The dark side of birds: melanism—facts and fiction

by Hein van Grouw

SUMMARY.—Melanism is generally defined as an increase of dark pigment in the plumage, resulting in a blackish appearance. Furthermore, melanism is often associated with mutations of one gene that encodes the melanocortin 1 receptor (MC1R), a protein involved in regulating melanin pigmentation. However, there is often no increase of pigment and melanism does not necessarily involve dark pigment alone. Also, many different mutations in many different genes promote melanism, which may explain why it is the commonest colour morph in birds. In the past, melanistic birds were sometimes mistakenly named as new species. Ironically, it now appears that melanistic birds do indeed differ from their normal-coloured conspecifics in more than just colour.

'Every morphism thus has implications in the field of genetics, ecology, selection theory, field natural history, and taxonomy.' (J. Huxley, 1955)

Melanism, from the Greek *melanos* (= dark-coloured), is generally defined as an increased amount of dark pigmentation (melanin). However, in this paper it will be demonstrated that an aberrant dark plumage is not necessarily the result of increased amounts of pigment, and that melanism can result in a paler plumage than normal.

Colour aberrations, especially melanism, have always confused ornithologists. In the past, when nothing was known concerning plumage pigmentation and mutations, aberrant-coloured birds were often viewed as being new taxa, and were even described scientifically. Perhaps the oldest and best-known example of a melanistic aberration named as a new species is Mountain Partridge *Perdix montana* (Brisson 1760). Brisson knew this 'species' only from the mountains of Lotharingen, France, hence *montana* (of the mountains). It proved, however, that '*montana*' occurred throughout Europe. Frisch (1763) described the same melanistic variety from Germany as 'Blackish-brown Partridge' (Schwarz-braune Rebhuhn, see Fig. 1) *P. fuscus*, and Latham (1823), based on two specimens in Bullock's museum (1795–1819) that were shot in Cheshire, north-west England, called them Cheshire Partridge. Subsequently, it became apparent that all of these 'species' were in fact

Figure 1. Hand-coloured copper engraving of '*Perdix fuscus*' from *Vorstellung der Vögel Deutschlands* (1763) by Johann Leonhard Frisch; the same mutation as Brisson's *Perdix montana*, i.e. a melanistic Grey Partridge *P. perdix* (Hein van Grouw, © Natural History Museum, London)

TABLE 1
Some examples of melanistic individuals named as new species.

'New' species	Actual species
Mountain Partridge, *Perdix montana* Brisson, 1760	Grey Partridge *Perdix perdix* (Linnaeus, 1758)
Sabine's Snipe *Scolopax sabinii* Vigors, 1825	Common Snipe *Gallinago gallinago* (Linnaeus, 1758)
Dicaeum aterrimum Lesson, 1830	Bananaquit *Coereba flaveola* (Linnaeus, 1758)
Pyrocephalus obscurus Gould, 1839	Vermilion Flycatcher *Pyrocephalus rubinus* (Boddaert, 1783)
Chestnut-coloured Partridge *Ortyx castaneus* Gould, 1842	Northern Bobwhite *Colinus virginianus* (Linnaeus, 1758)
Black Fantail *Rhipidura melanura* G. R. Gray, 1843	New Zealand Fantail *Rhipidura fuliginosa* (Sparrman, 1787)
Black Woodhen *Gallirallus fuscus* Du Bus, 1847	Weka *Gallirallus australis* (Sparrman, 1786)
English Rock Dove *Columba affinis* Blyth, 1847	Rock Dove *Columba livia* J. F. Gmelin, 1789
Rufous-bellied Coucal *Centropus epomidis* Bonaparte, 1850	Senegal Coucal *Centropus senegalensis* (Linnaeus, 1766)
Black-shouldered Peafowl *Pavo nigripennis* P. L. Sclater, 1860	Indian Peafowl *Pavo cristatus* Linnaeus, 1758
Perdix atro-rufa Soland, 1861	Red-legged Partridge *Alectoris rufa* (Linnaeus 1758)
Verreaux's Quail *Synoicus lodoisiae* J. Verreaux & des Murs, 1862	Common Quail *Coturnix coturnix* (Linnaeus, 1758)
Black Penguin *Eudyptes atratus* Hutton, 1875	Fiordland Penguin *Eudyptes pachyrhynchus* G. R. Gray, 1845
Tetrastes griseiventris Menzbier, 1880	Hazel Grouse *Tetrastes bonasia* (Linnaeus, 1758)
Monarcha ugiensis Ramsay, 1882	Chestnut-bellied Monarch *Monarch castaneiventris* J. Verreaux, 1858
Cory's Bittern *Ardetta neoxena* Cory, 1886	Least Bittern *Ixobrychus exilis* (J. F. Gmelin, 1789)
Sharpe's Rail *Stictolimnas sharpei* Büttikofer, 1893	Buff-banded Rail *Gallirallus philippensis (Linnaeus, 1766)*
Von Huegel's Snipe *Gallinago huegeli* Tristram, 1893	New Zealand Snipe *Coenocorypha aucklandica* (G. R. Gray 1845)
Willkonsky's Owl *Syrnium willkonskii* Menzbier, 1896	Tawny Owl *Strix aluco* Linnaeus, 1758

the same melanistic form of Grey Partridge *P. perdix*. Mistaking an aberrant-coloured bird for a new species (for more examples see Table 1) usually occurred if the aberration was quite common in the relevant species / population.

Once an aberration like melanism represents a certain percentage of the entire population, then the aberration is often considered a natural colour morph within that species. Overall, melanism is reported to be the commonest form of polymorphism in birds (Mundy 2006). To define, however, whether melanism can be viewed as a recognised morph or as an only occasional aberration is not clear cut. Further, besides their colour, melanistic birds often also differ in behaviour resulting in, for example, different habitat preferences.

Under appropriate conditions, melanistic morphs may therefore separate themselves from their typical-coloured conspecifics and consequently evolve into new taxa. That this is true shall be demonstrated here and the examples also confirm a 60-year-old evolution theory that states that there is a link between polymorphism and the faster evolution of new species. The examples presented, however, all involve melanism according to the traditional definition: increased amount of dark pigment. Whether other forms of melanism also promote speciation will also be discussed.

