



UNOP

Unión de Ornitólogos del Perú

Boletín informativo
ISSN 2220-9212

<https://sites.google.com/site/boletinunop/>

ÍNDICE

Diversidad de aves silvestres y correlaciones con la cobertura vegetal en parques y jardines de la ciudad de Lima. Sergio Nolzco: 4-16.

Cocoi Heron (*Ardea cocoi*) recorded in the Pisco - Paracas area, Peru. Altamirano-Sierra, A. & J. C. Reyes: 17-18.

Primer registro de *Caracara plancus* para el departamento de Cusco, Perú. D. Matthias Dehling: 19-20.

Nuevos registros del zorzal ecuatoriano (*Turdus maculirostris*) en los Andes del norte del Perú. Segundo Crespo & Jorge Novoa: 21-25.

The Nature of melanism and some other colour aberrations in the Vermilion Flycatcher (*Pyrocephalus rubinus obscurus*). Hein van Grouw & Sergio Nolzco: 26-37.

Bibliografía de las Aves de Perú 2010. Manuel A. Plenge: 38-44.

Reporte del Comité de Registros de Aves Peruanas del periodo 2008 – 2009. CRAP: 45-52.

The nature of melanism and some other colour aberrations in the vermilion flycatcher (*Pyrocephalus rubinus obscurus*)

Hein van Grouw¹ & Sergio Nolazco²

h.van-grouw@nhm.ac.uk

1. Natural History Museum at Tring

Akeman Street, Tring, Herts

HP23 6AP - United Kingdom

2. Centro de Ornitología y Biodiversidad (CORBIDI)

Calle Sta. Rita 105 Oficina 202, urb. Huertos de San Antonio, Surco, Lima - Perú

ABSTRACT

The high frequency of melanism in the Vermilion Flycatcher *Pyrocephalus rubinus obscurus* Gould 1839 at Lima city (Perú) polymorphic population give rise to some hypotheses, mostly, orientated to explain the pattern of phenotypic frequencies as a consequence of external selective mechanisms. For a better understanding of this special case and other plumage colour aberrations in *P. r. obscurus*, we give a review on terminology and nature of melanism. Also our findings for a dominant inheritance of melanism in the subspecies are presented as well as evidence of non-assortative mating based on plumage colouration and descriptions of other less common colour aberrations.

Key words: polymorphism, melanism, melanocortin 1-receptor, assortative mating, natural selection, Lima city.

INTRODUCCIÓN

The widely distributed Vermilion Flycatcher (*Pyrocephalus rubinus*) exhibit an interesting case of polymorphism at Lima city where more than 60% of the population is melanistic (Ballón 1994), in contrast to the usual bright plumage exhibit in all other populations from urban areas to mature native forests throughout its range. The first documented record of this dark morph is a specimen collected in 1835 at Lima by Charles Darwin and named by John Gould as (*Pyrocephalus obscurus*) in 1839 (figure 1).

RESUMEN

La alta frecuencia del melanismo en la población polimórfica del turtupilín (*Pyrocephalus rubinus obscurus*) (Gould 1839) en la ciudad de Lima (Perú) da origen a muchas hipótesis, mayormente orientadas a explicar el patrón de frecuencias fenotípicas como consecuencia de mecanismos de selección externos. Para un mayor entendimiento de este caso especial y otras aberraciones en la coloración de plumajes en *P. r. obscurus*, realizamos una revisión de la terminología y naturaleza del melanismo. Además, presentamos nuestros descubrimientos en esta subespecie, tales como la dominancia hereditaria del melanismo, la evidencia de apareamiento aleatorio basado en la coloración del plumaje y las descripciones de otras aberraciones de coloración menos comunes.

Palabras Clave: polimorfismo, melanismo, receptor 1 de melanocortina, apareamiento asortativo, selección natural, ciudad de Lima.

In 1884, Władysław Taczanowski cited Stolzmann specifying that the two phenotypes were common in Lima surroundings. He also pointed out, by referring to Jelski, that non-melanistic individuals were more seen in orchards and groves, while melanistic ones were seen in open areas like corn fields. In 1941, John T. Zimmer recognized the two morphs as a same subspecies (*P. r. obscurus*), but in contrast to Jelski's observations, he pointed out that the two morphs coexists in the same type of environments. He also

considered that this melanistic phenotype was found occasionally as far as Cocachacra (Arequipa), probably corresponding to birds of the subspecies *P.r.cocachacrae*.



