

swamp was seen to be followed—like gulls behind a plough—by a dozen Lily-trotters, *Actophilornis africanus* (Gmelin) eagerly darting hither and thither to feed on the aquatic life being stirred up.

A somewhat similar incident was witnessed in Uganda on the River Nile, in the Murchison Falls National Park, a little later when a frightened crocodile moved through a shallow pool covered with floating vegetation, mainly Nile cabbage (or lettuce), *Pistia stratiotes*. A Lily-trotter, with butterfly-wise flicks of its wings, skipped across the backs of two other crocodiles to pick up the aquatic organisms which had been disturbed. In the course of the same trip, a Goliath Heron, *Ardea goliath* Cretzschmar, was seen standing on the back of a semi-submerged hippopotamus—one of a small huddle—close to the bank.

In Uganda's Queen Elizabeth National Park, at a place where a wallow harboured a huddle of 90+ hippos alongside a breeding colony of the Yellow-backed Weaver, *Ploceus melanocephalus dimidiatus* (Antinori and Salvadori), these weavers were incessantly flying down and perching on the animals, on which were also perched one Hammerkop, *Scopus umbretta bannermani* C. Grant, and a few Buff-backed Herons or Cattle Egrets, *Bubulcus ibis* (Linn.). In another wallow in this Park, where an astonishing huddle contained 200+ hippos, a few of these creatures, which were nearest to a Nile cabbage-covered shallow lagoon had Cattle Egrets on their backs.

At a wallow in the same Park where several bull buffaloes, four giant forest hog and one warthog were disporting, it was noticed that Oxpeckers, *Buphagus africanus* Linn. were in attendance on the buffaloes and warthog, but not on the very hairy (coarse long-haired) giant hog.

Albinism and melanism in birds (as illustrated by the Mallard) and their possible significance

by JAMES AND JEFFERY HARRISON

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INTRODUCTION

This communication is to be regarded as supplementary to our previous papers (1957, 1961). Albinism and melanism often appear as striking discontinuous variations in many different species, but one has also to recognise the fact that in dimorphic species such phases form part of a normal morphology.

Examples come readily to mind, one of the best known being, of course, the melanistic mutant of the covert pheasant, *Phasianus colchicus* var. "tenebrosus", other instances being the black phases of Montagu's Harrier, *Circus pygargus* (Linnaeus), Arctic Skua, *Stercorarius parasiticus* (Linnaeus) and Reef Heron, *Egretta schistacea* (Ehrenberg). In East Africa the Little Egret, *E. garzetta* (Linnaeus) has melanistic phases ranging through a pale lavender grey, sooty grey, slaty grey to a blackish slate, while as an example of a species having a blue form one may cite the Lesser Snow Goose, *Anser coerulescens coerulescens* Linnaeus.

Genetically albinism is explained by the recombination of recessive genes giving rise to a state of recessive dominance, while the dominance

of black over white is known to be due to lack of tyrosinase, the precursor of melanin in the white individuals.

The genetic investigation of such phases in the wild, however, presents great difficulties. Melanism forms a not unusual character of sexual dimorphism in some species, a familiar example being provided by the jet black male of the Blackbird, *Turdus merula* Linnaeus, while again it can appear precipitously and mysteriously as in the case of a female Red-billed Dioch, *Quelea quelea* (Linnaeus) reported by Disney, Lofts and Marshall (1961) and apparently due to captivity conditions, as many thousands of wild specimens had been examined without a single case of melanism being observed. This problem has since been investigated by Lofts (1961) and it was established that captivity melanism could be reversed by a brief exposure to ultra-violet light during the moult.

It is well known that through the pressure of natural selection many melanistic forms enjoy a survival advantage, for instance in areas of industrial contamination, or on dark soils, as in the cases of the black form of the Peppered Moth, *Amphidiasis betularia* (Linnaeus) var. "*double-dayaria*", and the Peat Partridge, *Perdix perdix sphagnetorum* (Altum).

The classification of albinistic subjects may still be regarded as somewhat arbitrary, and the condition can range through rather haphazard mosaics, resulting from the mating of an individual carrying a recessive gene for white with a normal individual. In such cases varying degrees of the pied state result in the progeny, conforming to the laws of Mendelian inheritance, and these always have normal coloured irides, though the other soft parts may share in the pied condition.