Melanins and plumage coloration

The main pigments in birds that afford plumage its colour are melanins and carotenoids. As only melanins are responsible for melanism, carotenoids will not be discussed further here. Melanin occurs in two discernible forms: eumelanin and phaeomelanin (Lubnow 1963). Depending on their concentration and distribution within the feather, eumelanin is responsible for black, grey and / or dark brown feathers, whereas phaeomelanin is responsible for warm reddish brown to pale buff colours. Both melanins together can produce a wide range of greyish-brown colours. Melanin is produced by cells called melanocytes located mainly in the skin and feather follicles (from which the feathers grow). Melanocytes within the feather follicles produce melanin, which is added to the feather cells as the feather grows. However, melanin distribution does not always occur at a constant rate. In most species, the feathers have certain patterns and / or colour differences caused by the type, amount and distribution of melanin. During feather growth, sudden changes from the production of eumelanin to phaeomelanin can occur, giving rise to different patterns.

In mammals, several genes regulate the production and deposition of the two distinct types of melanin (Lamoreux 2010), of which the two most important are the extension (MC1R) and agouti (ASIP) genes. The agouti gene regulates the distribution of eumelanin and phaeomelanin on each hair and over the surface of the body, while the extension gene is responsible for controlling the type of melanin being produced: eumelanin or phaeomelanin. Melanin cells do not produce both types of pigment simultaneously, but they can rapidly switch from one to the other. This complex control of melanin patterning is often referred to as the melanin-type switching mechanism. Primary control over this switch is exerted by both the agouti gene, which encodes the agouti signalling protein (ASIP), and the extension gene that encodes for the melanocortin 1 receptor (MC1R), with which ASIP interacts. Normally, these genes together determine which of, where and when the two types of melanin will be manufactured by the pigment cell during hair development (Lamoreux 2010).

Research shows that, in birds, a comparable extension gene is responsible for the production of melanin (Kerje *et al*. 2003, Mundy 2005, Vidal 2010a,b). How the melanin-type switching mechanism in birds works is still poorly known. However, it is reasonable to assume that a comparable agouti gene is present in birds as well, as many species possess feathers with distinct patterns of both melanin types. Several studies have indicated an avian equivalent of the agouti gene in Japanese Quail *Coturnix japonicus* (Hiragaki *et al*. 2008, Nadeau *et al*. 2008). So evidence suggests that there is a gene in birds responsible for melanin-type switching, which regulates the distribution of eumelanin and phaeomelanin on each feather. For convenience, it will be also termed the agouti gene in this paper.

In many bird species, however, (adult) plumage colour is determined by eumelanin alone. In spite of the lack of phaeomelanin, one can assume that in species with only eumelanin, an agouti locus is still involved in regulating the distribution of eumelanin within each feather. When inactivated by the presence of ASIP, the MC1R will not signal and the melanocytes will produce no melanin at all. The black-and-white patterns in the

flight feathers of, for example, Common Magpie *Pica pica*, Great Spotted Woodpecker *Dendrocopos major* and Common Hoopoe *Upupa epops* are probably the result of an agouti gene.

As mentioned, eumelanin does not always occur as black, but can also show as different shades of brown or grey. The pigment synthesis process is responsible for whether the eumelanin will be black or brown; incompletely oxidised eumelanin results in more brownish pigment granules, and grey is due to the way the black melanin pigment granules are arranged in the feather. These processes are controlled by other genes totally independent of the extension gene and / or the agouti gene. Most forms of melanism are heritable and inheritance patterns follow simple Mendelian principles.

Melanism and MC1R

Based on publications over the last 15 years, melanism in wild birds is often associated only with MC1R encoded by the extension gene, which determines the type of pigment produced inside the pigment cell by encoding (activating) the melanocortin 1 receptor. When activated, MC1R will send signals to the pigment cell to enable it to produce eumelanin. Without activation the pigment cells will produce phaeomelanin only.

Mutations of the extension gene can create a melanocortin 1 receptor that is constantly active, even of not stimulated, or conversely can lower the receptor's activity. Mutations for continually active MC1R are mostly inherited dominantly and result in a dark, black plumage, as mainly eumelanin is produced. Examples of these occur in the domestic chicken (Crawford 1990) and Bananaquit *Coereba flaveola* (Theron *et al*. 2001), and probably also in New Zealand Fantail *Rhipidura fuliginosa* (Caughley 1969) and Vermilion Flycatcher *Pyrocephalus rubinus* (van Grouw & Nolazco 2012) in which dark morphs are also dominant in inheritance. Mutations of the extension gene causing dysfunctional MC1R often result in a paler plumage based mainly on phaeomelanin, and these are mostly recessive. The mutation known as recessive red (symbol e) in the domestic pigeon / Feral Pigeon *Columba livia* is an example of this (van Grouw & de Jong 2009; Fig. 2D). A similar mutation occurs in Common Woodpigeon *Columba palumbus* (Fig. 3) and '*montana*', the reddish-brown morph of Grey Partridge (Fig. 4), is also a probable example of a mainly phaeomelanin-based plumage due to inactive MC1R.