Figure 1. Type specimen of *Pyrocephalus obscurus*, collected by Charles Darwin in 1835 and named by John Gould in 1839. Register number: BMNH 1855.12.19.389 (photo: Hein van Grouw, Natural History Museum Tring).

Despite the melanistic morph already being present in Lima when most part of the area was still covered by green fields and air was not polluted by car traffic and fabrics, nowadays there is a pattern of higher frequency of melanistic phenotypes from the highly urbanized core area of the metropolis declining to the outskirts of it (Ballón 1994). This may suggest the possibility of selection forces acting in benefit of dark morph individuals in highly urbanized areas. For a better understanding of this special case and other plumage colour aberrations in *P. r. obscurus*, we present a review on terminology and nature of melanism, including our findings for a dominant inheritance of melanism in the subspecies, evidence of non-assortative mating based on plumage colouration and descriptions of other less common colour aberrations.

MATERIALS AND METHODS

Collecting data

Besides the author's (HvG) own research, information from publications was compiled to summarize current knowledge on melanism and for descriptions of other aberrant plumage colourations documented here for the first time in this subspecies. For field data

collection, between January 2009 and November 2011 the author (SN) conducted mist net captures, mating observations and nest searches inside Lima city. Every bird captured was marked with a metal ring and a plastic coloured ring and released for individual identification, determining sex by behaviour in the case of melanistic birds. To find out if two birds are mating we used four reliable indicators: copulation, nest site selection interaction, nest construction interaction and active nest interaction. When a nest was identified we took notes on chick plumage phenotypes to determine if these were melanistic or non-melanistic morphs.

Analysing data

To confirm our hypothesis on dominant inheritance of melanism, we looked for nests of melanistic parents with non-melanistic offspring what would prove the dominance of the dark morph. Every bird captured was photographed to detect intra-sex variation on the intensity of melanistic morphs based on the assumption of a correlation between the intensity of darkness and the number of melanistic alleles. For assortative mating analysis we use count data on confirmed mating couples and test it using Pearson Chi square statistic.

Terminology

The knowledge on pigmentation development and genetics is mostly gained from studies of domesticated species such as mice and chickens. The genetic studies in mammals, and especially the mouse, are probably the most thorough ones. From an early stage in the study of animal genetics, it became obvious that different mammalian species had a similar series of heritable coat colour variants (Searle 1968). This was the start of scientific comparative genetics in mammals and a result of this was that similar mutations were allocated the same name in all species. The similarity was based on the relevant gene action on the pigmentation process and not necessarily on the appearance of the final coat colour, as this can differ between species. Despite the comparable nature of the pigmentation process in birds and mammals (Lubnow 1963), establishing some uniformity in the nomenclature of genes (loci) between mammals and birds has so far been sadly neglected. In this paper the names used for the different loci involved in the pigmentation process are based on mouse genetic nomenclature.

Melanins and plumage colouration

The main pigments in birds that give the plumage its colour are melanins and carotenoids. As only melanins are responsible for melanism, the carotenoids will not be discussed further in this paper.

Melanin can be distinguished in two forms: eumelanin and phaeomelanin (Lubnow 1963). Depending on 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. Both melanins together can give a wide range of greyish-brown colours.

Melanin is produced by cells called melanocytes which are found mainly in the skin and the 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 may occur, giving rise to these different patterns.

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

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

With the above knowledge in mind the process of production and deposition of melanin in bird feathers is, in a nutshell, controlled as follows.

The MC1R complex, encoded by the extension locus, determines the type of pigment that is produced inside the pigment cell. When activated by the melanocyte stimulating hormone (MSH), MC1R will send signals to the melanocyte to let it produce eumelanin. Without stimulation MC1R will not send signals and the melanocytes will produce phaeomelanin.