Such individuals are not true albinos, for they are constitutionally virile and well able to compete with individuals of normal colour. The true albino, with colourless (pink) irides and the other soft parts lacking all pigment, is to be regarded as pathological with a poor survival prospect. In previous papers (1957, 1961, *loc. cit.*) instances of a definite albinistic pattern have been given. Thus, in an inbred Mallard population this was seen as an increasing symmetrical albinism of the primaries of both sexes associated with the enlargement of the white neck ring in drakes and the appearance of a white chin spot. Both of these features gradually enlarge and coalesce and finally a completely white individual results. This effect is known to have come about without the influence of any white call-ducks and furthermore, similar patterns are found in the Mandarin, *Aix galericulata* (Linnaeus) and Salvadori's Duck, *Anas waigiensis* (Rothschild and Hartert).

The occurrence of albinism in an inbred population of the Grey Lag Goose, *Anser anser* Linnaeus is also noted from Castlecoole, Co. Fermanagh, Ireland by Deane (1954).

In the Carrion Crow, *Corvus corone* Linnaeus and the Jackdaw, *Corvus monedula* Linnaeus, a distinctive albinistic patterning takes the form of white wing-bars appearing on the primaries and secondaries, and occasionally this is associated with a white or light bar on the proximal part of the tail feathers, (J.M.H., 1957). As a further example of the leucistic pattern one may mention the "mottled" Rook.

Many species other than the ducks already mentioned have been recorded with symmetrical albinistic primaries, and this is particularly

frequent in the domestic pigeon, often in association with an albinistic tail.

The domestic Muscovy Duck, *Cairina moschata* (Linnaeus) is another excellent example, for a majority in this country now constantly have white primaries and white heads, while a grey-and-white barred and a leucistic variant also occur. A further example in which symmetrical depigmentation occurs with the production of white-banded wings is recorded by Fritz *et al* (1946). This was associated with a dietary deficient in lysine fed to bronze-wing turkey poults when it was established that from 1.1 % to 1.2 % is required to ensure normal growth and pigmentation, and that the condition could be reversed by administering crystalline lysine. Deficiency of pantothenic acid also gives rise to feather depigmentation.

The above findings are confirmed by the work of Vohra *et al.* (1956) on rats where greying of the hair resulted from a diet deficient in lysine. Kratzer *et al* (1950) referring to the work of Fritz *et al.* (*loc. cit.*) comment as follows, "From these experiments it may be concluded that lysine plays some rôle in the hair of rats as well as in the feathers of turkey poults". It is clear that lysine in some way, when deficient, interferes with the synthesis of melanin.

Albinistic patterning is not confined to birds, for in domestic mammals, the familiar "belted" variety is found in Galloway cattle and in saddle-backed pigs, while in the wild, an albinistic belted variant has been recorded in the Common Shrew, *Sorex araneus* (Linnaeus), by David Harrison (1957, 1961) and a bat *Scotophilus nigrita* Schreber, showing approximately symmetrical white wing markings, was obtained at Filabusi, Southern Rhodesia on 12th January, 1961. We are informed by Dr. David Harrison (*verbatim*) that symmetrical albinistic wing-patterning has so far been found in two families of bats, *viz.* in the Nycteridae and Vespertilionidae.

On 17th December, 1961, Dr. David Harrison obtained from Chevening a remarkable mutation in a dog fox, *Vulpes v. crucigera* Bechstein in which all four extremities are more or less white and which in general characters resembles the Asiatic form *V. v. pusilla* Blythe. A detailed description of this animal is in the course of preparation by him.

Such examples as these could be extended considerably, but they are sufficient to illustrate the point that they are in quite a different category to those of partial haphazard albinism, and in our opinion such are reversionary in origin.

Island and cave albinism are important to note for both these are isolating mechanisms favouring inbreeding and the exposure of recessive characters. Instances of the former are found in the Raven, *Corvus corax* Linnaeus in Iceland, though as a rarity, and formerly in the Faeroes, though now extinct, and in the Quail, *Coturnix coturnix* Linnaeus on the Azores. A well known instance in mammals is afforded by the white reindeer on Kolguev.

While all classes of Vertebrata show albinism it must be mentioned that in fish it is relatively rare. That the phenomenon is very widespread is emphasised by the fact that it occurs widely in the Invertebrata, a circumstance which stresses such cases as fundamental in nature.