As variation in MC1R encoded by the extension gene has been demonstrated to be associated with dark and pale plumages, Haas *et al*. (2009) tested whether this also applied to the colour differences between Carrion Crow *Corvus corone corone*, Hooded Crow *C. c. cornix* and their hybrids. However, they found neither any evidence of variation in MC1R related to the degree of melanism nor any significant genetic variation in the extension gene between the black and the grey crows. These results suggest melanism is attributable to other, additional causes. In addition to mutations of the extension gene, mutations of the agouti gene alone can also cause melanism. As described above, the agouti gene can influence 'communication' between the extension gene and the pigment cell by producing the agouti signalling protein, as ASIP inactivates MC1R independently and the melanocyte will then produce only phaeomelanin. Without ASIP interference, only eumelanin is produced. In this way ASIP normally regulates patterns of eumelanin and phaeomelanin pigment deposition in individual feathers by activating or inactivating the MC1R. Thus, mutations of the agouti gene, whereby no ASIP is produced, thereby causing MC1R to signal constantly, results in dark eumelanic (blackish) plumage that is mostly recessive in inheritance. The recessive dark morph of Montagu's Harrier *Circus pygargus* (Pandolfi 2000) is probably a mutation of the agouti gene. Mutations responsible for a constant production of ASIP, therefore producing only phaeomelanin, are mostly dominant, with an example

Figure 2. Feral Pigeons *Columba livia*: (A) wild phenotype, Leiden, the Netherlands, 19 August 2007; the grey wing-coverts and black wingbars are the result of different distribution of the same quantity of black melanin granules (Hein van Grouw); (B) T-pattern chequer, Leiden, the Netherlands, 19 August 2007; as a result of a dominant mutation of the pattern gene, the pigmentation over almost the entire wings is distributed as usually found only in the black wingbars, resulting in a blackish appearance, but the rump, tail and underparts are unaffected (Hein van Grouw); (C) Black, Leiden, the Netherlands, 19 August 2007; due to a dominant mutation known as 'spread', all pigment granules are equally spread, resulting in black plumage throughout (Hein van Grouw); (D) Recessive red, Pismo, California, USA; due to a recessive mutation of the extension gene that inactivates MC1R, phaeomelanin alone is produced (Robert Shriner)

of this found in Common Quail *Coturnix coturnix* (Fig. 5) and Japanese Quail (Hiragaki *et al*. 2008). The eumelanistic morphs in different isolated populations of Chestnut-bellied Monarch *Monarcha castaneiventris* on the Solomon Islands are the result of two different mutations. The eumelanic plumage of birds on the small island of Santa Ana is the result of a variation of the MC1R, while equally black birds on two other small islands, Ugi and Three Sisters, possess a mutation of the agouti gene (Uy *et al*. 2016).

To summarise, melanism can be due to mutations of the extension gene resulting in variation in MC1R, or mutations of the agouti gene resulting in variation in ASIP. Genetic studies in domesticated bird species, however, have identified many different genes which can cause different forms of melanism. Unsurprisingly, the commonest are extension and agouti, but there are many more, some reasonably common, and many can probably cause melanism in wild species too.

Figure 3. Common Woodpigeon *Columba palumbus* specimens (NHMUK 1930.8.14.1, NHMUK 2000.11.1, NHMUK 1923.3.8.1); the phaeomelanised plumage is probably the product of a similar mutation as 'recessive red' in Feral Pigeon *C. livia* (*cf.* Fig. 2D) (Harry Taylor, © Natural History Museum, London)

Figure 4. '*Perdix montana*', the phaeomelanistic variety of Grey Partridge *P. perdix*, NHMUK 1939.12.9.3717, Nasavad, Slovakia, 10 November 1932 (at left) and NHMUK 1939.12.9.3716, Norfolk, England, October 1911; the gene for this recessive mutation is present throughout the range of the species and is therefore a frequently recurring variety on the borderline of being recognised as a morph (Harry Taylor, © Natural History Museum, London)

Figure 5. 'Yellow' is a dominant mutation of the agouti gene in Common Quail *Coturnix coturnix* (NHMUK 1996.41.441, England) resulting in a coloration based on mainly phaeomelanin (Harry Taylor, © Natural History Museum, London)

Figure 6.. Hooded Crow *Corvus corone cornix* (left, NHMUK 1965.M.19466), Carrion Crow *C. c. corone* (right, NHMUK 2013.5.13) and their hybrid offspring, with in centre a first-generation hybrid (NHMUK 1965.M.19463), left of it a backcross Hooded Crow (NHMUK 1879.3.7.1) and right a backcross Carrion Crow (NHMUK 1925.2.12.1); both the Hooded Crow and all of the hybrids display many patterned feathers with black centres and grey fringes (Harry Taylor, © Natural History Museum, London)

Different forms of melanism

Several mutations in the domestic pigeon / Feral Pigeon, for example, are known to yield a blackish appearance without the quantity of melanin in the plumage being increased. In these cases, the melanistic forms are all due to a change in the arrangement of pigment granules, rather than more granules being present (van Grouw & de Jong 2009). The wild phenotype of *Columba livia* is slate blue-grey with a black tail-band and two black wingbars (Fig. 2A). The grey and black are the result of different distributions of the same amount of black melanin granules. In the grey parts the black granules are clumped and, due to the reflection of the light, what we see appears blue-grey. In the black parts the granules are spread equally and the colour appears black.

The two black wingbars are controlled by the pattern gene, symbolised as C, which regulates the way the pigment granules are arranged in specific feathers. Mutations of the pattern gene have resulted in both a bar-less phenotype and several phenotypes with black-spotted wings (chequered), while the remainder of the plumage pigmentation is scarcely affected. Only in the most extreme form, in which the wings are almost all black (T-pattern chequer, C^T), is the rest of the plumage obviously darker as well (Fig. 2B). The tail and rump, however, remain normal-coloured. Chequered pigeons are common, and among the semi-wild pigeons historically kept in large dovecotes for their eggs, squabs and dung in England (the ancestors of current Feral Pigeons) the trait was so common that Blyth (1847) considered them related to, but different from, Rock Dove. He named them *Columba affinis* (Latin *affinis* = related, allied). Another common melanistic mutation in the pigeon, unrelated to the pattern gene, also spreads the pigment granules equally and is therefore named 'spread' (symbol S). Spread, however, distributes all granules in the manner usually found only in the black wingbars and tail-band, resulting in entirely black plumage, including the rump and tail (Fig. 2C).