The agouti signalling protein inactivates the signalling of MC1R and makes the melanocyte produce phaeomelanin as long as the agouti locus encodes ASIP. So ASIP regulates patterns of eumelanin and phaeomelanin pigment deposition in individual feathers by activating or inactivating the signalling through MC1R.

In many species the (adult) colour is caused by eumelanin only, for example in most crows (Corvidae), gulls/terns (Laridae), tits (Paridae), woodpeckers (Picidae), parrots (Psittacidae), auks (Alcidae), oystercatchers (Haematopodidae) and the male European Blackbird (*Turdus merula*). However, in most species both types of melanin are present. There are no species in which only phaeomelanin occurs.

The Vermilion Flycatcher's colour is, besides red carotenoid, caused by eumelanin only. Phaeomelanin is not present in the species in spite of a brownish hint in the plumage. Hormones can affect the pigment synthesis and therefore the colouration (Kimball 2006). Usually, in the males the eumelanin synthesis

results in black pigment. The eumelanin synthesis in the females however is slightly different as a result of the absence of androgens (e.g. testosterone). In their case most of the eumelanin is not oxidised completely which results in more brownish eumelanin instead of black and that explains the duller and more brownish colour of the females. The difference between visual black and grey is due to the way the black melanin pigment granules are arranged in the feather. Eumelanin granules arranged in spread fashion will give the feather a black appearance. However if the granules are arranged in a clumped fashion, the light is reflected differently and what we see appears more grey.

In spite of the lack of phaeomelanin, one can assume that, in species with eumelanin only, an agouti locus is still involved in regulating the pattern of distribution of eumelanin, by activating or inactivating the signalling through MC1R. When it is inactivated by the presence of ASIP, the MC1R will not signal and the melanocytes will produce no melanin at all. In the case of the Vermilion Flycatcher in normal colouration eumelanin is not distributed equally all over the plumage. In both sexes the tips of the tail feathers and the outer webs of the outer tail feathers are almost free of eumelanin and therefore whitish. Also the flight and covert wings have less eumelanin in the tips and edges than in the rest of the feather. The under part body feathers (chin, throat, breast, belly and under tail coverts), and in the male also the feathers on top of the head are melanized in the down layer but (almost) completely free of eumelanin in the top half. In the female's breast plumage is besides in the down layer also eumelanin deposit along the shaft of the feathers what gives a streaking appearance.

In the female, visible carotenoids are only present in the top half of the feathers in the belly plumage and under tail coverts. In the male carotenoids are present in all under part plumage and in the feathers on top of the head but also only in the top half of these feathers and not in the down layer. Deposition of carotenoids in these feathers does not start immediately after the deposition of eumelanin has stopped and therefore a white line appears between the grey down layer (eumelanin) and the red top (carotenoid; see figure 2).

Melanism

Melanism has always confused ornithologists. In the past, when nothing was known about plumage pigmentation and mutations, aberrant coloured birds



Figure 2. Breast feathers of adult males. Normal coloured (left) and melanistic (right). In the normal coloured feather deposition of eumelanin is only in the down layer while eumelanin deposition in the melanistic feather is all over. The carotenoid is still present in the melanistic feather but not visible due to the overlaying eumelanin (photo: Hein van Grouw, Natural History Museum Tring).

were often seen as being new (sub)species, and were even scientifically named.

Melanism, from the Greek *melanos* (= dark-coloured), is often defined as an increased amount of dark pigmentation, resulting from the presence of melanin. However it is not always an increased amount of dark pigmentation that causes a dark appearance. In the domesticated pigeon (*Columba livia*) for example, the black appearance of a common melanistic form is due to a change in the arrangement of pigment granules instead of an increased amount of granules (van Grouw 2009). The wild type *Columba livia* is slate blue-grey with a black tail bar and two black wing bars on each wing. These two colours are the result of different arrangements of the same black melanin granules. In the grey parts the black granules are arranged in a clumped fashion and, due to the reflection of the light, what we see appears blue-grey. In the black parts the granules are arranged in an equally spread fashion and there the colour will appear black. Due to an autosomal dominant mutation in the pigeon (called 'spread' and symbolised as S) all the granules are now distributed in the manner usually found only in the black wing bars and tail bar and a self black plumage colouration is the result.

