, however, both Rollin and Sage may have been wrong. Rollin's experiments with captive birds did show that artificial food could cause loss of pigment, but the affected feathers were not solidly white and still showed remains of pigment, as seen in crows. No convincing evidence that the development of white feathers after a certain age has a straightforward heritable origin has been found so far. Rollin (1964) associated the occurrence of abnormal white feathers in wild birds with 'the haunts of man', but certainly for Blackbirds this is questionable. In the mid 1800s, when the Blackbird was still predominantly a rural bird and the bird table had yet to be invented, Blackbirds with white feathers were already being noted (Thompson 1849; Johns 1862), while Watters (1853) stated that '… white-marked varieties are nothing unusual.' Furthermore, many of the museum specimens with white feathers from my study sample were collected in the 1800s (the earliest in 1851). In addition, progressive greying is also rather common in the Fieldfare *T. pilaris* and Ring Ouzel *T. torquatus*, two species not typically closely associated with humans (plates 186 & 187).

Progressive greying thus remains something of an enigma. We know that white feathers are never present in the juvenile plumage but that they can develop any time after the bird reaches maturity, and in some individuals the condition is more progressive than in others. Since progressive greying in the Blackbird often also affects the pigment in the skin (like the heritable human pigment disease vitiligo), a heritable cause for this form cannot be ruled out. Although in most cases there is no evidence for a straightforward genetic basis to progressive greying, there are no clear external factors either. The lack of a demonstrable external cause for the condition may mean that 'becoming grey' is, in fact, a natural feature of the species, with a (complex) genetic component, just as it is in humans!

Ian York

184. Male Blackbird, UK, May 2014. In the third form of progressive greying, the entire plumage can be affected and the condition probably progresses more rapidly; these appear to be the birds that do become fully white (see plate 173).

Mary Payne

185. Female Blackbird, Stoke Mandeville, Buckinghamshire, April 2011. Probably not all birds affected by progressive greying become fully white, even if they live long enough. Note that although this bird has over 75% white feathers, the pigmentation in the feet is not or hardly affected.

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Harry Taylor, NHM

186 & 187. Ring Ouzels *Turdus torquatus* (specimens at the Natural History Museum, Tring: left, NHMUK 1987.24.313 and right NHMUK 1996.41.2325, both collected between 1882 and 1900) and Fieldfares *Turdus pilaris* (left, NHMUK 1996.41.2335; right, NHMUK 1987.24.321 (right), both collected between 1883 and 1890). Progressive Greying is not uncommon in these two species.

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Appendix 1. The abnormal plumage survey by the World Bird Research Station, Glanton, Northumberland

Calvert Noble Rollin (1906–2004) had a lifetime's interest in birds and their behaviour. After training as a metallurgical chemist, he worked for the North Eastern Marine Engine Company in Northumberland, at Wallsend. In 1930, upon the death of his father, Charles, he inherited Greystones, the family house at Glanton, and started the Bird Research and Educational Station, which opened to the public in 1931. During this time, he began to formulate his main areas of study into the daily behaviour of birds and, in particular, the dawn chorus.

The Second World War forced Rollin to return to his former job as a metallurgical chemist on Tyneside. However, at weekends he cycled to Greystones (a round trip of almost 120 km) and, during the week, spent all his spare time watching and studying birds on the Tyne, sometimes getting into trouble with the authorities as a possible German spy. After the war, he again left his job and returned to Glanton to continue his ornithological work, now also with a growing interest in abnormal plumage. He began comparative studies on domesticated birds to study the inheritance of plumage abnormalities, in an attempt to understand what he believed to be non-inherited plumage in wild birds. In 1952 he was asked to teach ornithology at the Extra-Mural Department of Newcastle University, which he did up to the 1980s. This work provided a reservoir of enthusiastic and willing adult students to help in his research. At this time, he expanded the scope of the research station at Glanton, which became known as the World Bird Research Station, and continued his long-term study of abnormal plumage.

The inspiration for that study were three young Song Thrushes *T. philomelos* and two young Blackbirds, which were hand-reared in May 1951 and which subsequently developed partly white plumage. Rollin assumed that the loss of pigment in these birds was due to diet. Continued field observations on Blackbirds in different areas convinced him that an intensive study of the distribution of abnormally coloured Blackbirds and related species was needed to ascertain whether the condition had any relationship with rural and urban environments. He began the study in early April 1962 with a public request for reports of any wild bird with odd white feathers, published in newspapers across the country. The final conclusions of that survey were never published, though interim results were reported (Rollin 1964).

Based on that 1964 paper and unpublished work, it is clear that Rollin recognised that the vast majority of cases of aberrant white feathers were not heritable and that the whitening was often progressive. He also believed that this phenomenon was solely due to diet and occurred mainly in urban areas. Calvert Rollin was well ahead of his time in his understanding of the nature of the colour aberrations in birds. Yet despite his efforts, an understanding of aberrant white feathering in Blackbirds (and other species) was still lacking. He would surely have been pleased to know that his work eventually encouraged further research into the phenomenon.