Figure 7. Melanistic Water Rail *Rallus aquaticus* (NHMUK 1939.12.9.3699, Ireland, 13 November 1902), with increased eumelanin, resulting in almost solid black plumage (Harry Taylor, © Natural History Museum, London)

Figure 8A. Melanistic Common Snipe *Gallinago gallinago* (NHMUK 1939.12.9.3643, Ireland), the same form as was previously described as Sabine's Snipe *Scolopax sabinii* Vigors, 1825; (B) Melanistic Common Quail *Coturnix coturnix* (NHMUK 1996.41.442, England, 1895), the same form as was previously described as Verreaux's Quail *Synoicus lodoisiae* Verreaux & des Murs, 1862 (Harry Taylor, © Natural History Museum, London)

It is reasonable to assume that dark morphs in species with predominantly slate-grey plumage are more likely to be the result of 'spread mutations' rather than increased melanin. A possible example is Northern Fulmar *Fulmarus glacialis* (Flood & van Grouw 2015). The difference in colour between Carrion Crow and Hooded Crow, however, is caused by the way the pigment is arranged (pers. obs.). As in both Hooded Crow and the hybrids, many individual, grey feathers are 'patterned' with black (Fig. 6), one can assume that melanism in crows is controlled by a pattern gene comparable with those in the pigeon.

Based on the above, melanism does not necessarily reflect an increase of pigment but may be the result of a changed distribution in the same quantity of melanin. Consequently, a better definition of melanism would be: a condition characterised by abnormal deposits of melanin in skin and feathers, as 'abnormal deposit' covers both a changed distribution and an increased amount. In general the appearance of a melanistic bird is dark, mostly blackish, but not always so. There are three ways melanism can affect birds' plumage: (1) all of the plumage is darker and appears blackish (eumelanin, Fig. 7), dark brown (both

Figure 9. Common Chaffinch *Fringilla coelebs*, Utö Island, Finland, 13 April 2013, with increased phaeomelanin resulting in predominantly reddish-brown plumage (Jorma Tenovuo)

melanins, Fig. 8) or reddish brown (phaeomelanin, Fig. 9); (2) normally dark markings are bolder and noticeably 'overrun' their typical boundaries (the rest of the plumage is often somewhat darker as well, Figs. 10–12); and (3) normal pattern and pigment distribution is changed, but the plumage is not necessarily darker (and can even be paler). See Appendix.

Melanism: accepted morph or aberration?

Melanistic forms are certainly not an uncommon phenomenon in birds. In certain species it is so common that the dark form represents a fairly large percentage of the entire population and is therefore considered to be a colour morph. In these cases the term 'dark morph' is often used instead of aberration. Northern Fulmar, Montagu's Harrier, Chestnut-bellied Monarch, Variable Oystercatcher *Haematopus unicolor*, Lesser Snow Goose *Anser caerulescens*, Common Pheasant *Phasianus colchicus*, New Zealand Weka *Gallirallus australis*, Pomarine Skua *Stercorarius pomarinus*, Arctic Skua *S. parasiticus*, Bananaquit *Coereba flaveola* and Blackcap *Sylvia atricapilla* (Fig. 12) are just a few examples in which a dark morph is accepted as a standard colour aberration within the species.

More than 300 bird species are known to exhibit polymorphisms (Galeotti *et al*. 2003) of which melanism is the commonest (Mundy 2006). Based on the many melanistic morphs in birds, dark forms are no more compromised than normal-coloured individuals (otherwise they would not have become established morphs). Genes (alleles) causing melanistic plumage are probably present in almost all species, as occasional dark individuals can be recorded in any population occasionally. In species in which no dark morph is recognised, single melanistic individuals often survive, and indeed breed. Therefore, in principle, what started as a colour aberration in a species can eventually become an established morph.

In general, a population is considered to be polymorphic when individuals of the same age and sex display one of several heritable colour variants for which the expression is not sensitive, or only at a low level, to the environment or body condition (Buckley 1987). It is difficult to decide, however, when a colour variant in a species can be considered a recognised morph or if it is only an occasional aberration. Ford (1945) seemed to be aware of that problem and defined polymorphism as 'the coexistence in one interbreeding

10A

10B

11

Figure 10. Melanistic White Wagtail *Motacilla a. alba*, Ardivachar, South Uist, Outer Hebrides, Scotland, September 2015; the normal black head markings have overrun their boundaries, whilst the rest of the plumage is darker as well (John Kemp)

Figure 11. Melanistic Great Tit *Parus major*, Rotterdam, the Netherlands, November 2008; the normal black head and breast markings have overrun their boundaries, whilst the rest of the plumage is darker as well (Harvey van Diek)

population of two or more sharply distinct and genetically determined forms, the least abundant of which is present in numbers too great to be due solely to recurrent mutation'. However, this is still vague: how many individuals are equivalent to 'numbers too great'?

Although one can assume that at least a certain percentage of the population needs to be of a different colour before a species can be identified as polymorphic, whether that must be 10%, 20% or even 50% of the population is unclear and debatable. For example, the melanistic form of Grey Partridge discussed earlier (Fig. 4) is occasionally recorded anywhere within the entire natural range of the species. Although this form comprises less than 10%, and probably < 1% of the Grey Partridge population, nevertheless in some works it is considered a recognised colour morph.

Melanism or new species?

In melanism the pigment granules are not changed in shape or size, thus express their full colour. Therefore the plumage of a melanistic bird is often not obviously aberrant, i.e. the plumage appears 'natural' but can be completely different to any known species. That melanistic birds were, especially in the past, mistaken for 'new species' is therefore understandable. Sometimes 'new species' were named on the basis of a single specimen with differently coloration, like Sharpe's Rail *Stictolimnas sharpei* (Hume & van Grouw 2014) and Chestnut-coloured Partridge *Ortyx castaneus* (Fig. 13). The latter was described by Gould (1842) because its different markings had persuaded him that it represented a distinct taxon. Eight years later, Gould (1850) was still convinced of its distinctiveness, as under *O. castaneus* he wrote 'The only example of this species that has come under my notice, I obtained in a living state at the sale of the collection of the late Zoological Gardens at Manchester. I must admit that I have always had a suspicion that the individual in question had assumed some unnatural style of colouring, and that it was merely a variety of *Ortyx Virginianus* or *O. Cubanensis*; but the rich chestnut colouring of the body, the black colouring of the forehead and throat, and the conspicuous markings of the sides and abdomen, are characters so different from what are observable in those species, that I have no other alternative than to describe and figure it as distinct.'