The definition of melanism is: a condition characterized

by abnormal deposits of melanin in skin, hairs and feathers. That means that melanism is not necessarily an increase of pigment but may be the result of a changed distribution or "abnormal deposit" of the same amount of melanin.

In general the appearance of a melanistic bird is dark, mostly blackish, but not always.

There are three ways melanism can affect birds' plumage.

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

Melanism is the only mutation in which there is no loss of pigments or changes in the shape or size of the melanin granules. Therefore the plumage of a melanistic bird is not obviously aberrant, i.e. the plumage looks 'natural' but often completely different to any known species. So is therefore understandable that those melanistic birds were, in the past, mistaken for 'new species'.

Perhaps the oldest and best known example of a melanistic aberration named as a distinct species is the Mountain Partridge (*Perdix montana*) Brisson, 1760. In Brisson's time this 'species' was only known to live in the mountains of Lotharingen, France, which resulted in it being named *montana* (of the mountains). However, it was subsequently revealed to be a melanistic form of the Grey Partridge *Perdix perdix*.

Another example is Sabine's Snipe *Scolopax sabinii* Vigors, 1825. This dark coloured snipe was in fact a melanistic form of the Common Snipe *Gallinago gallinago*.

Other examples include:

- The now well-known 'black-shouldered' mutation found in Indian Peafowl *Pavo cristatus* was first described as the Black-shouldered Peafowl *Pavo nigripennis* Sclater, 1860.
- The melanistic form of the Red-legged partridge

Alectoris rufa in France what was named *Perdix atrofufa* Soland, 1861.

- *Synoicus lodoisiae*, Verreaux & des Murs 1862, a melanistic Common Quail *Coturnix coturnix*.

- The dark coloured Willkowsky's Owl *Syrnium willkowskii* Menzbier, 1896 from the Caucasus was considered to be a new species, but appeared to be a melanistic form of the Tawny Owl *Strix aluco*.

The examples above, and there are many more, are mostly based on aberrations that occur quite commonly in the relevant species/populations. So the idea that the aberrant coloured birds have been interpreted as another species is easy to understand. Melanistic forms in species are certainly not an uncommon phenomenon in birds. In certain species it is even so common that the dark forms represent a fairly large percentage of the whole population and therefore considered to be a colour morph within the species. In these cases the term 'dark morph' is often used instead of aberration.

Northern Fulmar *Fulmaris glacialis*, Montagu's Harrier *Circus pygargus*, Lesser Snow Goose *Anser caerulescens*, Common Pheasant *Phasianus colchicus*, Weka *Gallirallus australis*, Pomarine Skua *Stercorarius pomarinus*, Arctic Skua *Stercorarius parasiticus*, Bananaquit *Coereba flaveola* and Blackcap *Sylvia atricapilla* are only a few examples of species in which the dark morph is accepted as a standard colour feature within the species.

Similarly in the Vermilion Flycatcher, the subspecies *obscurus*, which occurs in West Peru (Lima region), has a dark morph that is well established. In fact the name *obscurus* was given by Gould (1839) to a melanistic bird as he thought that the uniform dark cinereous birds from the Lima region were a distinct species. The uniform dark plumage is due to the fact that the deposition of eumelanin is equally spread all over the plumage. However, not uncommon in the dark individuals is to find some amelanistic feathers as well (Figure 3, 4 and 5). These feathers lack melanin completely (carotenoids are still present). The precise cause for this is unknown but it is probably due to Progressive Greying. Progressive Greying is defined as the progressive loss of melanin pigment cells with age (van Grouw 2012). From the onset of the condition, the bird will gain an increasing



Figure 3. Melanistic male (sex determined by behaviour) with amelanistic flight feathers (photo: Sergio Nolzaco, Lima city).



Figure 4. Melanistic male (sex determined by behaviour) with amelanistic feathers on face and crown. This does not affect the normal deposition of red carotenoids observed on non-melanistic birds (photo: Sergio Nolzaco, Lima city).