It is necessary here to refer to traumatic albinism. In mammals Duerst

(1926) and Schultz (1918) have shown that this state can be induced by the experimental infliction of wounds which, on healing, have grown long white hairs. In birds the repeated plucking of feathers from the same area has resulted in depigmentation. Noorduijn (1905), Pearl and Boring (1914), Krizenecky (1930) have confirmed that albinism resulted by plucking in two different breeds of domestic fowl and the same author (*loc. cit.*) records another case of asymmetrical albinism in a Green Woodpecker, *Picus viridis* Linnaeus in which the right wing showed two white secondaries and some white wing-coverts which it was presumed were due to healed gun-shot wounds. Nero (1960) working on the Red-winged Blackbird, *Agelaius phoeniceus* (Linnaeus) has obtained somewhat anomalous results to traumatic albinism by plucking, for by producing forced moults in the black innermost wing-coverts he succeeded in the third regeneration in producing pied feathers. Significantly he also succeeded in producing a definite depigmentation from the bright red of the "epaulets" of the fully adult male to an orange-brown colour by repeated plucking. In the experiments carried out he was able to exclude sex hormone as responsible for the changes produced. However, even this experimental depigmentation was not entirely constant for one specimen regrew scarlet "epaulets" which were actually brighter than those of the normal bird, and it was noted that some individuals regrew depigmented, *i.e.* orange-brown feathers which were also black spotted. It is, however, stressed that the "epaulets" in immatures are normally highly variable ranging in colour from yellow to reddish-orange.

It would seem, therefore, that although it has been established that traumatic albinism and traumatic depigmentation occur, the aetiology of the condition is uncertain and experimental responses are variable. It is our opinion that as a natural phenomenon it cannot but be regarded as a rare cause for either state in the wild. Such cases would appear to be on a parallel with the sudden blanching of the hair in a human subject following a severe illness, shock following trauma or grievous emotional disturbance. Some cases of depigmentation in game birds could also possibly result from traumatic shock resulting in an endocrine imbalance. This loss of melanin is referred to by Fox and Vevers (1960) in the following terms "As a final instance of loss of melanin it may be noted that injury can be responsible for the disappearance of melanocytes. Thus they may be destroyed in the dermal papillae of hairs by X-ray, after which subsequent hairs are white. In bay and chestnut riding horses, new hair growing from healed saddle sores is likewise white."

DISCUSSION

The inter-relationship between natural selection and habitat is universally admitted and it is not without interest to examine some of the very contrasting colour types which can coexist and survive equally successfully in a marine or coastal environment. The contrastingly pied Alcidae bear this out. Of especial interest within this group one may mention as typical amongst others the Common Guillemot, *Uria aalge* (Pontoppidan) and the Black Guillemot, *Cephus grylle* (Linnaeus) with its wholly black mutant form *C. g. "motzfeldi"*. Examples in the Anatidae are afforded by the European Scaup, *Aythya marila* (Linnaeus) and New Zealand Black Scaup, *A. novaeseelandiae* (Gmelin).

Exactly parallel examples of species inhabiting a coastal terrain are to be found in the Oystercatchers, for the New World representative of *Haematopus ostralegus* Linnaeus, *H. o. palliatus* Temminck coexists on the western coast of North America with the Black Oystercatcher, *H. o. bachmani* Audubon. In Australia also the Sooty Oystercatcher, *H. fuliginosus fuliginosus* Gould further exemplifies the point that neither a marine nor a coastal habitat would appear to impose very rigid adaptations on the bird-life inhabiting them, whereas a terrestrial environment indisputably demands a closer assimilation as a condition of survival.

These generalisations are not irrelevant to our subject as can be seen from the series of Mallard, *Anas platyrhynchos platyrhynchos* Linnaeus of both sexes in illustration. From what may be described as an average normal drake, and an average normal duck, the full range of variation from the pure white to the melanistic mutation and the so-called "Cayuja" type Mallard is shown.