On most occasions, the confusion was based on melanistic forms that occurred, or still occur, quite commonly in the relevant species / populations. That more individuals were found was, for many ornithologists, evidence that these aberrant birds were indeed distinct species. For example, Menzbier (1896) wrote in his description of Willkousky's Owl 'At first I thought that this specimen was but a merely individual melanism [*sic*] of *Syrnium aluco* [Tawny Owl]; but in the spring of this year I received from Mr. Willkousky a skin of another specimen coloured in the same manner as the first, which had been obtained in a

Figure 12. Melanistic morph of Eurasian Blackcap *Sylvia atricapilla heineken*, Madeira, 27 April 2008; the normal black head markings have overrun their boundaries, whilst the rest of the plumage is darker as well (Hadoram Shirihai)

Figure 13. Gould's Chestnut-coloured Partridge *Ortyx castanea*, which was a melanistic Northern Bobwhite *Colinus virginianus*; the normal black head markings have overrun their boundaries, whilst the rest of the plumage is darker as well, the latter mainly due to increased phaeomelanin hence 'Chestnut-coloured' (Hein van Grouw, © Natural History Museum, London)

vineyard in the district of Shushov. After a careful examination of this specimen, I am now convinced that this Owl is a very good new species, differing from *Syrnium aluco* both in its general colour and character of markings…'. Although rare, melanistic Tawny Owls (Fig. 14A) are still occasionally recorded throughout Europe (and unconnected to the grey and rufous colour morphs of this species). In other *Strix* species, dark forms are also known and are less uncommon. In Ural Owl *S. uralensis* (Fig. 14B), for example, the melanistic form is often treated in the literature as a recognised morph.

Another example of a dark morph that was confused for a new species is the Weka *Gallirallus australis*. In 1847, a dark-coloured rail from New Zealand was described and named *Gallirallus fuscus* by Du Bus. In 1869, Buller described the Black Woodhen *Ocydromus nigricans*, which occurred only on the south-west coast of South Island. Having compared the type specimens of *fuscus* and *nigricans*, Buller (1873) concluded they were the same species, 'which is quite distinct…, but different from South Island Woodhen *O. australis* [= Weka]'. Buller also remarked that Black Woodhen 'inhabits the sea-shore and feeds among the kelp and seaweeds', unlike *australis* which inhabits mainly forest, woodland, scrub and grassland. Differences in behaviour / habitat together with differences in colour also occur in other species. There are, for example, differences in foraging behaviour between the white and dark morphs of Pacific Reef Heron *Egretta sacra* (Rohwer 1990). The differences occur both in the habitat used for feeding as well as the techniques used. Different perch site selection is recorded in Red-tailed Hawks *Buteo jamaicensis* (Preston 1980). Pale-coloured hawks occupy open perch sites, while dark hawks more frequently select perch sites

Figure 14A. Melanistic Tawny Owl *Strix aluco*, Switzerland, April 2015 (Bertrand Ducret); (B) melanistic morph of Ural Owl *Strix uralensis*, southern Poland, May 2008 (Chris van Rijswijk)

characterised by dense stem cover, and it is suggested that the morphs are associated with perch sites that best conceal them from prey. These examples are certainly not exceptions as will be demonstrated further below.

Melanism-dependent selection: yes or no?

Assuming that the plumage coloration of each species has evolved under natural selection over a long period to produce a colour / pattern best suited for survival, why do colour morphs also survive? In general, polymorphism is expected to have important effects on fitness. Some research has investigated the fitness effects of melanistic morphs, and positive effects have been found, for example, in Feral Pigeon. It appears that the plumage colour of juvenile Feral Pigeons is associated with features that influence its survival to adulthood in an urban environment. Strongly melanistic fledglings are more likely to attain adulthood, compared to the wild phenotype (Haag-Wackernagel *et al.* 2006). There is also some evidence in Feral Pigeons that melanistic males have a longer breeding season and are more fertile than the wild phenotype (Murton *et al.* 1973). Coloration per se may not directly influence survival, but there appears to be a link between plumage coloration, especially melanism, and behavioural and physiological characteristics associated with survival. In general, more strongly melanistic individuals are more resistant to stress, more aggressive and differ in metabolism (Roulin & Ducrest 2011, Poelstra 2013, Corbel *et al.* 2016). In Feral Pigeon this may explain why more melanistic phenotypes occur in the centre of large cities, while in small towns and natural or rural habitats the wild phenotype is more common.

Figure 15. Feral Pigeons *Columba livia* with phaeomelanised plumage (ash-red) but different wing patterns: (A) Barred (the white primaries and head feathers are the product of leucism), (B) Chequer and (C) T-pattern chequer, Leiden, the Netherlands, 19 August 2007 (Hein van Grouw)

Thus, in some cases, colour morphs of a species may behave differently due to their respective physiological properties. Eventually, colour morphs may evolve into distinct taxa. An example of this is perhaps Carrion Crow vs. Hooded Crow. Besides differences in plumage (melanistic versus non-melanistic), they also differ in vocalisations and habitat selection, the latter especially during the breeding season (Rolando & Laiolo 1994). Nevertheless, in the areas of overlap they do interbreed and, although melanism in crows is probably based on more than one gene, the alleles for black appear dominant (pers. obs., based on colour of first-generation offspring and that of backcrosses to the parental species; Fig 6). Although Carrion Crow and Hooded Crow hybridise, pair composition is not random (Saino & Villa 1992, Rolando 1993, Risch & Andersen 1998). Also, hybrids prefer to breed with 'grey' crows rather than 'black' crows (Rolando & Laiolo 1994), which may suggest that the Hooded phenotype is the original colour. The preference for 'grey' may also explain the non-random pair formation in areas of overlap, if Hooded Crows only select a melanistic partner in the absence of their own phenotype. In general, reproductive success, defined as the number of chicks reared to about fledging, is greater in Carrion Crows than Hooded Crows (Saino & Villa 1992). This may reflect the fact that Carrion Crow is more aggressive (Saino & Scatizzi 1991) and more stress-resistant (Poelstra 2013).