Figure 5. Melanistic male (sex determined by behaviour) with amelanistic feathers, mainly on back, belly and flanks. Carotenoids deposition is not affected. Visible carotenoids at the back of this bird may be present in non-melanistic birds but masked by melanin (photo: Sergio Nolzaco, Lima city).

number of feathers without melanin after every moult. Progressive Greying may be or may not be inheritable; some forms may be related to age while in others the progressive loss of pigment cells may be due to disorders such as vitiligo or food deficiency. Progressive greying is mostly found in species that are black naturally like European Jackdaw *Corvus monedula* and European Blackbird (van Grouw 2012). In the latter species it is far more common in the black males than it is in the brown females.

Gaining white feathers with age in melanistic varieties in the Domesticated Duck *Anas platyrhynchos* is a common phenomenon (Crawford 1990).

Melanism is the most common polymorphism represented in birds (Mundy 2006). Many colour aberrations, including melanism, are heritable and show inheritance patterns that follow simple Mendelian principles involving one locus or a several loci.

Genetic basis of Melanism

Genetic studies in both mammal and bird species have identified several genes involved in melanism. Not surprisingly the most common are agouti (A) and extension (E).

Above is described how the normal production and deposition of the two distinct types of melanin is regulated. A tight cooperation between the melanocortin 1 receptor and the agouti signalling protein regulates the time, type and location of pigment resulting in the species specific feather patterns. However, mutations of the extension gene can create a melanocortin 1 receptor that constantly signals, even when not stimulated, or conversely can lower the receptor's activity. Alleles for constitutively active MC1R are mostly inherited dominantly and result in a black plumage colour. Alleles for dysfunctional MC1R result in a light plumage colour and are mostly recessive.

Beside mutations at the extension locus mutations of the agouti gene can cause melanism as well. A so called loss-of-function mutation in agouti, whereby no ASIP is produced and therefore MC1R will signal constantly, results in dark eumelanin plumage. Melanism caused by agouti alleles is mostly recessive



Figure 6. Melanistic chick (down) and non-melanistic chick (up). These birds are siblings from two heterozygous melanistic parents and a proof of dominant inheritance of melanism in *P. r. obscurus* (photo: Sergio Nolazco, Lima city).



Figure 7. Probable homozygous female (sex determined by behaviour). Note darker colouration appearance in comparison to heterozygous female at figure 8 (photo: Sergio Nolazco, Lima city).



Figure 8. Heterozygous female (sex determined by behaviour), mother of chicks at photo 6. Duller colouration appearance of underparts make carotenoids more visible and may be confusing but note there are no streaks on breast (exhibited by non-melanistic females) due to melanin spread inside whole breast feathers (photo: Sergio Nolazco, Lima city).

in inheritance, while alleles responsible for a constant production of ASIP, and therefore producing only phaeomelanine, are mostly dominant.

The inheritance of melanism in the Vermilion flycatcher was unknown until recently. The presumption of the authors was that it would be dominant but this was mainly based on the high amount of melanistic individuals in the population. However, a high proportion of dark specimens in a



Figure 9. Probable homozygous male (sex determined by behaviour). Such darker melanistic birds are always males (photo: Sergio Nolazco, Lima city).

population is not necessarily due to a dominant gene causing the dark morph. The dark colouration may have a positive influence on survival and maybe in proportion more melanistic youngsters reach adulthood than normal coloured ones.

Recently however the authors found proof for dominant inheritance as a normal coloured young was found, together with a melanistic sibling, in a nest of two melanistic parents (figure 6). The dominant nature



Figure 10. Heterozygous male (sex determined by behaviour), father of chicks at figure 6. In these male birds it is very difficult to determine sex just by plumage colouration as they look very similar to female homozygous birds (photo: Sergio Nolzco, Lima city).

of the gene for melanism may explain the difference in intensity between melanistic specimens (Figure 7, 8, 9 and 10). The darkest specimens may be homozygous for melanism while the less dark birds carry only one gene for melanism in their genome (heterozygous). More observation and research is necessary to clarify this but fact is that both parent birds mentioned above are heterozygous and not intensely dark.

Given the dominant inheritance the dark plumage is likely due to a mutation of the extension gene that constantly activates the MC1R. However, exceptions are possible and therefore a mutation at the agouti locus whereby the absence of ASIP the final cause for the dark plumage is can't be ruled out.