In a paper Sage (1955) suggests that the type of Mallard in which there is a general darkening of the plumage, the under parts of which vary from a rather dark bay to a richer somewhat chestnut colour, results from hybridisation with *A. clypeata* Linnaeus. This condition is often linked with the white chin spot and the white patch on the breast, both variable in extent as we have shown in our recent paper (1961 *loc. cit.*). We have now examined numerous individuals showing these characters and find ourselves unable to subscribe to the suggestion that these are hybrid *A. p. platyrhynchos* x *A. clypeata*. In our paper referred to above, the same incipient mutation is shown in the plate depicting a drake and duck of *Aix galericulata*, while we have a drake (wild shot) of what is apparently a hybrid between *A. p. platyrhynchos* and *Cairina moschata* which shows a similar combination of characters associated with frank melanism.

Are we then, on Sage's interpretation, to assume that in these quoted cases there is *A. clypeata* blood to account for the variable white marking at the root of the neck? We think not, and regard this special type of variation as due to an excess of melanin and the white breast markings as due to variable albinistic patterning referred to in our previous communication.

Probably the only other species of which a sufficiency of material exists and in which a similar gradation of characters of this nature could be demonstrated is the covert pheasant, *Phasianus colchicus* Linnaeus, a species which, like the Mallard, has been subjected to the same selective pressures under domestication and semi-domestication by man.

It is significant that symmetrical white primaries occur constantly in the chicks of the melanistic mutant pheasant, *P. c.* var "*tenebrosus*" in the first definitive plumage, as well as albinism of the head and neck. A similar mutation is found sporadically also in the juvenile plumage of some otherwise normally-coloured birds of this species.

Further instances can be seen in the many varieties of the domesticated pigeon where, for example, in the Fan-tail there is a pure white as well as a wholly black variety, while, of course, many rather nondescript varieties frequently show symmetrical white primaries.

It has already been stated that albescence, as well as, doubtless, many

other mutations depend upon the recombination of recessive genes giving rise to recessive dominance. This, of course, explains the genetic mechanism involved, but does not in any way account for the very widespread prevalence of albinism in the animal kingdom.

We feel that in view of this overall prevalence the phenomenon must depend upon some deep and fundamental cause. Albescence *per se* cannot be regarded as a pathological state for reasons already given.

While of course speculative, we would suggest that albinistic patterns, and probably also some of the other heterochromisms are atavistic in origin. It is, in our view, most probable that all early forms of life were self-coloured and that patterning came in at a much later stage in the evolution of all species. A curious structural alteration is associated in the Water Hen, *Gallinula chloropus* (Linnaeus) as recorded by Fitzherbert-Brockholes (1885), Stevenson (1885) and Forrest (1901) and recently in a Jay, *Garrulus glandarius glandarius* Linnaeus, by one of us (J.M.H., 1951) in connection with atavistic characters. These so-called "hairy albescents" show a primitive type of feather structure in which the intricate interlocking mechanism of barbs, barbules and hooklets is lacking, the plumage in consequence being hair-like, loose and soft. These cases lend further support to the suggestion that albinism is basically atavistic.

That this curious alteration in feather structure is inherent possibly in many species, though only a rare mutation in nature, would seem proved by the production by selective breeding of "frizzled" or "silky" mutants in both poultry and canaries.

Intensive in-breeding and similar factors operating in the wild would result in setting this process of patterning in reverse, as we believe we have shown in the Mallard series in illustration of this and our previous paper (1961 *loc. cit.*) already referred to.

In conclusion we would suggest that this phenomenon as seen in the Mallard is worthy of specialised and detailed genetic analysis. Ecologically the Mallard is successful equally as a coastal and inland species. In its long evolutionary history there may have been stages when it was self-coloured. From this, in an aquatic habitat, it may well have developed any of the well known and varied varieties including both a white and a melanistic form before acquiring by suffusion the pattern and morphology as we know it to-day, for as already stated, black species, contrastingly pied species and white forms can all survive equally successfully in such a habitat.

In this connection we would suggest that the Black Duck, *Anas sparsa* species complex, and the Hawaiian Duck, *A. p. wyvilliana* all represent forms which have evolved from the melanistic phase of the Mallard.

On this basis it is possible to offer a broad explanation of the different colour aberrations, particularly albinistic and melanistic varieties, to which the Mallard is subject, and indeed similar mutations in other species might well be strictly comparable on the premise that in evolution self-colour almost certainly preceded patterning.