Carrion Crow and Hooded Crow inhabit separate but adjoining ranges in Europe, with some narrow areas of overlap. The popular hypothesis to explain the differences between them are that they diverged from a common ancestor and, during an extended period of geographical separation, these populations underwent genetic differentiation before meeting again. Genetic studies, however, reveal no significant molecular differentiation

(Haring *et al.* 2007, Haas *et al.* 2009), suggesting that the forms have either not been separated, or at least not for long. Another possible scenario, however, is that at some point a colour aberration occurred, probably the melanistic form, and that, due to different behaviour and physiology related to melanism, this form finally evolved into a distinct taxon. A similar phenomenon appears to have produced the dark-coloured Basalt Wheatear *Oenanthe lugens warriae*, a subspecies of Mourning Wheatear *O. lugens*. Until recently, the dark-coloured birds were considered to be a dark morph of nominate *O. lugens*. The breeding range of Basalt Wheatear is, however, restricted to the basalt deserts of eastern Jordan and southern Syria, with no or little evidence of hybridisation with Mourning Wheatear (Shirihai *et al.* 2011, Khoury *et al.* 2013). Although genetically insignificantly differentiated from nominate Mourning Wheatear, Basalt Wheatear differs sufficiently in plumage colour, breeding habitat selection and biometrics to recognise it taxonomically (Shirihai *et al.* 2011). Thus it appears that dark morphs, due to their different behaviour, can evolve into new taxa.

That the above scenarios are more than a hypothesis was demonstrated by Hugall & Stuart-Fox (2012), who showed that bird species with multiple plumage colour forms within the same population speciate faster than those with only a single colour morph. Earlier, Gray & McKinnon (2007) had already suggested that coloration differences among individuals may directly promote speciation events. All of this research was, however, not new as the tendency of colour polymorphs to evolve more quickly had been predicted more than 60 years earlier by the evolutionary biologist, Sir Julian Huxley (1955). Whether he was misunderstood by his contemporaries, or was simply not taken seriously, the proof appears to be available. And if we do not believe in the above examples among crows and wheatears, differences in behaviour / habitat choice by melanistic morphs occur in other species in which the dark morph is still considered to be the same taxon.

In Senegal Coucal *Centropus senegalensis*, for example, two colour morphs occur in the populations of Ghana and Nigeria. The typical form, with creamy-white underparts and black more or less confined to the crown, occurs throughout the species' range without any strong habitat preference but is less associated with wet areas (Erritzøe *et al.* 2012). The dark form, however, with an all-black head and breast, and reddish-brown belly, which was recognised taxonomically in the past (see Table 1), occurs mainly in coastal Ghana and Nigeria, as well as Ivory Coast and Liberia. The two morphs interbreed freely, but the dark morph appears to prefer especially wet areas, with higher rainfall and is therefore more dependent on certain habitats than the typical form.

Another example is Vermilion Flycatcher, wherein the population around Lima, Peru, is polymorphic, with dark and red morphs occupying the same areas and interbreeding randomly. However, just as in Feral Pigeons, the dark phenotype is commoner in the more urbanised areas of the city, while towards the outskirts the number of red morphs increases (van Grouw & Nolazco 2012). This suggests that certain fitness effects related to the melanistic morph are beneficial in highly urban environments, e.g. stress resistance. Mate selection does not (yet) appear to be based on colour, but this can be explained by the fact that, although melanism may indirectly favour the fitness of dark individuals in an urban environment, evolution in the species is still in its relative infancy.

A similar process appears to have occurred in Bananaquit; black morphs occur in several populations within the species' range. On several of the islands off northern Venezuela the populations only comprise black morphs, which are recognised as subspecies (*melanornis*, *lowii* and *laurae*), underlining the statement that melanism promotes speciation. On the islands of Grenada and St. Vincent the populations are (still) polymorphic, but the two morphs occupy different habitats. Melanistic birds occur in moist forest at all altitudes, whereas (normal) yellow-and-black birds persist only in dry lowland habitats.

Although already separated by habitat preference, in the few, narrow areas of overlap pair composition is random (Wunderle 1981), but some post-mating isolation (= unsuccessful fertilisation and development) is suspected (MacColl & Stevenson 2003), suggesting that speciation has commenced.

Nevertheless, it must be stated that in other species, e.g. Lesser Snow Goose *Anser c. caerulescens*, intensive studies have failed to find definitive evidence of natural selection for morphs (Cooke *et al*. 1995). This does not mean, however, that such selection does not exist.

Discussion

Morphism, a term introduced by Huxley (1955) to denote genetic polymorphism as opposed to other kinds of polymorphism such as seasonal, cyclical, geographical, etc., appears to be an important factor in promoting speciation. Note, however, that polymorphism does not of necessity lead to speciation, as this depends also on many other factors. Morphism in a species probably is initiated as an occasional colour aberration. If a selective balance operates between the aberrant and normal colour morphs, based on selective advantage vs. disadvantage, the aberration may become an established morph. Pigment aberrations often combine with different behaviour and physiology, and these differences may prove advantageous in certain habitats, ultimately leading to speciation.

As mentioned earlier, recent studies have revealed that in birds, strongly melanistic individuals are more resistant to stress, more aggressive and differ in their metabolism. Legendre (1941) had already noted that the melanistic morph of *Phasianus colchicus* is more vigorous and robust than normal-coloured individuals. The mutation occurred for the first time within feral populations in England in the late 1800s, and has persisted ever since. Also, in other countries where the species was introduced, it flourished. In this, and all other given examples of strongly melanistic morphs with positive effects for fitness, the melanin involved is eumelanin alone. But what of phaeomelanin; do strongly phaeomelanised individuals possess the same link between plumage colour and behavioural and physiological characteristics associated with survival, as eumelanised individuals? Although '*montana*', the reddish 'morph' of Grey Partridge, persistently re-appears due to the recessive nature of the mutation, there is no evidence that this phaeomelanised variety increases numerically anywhere in the species' natural range.