Plumage colour-dependent selection; yes or no?

Over 300 bird species are known for exhibiting polymorphisms (Galeotti *et al.* 2003). In general polymorphism is expected to have important effects on fitness and survival. Some research is done at the fitness effects of melanistic morphs and positive effects are found for example in the Feral pigeon *Columba livia* (Murton *et al.* 1973; Haag-Wackernagel *et al.* 2006). It appeared that the plumage colour of juvenile Feral pigeons is associated with features that influence its survival to adulthood in the urban environment. Strongly melanized fledglings are more likely to become adults, compared with the wild type colour (Haag-Wackernagel 2006).

Colouration per se may not have a direct influence on survival, but there could be a link between plumage colouration and behavioural and physiological characteristics associated with survival. In general, Feral pigeons in the centres of large cities show more melanized phenotypes and fewer wild type colouration than Ferals of small towns and in natural or rural areas.

There is also some evidence in Feral pigeons that melanistic males have a longer breeding season and are more fertile than the wild-type (Murton *et al.* 1973).

Differential fitness could also play a role in the higher frequency of melanistic Vermilion flycatchers in the urban areas of Lima compared with the normal coloured ones in the more rural environments. The main hypothesis is an adaptive advantage for camouflage against predators for melanistic birds. However, given that the bright plumage morph is very common in other highly urbanized areas across its global distribution range, it is reasonable to assume that the high frequency of melanistic vermilion Flycatchers in Lima can't be explained as natural selection on camouflage only. Therefore other causes for the survival rates of melanistic vs. non-melanistic birds might be considered. In the Feral pigeon for example, evidence for higher fertility and a tendency towards having a longer breeding season is found in the melanistic morphs (Murton *et al.* 1973). According

to Ballón (1994) there is a higher frequency of melanism in Rímac river basin, while a lower frequency corresponds to areas closer to Chillón and Lurín rivers. However, he came to his findings without measuring the degree of urbanization for each bird count plot. His findings do not rule out the possibility of an originally small and isolated population with a high frequency of melanistic individuals located in Rímac river basin before urbanization. Lima city as a first point started in Rimac river basin and expanded in later days to other areas like Lurin and Chillon basin. Therefore the actual pattern of phenotypes can be the result of recent hybridization between former isolated populations which are now connected due to the urbanization.

Pearson's chi square test for hypothesis on plumage colouration assortative mating for *P. r. obscurus* show no significant evidence at $\alpha=0.05$ ($\text{Chi}^2=1.75$, $\text{df}=1$, $p=0.19$; table 1). So, other traits may be acting on partner selection such as territory quality. But what are the implications of this? If there is no kind of sexual selection directly linked to plumage colouration itself, phenotypic frequency patterns might be different than expected and simply based on the natural selection of fitness. It might be considered that melanism indirectly favours the fitness of the dark individuals (in urban environment) but evolution in the species is not that far yet that it already affects the partner choice based on dark colouration. If the urban environment indeed plays an important role is not clear as the dark morph was already very common in the 19th century (Taczanowski 1884), before urbanisation. It is possible that the differences in frequency are still the result of recent hybridisation between an original melanistic population and non-melanistic populations after Lima city expanded.

Other aberrant plumage colourations in *P.r.obscurus*

Besides melanism there are many other genetic mutations which cause colour aberrations in birds. The mutation Brown is widespread amongst all bird species and it is probably the most frequently encountered heritable colour aberration in birds in general (van Grouw 2006, 2010, 2012). The mutation Brown is defined as a qualitative reduction of eumelanin. In this mutation the number of eumelanin pigment granules remains unchanged but the appearance of the pigment is changed: the eumelanin synthesis process is incomplete as the eumelanin is not fully oxidised. As a result the pigment will not become black but will remain dark brown, although the quantity of pigment remains the same. The phaeomelanin, if present, is unaffected.