The virtually universal prevalence of such discontinuities throughout nature supports the hypothesis that the phenomena discussed are basically fundamental in origin and are to be regarded as reversions to less specialised ancestral types. That they are discontinuities is in itself sig-

nificant and evidence that such are retrograde and that they do not represent progressive evolution.

It is clear that in so far as depigmentation is concerned there is ample experimental evidence of its production and reversal by manipulation of



Range of variation in Mallard from the average normal drake and duck to albinism and melanism.

the diet in respect of the lysine content as well as by physical agents. Since a fractional amount of lysine is vital to normal pigmentation and growth, a very sensitive balance is demonstrated.

In work previously published by one of us (J.M.H., 1957. *loc. cit.*) on similar white wing-barring in corvines, in-breeding was advanced as probably causative, and it is of course well known that in-breeding favours mutation, while the relationship between a possible lysine deficiency and white wing-barring in birds living free remains obscure. As carrion feeders

one would have thought that corvines would be the last to suffer from a lysine deficiency as a cause of white wing-barring since that substance results from the decomposition of proteins which constitutes a large part of the dietary of crows.

SUMMARY

In this paper we have considered the problems and implications of albinism and melanism in birds.

A broad classification of albinism is given and a sharp distinction is drawn between haphazard mosaic albinism and symmetrical albinistic patterning; also between the true and pathological albino and the white, but nevertheless virile and otherwise normal variant. Island, cave and traumatic albinism are discussed as also the depigmentation associated with lack of certain biochemical factors.

Many instances of albinism and melanism are regarded as atavistic states, and white and black plumages in birds are regarded as originating from such in response to natural selection. Symmetrical albinistic patterning is also regarded as atavistic in origin and as derived from self-coloured atavistic forms. The association of a structural alteration in feathers in the presence of albinism is noted.

The swing from pure white to black individuals in the Mallard is demonstrated by specimens and certain normally black species are regarded as the result of evolution from early melanistic phases.

It is suggested that contrasting colour phases can coexist in an aquatic or coastal habitat equally successfully and that this circumstance finds convincing support in the diametrically opposed phases of various species found coexisting in such environment.

Natural selection acts far more stringently in terrestrial habitats, as is evident by the very restricted distribution of certain species found only on certain soils and in cases where the melanism has little, if any, bearing on sexual dimorphism.

The principles involved postulate that self-colouring, including possibly total absence of colour, i.e. a white phase preceded the suffusion of pattern in all early forms of life, a speculative surmise which finds support in the widespread prevalence of albinism, not only in the vertebrate but also in the invertebrate animal kingdom.

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Some recommendations for a revised check-list of the genera and species of grebes (Podicipitidae)

by K. E. L. SIMMONS

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The grebes form a small, well-defined group very suitable for taxonomic study along modern lines. Rather surprisingly, the only recent check-list (not quite complete) is that of Peters (1931), though Hellmayr and Conover (1948) dealt with the numerous American forms. The present note gives some recommendations for a revised list of the genera and species of the Podicipitidae, based on a recently completed survey of the biology and morphology of the family to be published in full elsewhere, together with a detailed discussion of conclusions only mentioned or summarized briefly here. I would be most grateful for any comments on, or criticisms of this preliminary statement from interested workers, either with reference to the key problem of the biological aspects of the proposed classification or to its purely nomenclatural side.

The basic work on skins was done in the National Collection at the Bird Room of the British Museum (Natural History) by kind permission of the Director. I am indebted to the staff of the Bird Room for facilities.

PETERS' (1931) ARRANGEMENT

Peters (1931) listed thirty-nine forms which he arranged in five genera and eighteen full species. His arrangement may be summarized as follows:

Genus POLIOCEPHALUS. Subgenus TACHYBAPTUS.

Species: (1) *P. ruficollis* (ten races); (2) *P. pelzelinii* (monotypic) (3) *P. dominicus* (three races).

Subgenus POLIOCEPHALUS.

Species: (1) *P. rufopectus* (monotypic); (2) *P. poliocephalus* (two races).

Genus COLYMBUS.

Species: (1) *C. rolland* (monotypic); (2) *C. chilensis* (monotypic); (3) *C. occipitalis* (two races); (4) *C. taczanowskii* (monotypic); (5) *C. auritus* (monotypic); (6) *C. nigricollis* (three races); (7) *C. cristatus* (four races); (8) *C. grisegena* (two races).



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