A form of melanism that is dominant in inheritance and also results in predominantly phaeomelanised plumage (different from Gould's *castaneus*) occurs in Northern Bobwhite *Colinus virginianus*. This red mutation is weaker and less fertile than normal individuals and, although it achieved a probable frequency of *c*.15% for a few years within a small area, it has failed to persist in the wild even when purposely bred and released (Cole *et al*. 1949).

Another example is the Feral Pigeon. A dominant mutation, known as dominant red or ash-red (symbol B[A], van Grouw & de Jong 2009), lacks almost all eumelanin in the plumage, resulting in pale, ash-grey body, flight and tail feathers, with additional phaeomelanin in the neck feathers and wing pattern. Ash-red is a very common mutation in many breeds of domestic pigeons, but relatively rare in feral populations (pers. obs.). In Vienna, for example, <5% of the city's feral population is ash-red (Haag-Wackernagel *et al* 2006), which appears unexpected given that the mutation is dominant in inheritance over the black / grey wild phenotype. In fact, it is dominant and sex-linked, thus all male offspring (= 50% of all offspring) of an ash-red female crossed with a wild phenotype male are ash-red. Depending on whether an ash-red male is homozygote (pure) or heterozygote (impure) for the mutation, when mated with a wild phenotype female either all offspring or 50% will be ash-red—both males and females in the latter. Thus any ash-red pigeon, irrespective of its sex and mate, will produce at least 50% ash-red offspring. Based on this, one would

expect a much higher percentage of ash-red individuals in Feral Pigeon populations, meaning that there is presumably high mortality among juvenile ash-red pigeons. Ash-red is independent of the wing pattern, thus ash-red pigeons come in barred, chequered and T-pattern chequered wing patterns (Fig. 15; see Different forms of melanism). According to research in Vienna, ash-red barred juveniles have a high probability of reaching adulthood, while ash-red juveniles with chequer or T-pattern chequer have a rather low survival rate (Haag-Wackernagel *et al*. 2006). This is remarkable as eumelanised juveniles with chequer or T-pattern chequer wings possess a higher success rate, compared to their barred counterparts. These findings suggest that, at least among Feral Pigeons in cities, negative effects on fitness are linked to strongly phaeomelanised plumage. Whether the same applies to Feral Pigeons in rural areas, or for other species in their natural habitat is unknown. However, what is known is that there is much more to the phenomenon of melanism than an increase of dark eumelanin resulting in dark plumage alone.

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Address: Bird Group, Dept. of Life Sciences, Natural History Museum, Akeman Street, Tring, Herts. HP23 6AP, UK, e-mail: h.van-grouw@nhm.ac.uk

Appendix

If darkish-coloured birds were not sufficiently confusing, forms of melanism causing a completely different, but very natural-looking pattern have baffled ornithologists even more. These forms often cause an extreme variation of the original plumage. The colour of the melanin itself (the shape or size of the pigment granules) is unaffected, but the way it is distributed over the feathers is, resulting in wholly different markings and patterns (Figs. 16–17), and even an overall paler appearance (Fig. 18). In sexually dimorphic species, the appearance of females alone may be significantly paler, whereas males are often less affected and may be slightly darker, resulting in an even more extreme difference between the sexes. A well-known example is Black-shouldered Peafowl, named *Pavo nigripennis* by Sclater (1860) which is a colour mutation of Indian Peafowl *P. cristatus*. Males hardly differ from normal-coloured birds, except in having solid black 'shoulders', hence their name, rather than the normal barring (Fig. 19). Females, however, are considerably paler with different markings and appear strikingly different from normal-coloured individuals (Fig. 20). This extreme

Figure 16. Specimen of Red-legged Partridge *Alectoris rufa* with a form of melanism that has changed the usual pattern and markings (left, NHMUK 1923.1.29.1) and a normal-coloured individual (right, NHMUK 1907.12.20.7); due to a mutation, the black head and throat markings are altered and the solid-coloured back, shoulders and wing feathers (based mainly on eumelanin) now exhibit distinctive patterns based on both melanin types, and some parts resemble the flanks plumage (Harry Taylor, © Natural History Museum, London)

Figure 17. Chukar *Alectoris chukar* (NHMUK 1939.12.9.3715), same mutation as in Fig. 16. (Harry Taylor, © Natural History Museum, London)

Figure 18. Hazel Grouse *Tetrastes bonasia* (NHMUK 1987.24.122) with a form of melanism that has altered the typical pattern and markings, resulting in a paler appearance (Harry Taylor, © Natural History Museum, London)

sexual dimorphism convinced Sclater (1860) to name Black-shouldered Peafowl as a species and not a hybrid or domestic variety: 'I cannot consider it a domesticated variety, because of the differences in both sexes appear to be constant, and to descend to the progeny…'. Similar mutations occur in Mallard *Anas platyrhynchos* (Fig. 21) and Asian Blue Quail *Synoicus chinensis* (Fig. 22).

Pattern-changing mutations have not only been mistaken for new species. In Black Grouse *Lyrurus tetrix*, for example, Meyer (1887) believed they were hybrids instead. Hybrids between Black Grouse and ptarmigan *Lagopus* sp. were well known in Meyer's time and he considered the hybrids to differ in the degree of feathering on their feet, depending on which species was the male parent: if the latter was a ptarmigan, then the offspring had ptarmigan feet (Fig. 23), whereas if the male was a Black Grouse then it had feet like this species (Fig. 24). Whether ptarmigan-footed hybrids' male parents are indeed always ptarmigans is unknown, but Black Grouse-footed birds he depicted were Black Grouse and not hybrids. The totally different feather markings and patterns due to mutations, which gave the birds a more whitish appearance, fooled Meyer. Apparently, he never observed a male affected by the same mutation, or at least he neither

Figure 19. Normal-coloured and black-shouldered male Indian Peafowls *Pavo cristatus*; apart from parts of the wing and shoulders, this mutation does not affect the rest of male plumage (Hein van Grouw)