In many species, like the Vermilion Flycatcher, eumelanin that is not fully oxidised is part of the original plumage colour. So in these cases, as a result of the mutation Brown, the original dark brown feathers will turn light brown, because the eumelanin will be less oxidised than in the original colouration (figure 11). Aberrations due to incompletely oxidised eumelanin are very sensitive to sunlight and will bleach quickly and strongly. Therefore old plumage is often almost white and for that reason sometimes hard to distinguish in the field. For a correct identification, try to see parts of the plumage that should be less influenced by sunlight, such as the inner webs of flight feathers when the bird is stretching its wings. This should determine whether the plumage has been bleached differentially by the light. 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.



Figure 11. 'Brown'. Note light brown colouration due to less oxidised eumelanin. Carotenoids are not affected by this mutation (photo: Alejandro Tabini, Lomas de Lachay).

The inheritance of Brown is recessive and sex-linked in all bird species. The sex-linkage means that a Brown individual with normal-coloured parents is always female and this is why only Brown females are seen in the wild. 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 (van Grouw 2012).

The red carotenoid pigment is not affected by the mutation Brown and remains clearly visible. Changes in carotenoid colouration are mainly not heritable and are caused by food deficiency. Although carotenoid

mutations are rare; they do occur. The most common mutation is a 'dilution' of the colour. Dilution can be defined as a quantitative reduction of pigments. So in dilution mutations the amount of pigment is reduced but the actual pigment itself is not changed. Therefore, due to a lower concentration of pigment than normal, a 'weaker' or 'diluted' colour is observed. Dilution of melanins only is quite common but carotenoid dilution is rare. Dilution of melanins does not affect carotenoid and visa versa. Carotenoid dilution in the Vermilion Flycatcher will cause an orange colour in combination with normal melanin pigmentation (Photo 12). Melanin dilution will give a pale greyish bird with the normal red colouration in the head plumage and under parts.



Figure 12. 'Carotenoid Dilution'. All typical red carotenoids turn orange due to a quantitative reduction of this pigment. The melanins are not affected by this mutation (photo: José Luis Venero, Pantanos de Villa, 1983).

CONCLUSION

Common melanistic phenotype in the Vermilion Flycatcher, subspecies *obscurus*, is a consequence of dominant inheritance. The variable degree of intensity exhibited within each sex suggests to be the result of being either homozygous or heterozygous for the gene causing melanism. Other, rare, plumage colouration aberrations in the subspecies are 'Brown' and 'Carotenoid Dilution'.

Mating couples were composed by individuals of the same and different morphs with no evidence on assortative mating related to plumage colouration. The actual pattern of higher melanistic phenotype frequencies on the highly urbanized area and lower

frequencies to the outskirts may be a result of natural selection forces acting in favour of melanistic birds at urban sites. However, it might be considered that the urban environment does not influence the survival rate of the melanistic individuals and that the phenotype frequency is still a result of a recent hybridization between previous isolated populations.

Further research on this topic is necessary to understand the mechanisms controlling actual phenotype frequencies pattern.

Acknowledgments

Thanks to Alejandro Tabini, José Luis Venero and Ernesto Málaga for their photographic contributions, Lourdes Falen, Rosaura Watanabe, Eveling Tavera, Cynthia Sánchez and Angélica Rodríguez for their help in field data collection, CORBIDI for ring donations and institutional support, Botanical Garden from 'Patronato Nacional del Parque de las Leyendas' and 'Universidad Nacional Agraria La Molina' for allowing us to work inside their properties. Special thanks to Robert Jiménez and Carmen Deza for their interest in the topic and their continuous support for working inside the Botanical Garden.

REFERENCES

- Ballón, G. 1994. Frecuencia Fenotípica y Genotípica de *Pyrocephalus rubinus obscurus* Gould (Aves: Tyrannidae) en la ciudad de Lima, Perú. Tesis para optar el título profesional de biólogo. Universidad Nacional Mayor de San Marcos. Lima, Perú.
- Crawford, R.D. 1990. Developments in Animal and veterinary Sciences, 22: Poultry breeding and Genetics. Elsevier, Amsterdam.
- Galeotti P., Rubolini D., Dunn P. O. and Fasola M. (2003). Colour polymorphism in birds: causes and functions. *Journ. Evol. Biol.* 16: 635-646.
- Gould, J. (1839). *Zoology of the voyage of H.M.S. Beagle*, 3, Birds: 45.
- Grouw, H. van, 2006, Not every bird is an Albino; sense and nonsense about colour aberrations in birds. *Dutch Birding* 28(2): 79-89.
- Grouw, H. van, 2010. How to recognise colour aberrations in birds (in museum collections). *Journal of Afrotropical Zoology*, special issue-2010: 53-59.