Figure 20. Normal-coloured and black-shouldered female Indian Peafowls *Pavo cristatus*; the 'black-shoulder' mutation has a major effect on female plumage (Hein van Grouw)
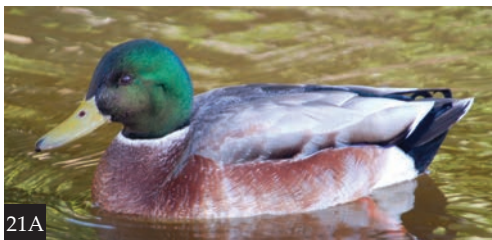

Figure 21. A form of melanism in Mallard *Anas platyrhynchos* that affects female plumage much more than male plumage (Hein van Grouw)

mentioned nor illustrated one, as otherwise he probably would have realised his mistake (Figs. 25–26). These mutations were not uncommon in Scandinavia and Russia, and in the early 1900s in the Bjerkreim area, Norway, were sufficiently numerous that Schaaning (1921) described them as a new subspecies, *Lyrurus tetrix bjerkreimensis* (Fig. 27), because '…the plumage of the male is similar to the spring plumage of male Willow Ptarmigan *Lagopus lagopus*.'

Figure 22. Forms of melanism (C and D) in Asian Blue Quail *Synoicus chinensis* that affect female plumage much more than male plumage (Pieter van den Hooven)

Figure 23. Pl. 14 in A. B. Meyer (1887) *Unser Auer-, Rackel- und Birkwild und seine Abarten* showing Black Grouse *Lyrurus tetrix* × ptarmigan *Lagopus* sp. hybrids (Hein van Grouw, © Natural History Museum, London)

Figure 24 (facing page). Pl. 15 in A. B. Meyer (1887) *Unser Auer-, Rackel- und Birkwild und seine Abarten* showing what Meyer believed to be Black Grouse *Lyrurus tetrix* × ptarmigan *Lagopus* sp. hybrids; however, these birds are aberrant-coloured female Black Grouse (*cf*. Figs. 25–26) (Hein van Grouw, © Natural History Museum, London)

Figure 25. Form of melanism in Black Grouse *Lyrurus tetrix* (NHMUK 1996.41.320, male, and NHMUK 1987.24.143, female) that alters the pattern and markings, resulting in a paler appearance than normal; compare the female with left-hand bird in Fig. 24. (Harry Taylor, © Natural History Museum, London)

Figure 26. Another form of melanism in Black Grouse *Lyrurus tetrix* specimens at Zoological Research Museum Alexander Koenig, Bonn, which alters the pattern and markings, resulting in a paler appearance than normal; compare female with right-hand bird in Fig. 24. (Hein van Grouw)
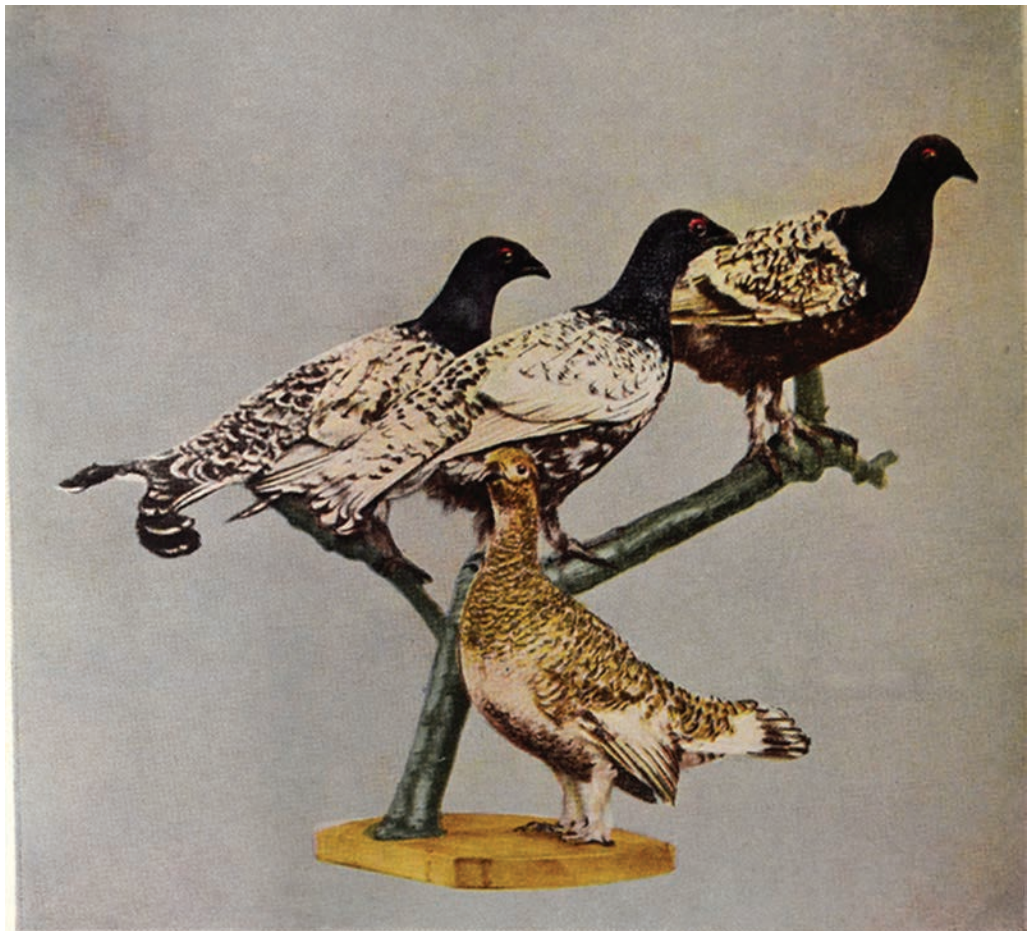
„BJERKREIM-ORREN"

Lyrurus tetrix. Varietet: 3 ♂♂♂ og ♀ i Stavanger Museum

Figure 27. Depiction in Schaaning (1921) of another form of melanism in Black Grouse *Lyrurus tetrix* that changes the pattern and markings, resulting in a paler appearance than normal (Hein van Grouw, © Natural History Museum, London)