Grouw, H. van, 2012. What colour is that Bird, Part 1: How to recognize and name colour aberrations in birds, *British Birds* (in press).

Grouw, H. van and J. de Jong. 2009. *Genetica bij Duiven, Modern Mendelisme en meer voor de Duivenliefhebber* (Genetics in the Pigeon, Modern Mendelism and more for the Pigeon Fancier). NBS, Surhuisterveen.

Haag-Wackernagel, D. 2006. Phenotype-dependent selection of juvenile urban Feral Pigeons *Columba livia*. *Bird Study* 53: 163-170

Hiragaki T., Inoue-Murayama M., Miwa M., Fujiwara A., Mizutani M, Minvielle F. and Ito S. 2008. Recessive black is Allelic to the yellow Plumage Locus in Japanese Quail and associated with a Frameshift Deletion in the ASIP Gene. *Genetics* 178: 771 - 775.

Kerje S., Lind J., Schütz K., Jensen P. and Andersson L. (2003). Melanocortin 1-receptor (MC1R) mutations are associated with plumage colour in chicken. *Animal genetics* 34(4): 241-248.

Kimball, R.T. 2006, Hormonal control of coloration. In: Hill, G.E. and K.J. McGraw, 2006. *Bird Coloration, Volume I Mechanisms and Measurements*, Harvard University Press.

Lamoreux M.L., Delmas V., Larue L. and Bennett D.. 2010. *The Colors of Mice a Model genetic Network*. Wiley-Blackwell, Chichester, UK.

Mundy, N.I. 2005. A window on the genetics of evolution: MC1R and plumage colouration in birds. *Proceedings of the Royal Society B* 272: 1633-1640.

Mundy, N.I. 2006. Genetic basis of color variation in wild birds. In: Hill, G.E. and K.J. McGraw, 2006, *Bird Coloration, Volume I Mechanisms and Measurements*, Harvard University Press.

Murton R.K., Westwood N.J. and Thearle R.J. (1973). Polymorphism and the evolution of continuous breeding season in the pigeon *Columba livia*. *Jour. Reprod. Fert. Suppl.* 19: 561-575.

Hiragaki T., Inoue-Murayama M., Miwa M., Fujiwara A., Mizutani M, Minvielle F. and Ito S. (2008). Recessive black is Allelic to the yellow Plumage Locus in Japanese Quail and associated with a Frameshift Deletion in the ASIP Gene. *Genetics* 178: 771 - 775.

Taczanowski, W (Ladislav) (1884). *Ornithologie du Pérou*. Vol. II. Oberthur, Paris.

Vidal, O., J. Vinas and C. Pla. 2010a. Variability of the melanocortin 1 receptor (MC1R) gene explains the segregation of the bronze locus in turkey (*Meleagris gallopavo*). *Poultry Science* 89; 1599-1602.

Vidal O., Araguas R.M., Fernández E., Heras S., Sanz N. and Pla C. 2010b. Melanism in guinea fowl (*Numida meleagris*) is associated with a deletion of Phenylalanine-256 in the MC1R gene. *Animal Genetics* 41: 656-658.

Zimmer, J.T. (1941). *Studies of Peruvian birds. XXXVIII. The genera Oreotriccus, Tyrannulus, Acrochordopus, Ornithion, Leptopogon, Mionectes, Pipromorpha, and Pyrocephalus*. 1126:25pp.

Mating couples combinations	Observed	Expected
<i>Female melanistic x male melanistic</i>	18	16
<i>Female non-melanistic x male non-melanistic</i>	8	6
<i>Female melanistic x male non-melanistic</i>	10	12
<i>Female non-melanistic x male melanistic</i>	6	8

Table 1. Mating couples combinations between melanistic and non-melanistic individuals. Observed values based on 42 confirmed mating couples and its expected values by chance.