covered with jungly rain forest, its tall trees and undercover closely packed, and interlaced with a tangle of rope-like lianas.

The presence of the Lyre-tail in this forest became evident almost at once. At 8 a.m. on the 4th of April, as my guide and three other men were entering the village with me, the unmistakable sounds made by a Lyre-tail in flight came through the crisp air from the direction of the forest. We stood listening, fascinated by the noise, which seemed at first to come from afar, yet gradually to approach us. We agreed that its maker must be about three-fourths of a mile away as the performance ended. This was a morning of brilliant sunshine, yet with mist in the valley. The Lyre-tail gave its serenade four times, only at intervals.

Thereafter it seemed to repeat its performance almost daily until the 4th of May. We listened to it on thirteen different days during that period, sometimes only once in a day, but more often two, three, or four times, and on the 19th of April even five times. On the 12th of April a Lyre-tail was judged to have passed within 200 yards of the village in one long continuous flight of almost a half-mile. We heard the bird only on sunny mornings, around 8 or 9 o'clock, but none was heard after the 4th of May, although I remained in the vicinity until the 12th of June. On wet, misty mornings the Lyre-tail remained silent, at least until the fog had been dissipated and the sun came out warm and brilliant.

Many natives, here of the Yakoba tribe, were familiar with the noise and referred to it as "zierre"; but not one of them seemed to know it was produced by a small bird. A group of men and women from a place one full day's walk to the south-east of Yále assured me that they frequently heard the same sounds while working in their coffee plantations. I was convinced they knew it well, but all my efforts to secure a specimen of *Melichneutes* went unrewarded.

On my way back to the coast I stayed for thirteen days at Man, but never did I hear the Lyre-tail there. In any case we may now be certain that the range of the elusive Lyre-tailed Honey-Guide is not restricted to the rain forests of Lower Guinea, including Southern Nigeria, but extends westward to the high forests of the Nimba Mountains, near the junction of the Ivory Coast, Guinea, and Liberia. This is at approximately 7½ degrees of north latitude and 8 degrees of west longitude, some 170 miles inland from the coast.

A Gadwall with a white neck ring and a review of plumage variants in wildfowl

by James M. and Jeffery G. Harrison

Received 27th December, 1962

Through the kindness of the Wildfowl Trust, we have recently received on loan the skin of an adult drake Gadwall *Anas strepera* Linnaeus with a pronounced white neck ring. The bird was shot by Lord William Percy on 25th February, 1913 on South Uist, Outer Hebrides, and was presented to the Trust by him together with the rest of his wildfowl collection.

In our previous note (Harrisons 1959 A) we have recorded this variant in three out of twelve drake Gadwall in our collection, so that it is reasonably common. This example is, however, quite the most marked of any

we have seen, the ring being almost comparable to that of a drake Mallard Anas platyrhynchos Linnaeus, as can be seen from the photograph. In addition, the ground colour of the neck and throat, instead of being whitish-brown, is pale chestnut, which also extends to a lesser degree onto the cheeks. On account of these two striking variations, Lord William Percy had labelled the bird as a hybrid Gadwall X Pintail Anas acuta Linnaeus, which is an understandable error.

On re-examining our series of Gadwall, we find that one of our three examples (November 1933, Rainham Hall, Kent) also shows this chestnut colour on the throat and neck, as does a further unrecorded example with a white neck ring shot in north Kent in November 1959 (coll. J.M.H.) and it would seem that these two variant characters may be linked.

The South Uist bird and the one we recorded from Lough Erne, Co. Fermanagh, were presumably of Icelandic nesting stock and it is noteworthy that on 1st July, 1962 a drake Gadwall was seen by one of us (J.G.H.) with a well-marked white neck ring, in Reykjavik.

The presence of the white neck ring variant in drake Gadwall probably provides further evidence of the close relationship of this species to the Falcated Teal Anas falcata Georgi, in which the drake as part of the elaborate pattern of the head and neck, also has a constant and well developed white neck ring. We were wrong in attributing this character in our earlier paper (loc. cit.) on Gadwall variants to a Mallard relationship.

Discussion: It is desirable to consider the significance of this and the other variant characters which have been described in wildfowl, both with and without the influence of interspecific hybridisation. C. J. O. Harrison (1963) considers that these variant characters have no greater phylogenetic significance than that the species displaying them belongs to the Anatidae, or even to some higher taxonomic unit, whereas we regard many of these characters as indicative of a closer relationship at the levels of genus and species. That plumage characters are sufficient to justify this assumption is supported by Delacour (1956) who writes: "There is even good evidence that the Shovelers do not constitute a monophyletic group: the South American Red Shoveler (platalea) and the Cinnamon Teal (cyanoptera) on the one side; the Australian-New Zealand Shoveler (rhynchotis) and the Blue-winged Teal (discors) on the other, greatly resemble each other in plumage pattern, so nearly that the closest relationship must be assumed*".

The following variants appear to provide additional evidence of affinity in races or in species well known to be closely related on other morphological and behavioural characters:—

1. VARIANTS WITHIN THE SPECIES

- (a) The spotted breast shield of the Mallard. This is present throughout the range, but only as an unusual variant in the typical race Anas p. platy-rhynchos, being increasingly common in the Icelandic population and constant in the sedentary Greenland race Anas p. conboschas Brehm (Harrison, J. G. 1944). This is a good example of Huxley's morphic cline.
 - (b) The black V on the chin of the Eider. This is constant in drakes of the

^{*}Our italics.

Pacific Eider Somateria mollissima v-nigra and is found occasionally in the other races (Delacour 1959). It is a constant feature of the King Eider, Somateria spectabilis Linnaeus, and is therefore another example referable to Group 2. It is even present in "ghost" form in a first summer drake obtained in west Greenland in 1963.

(c) Transient white neck ring in Pintail. See white neck spots and rings, Group 3a.

2. VARIANTS RESEMBLING A CLOSELY RELATED SPECIES

- (a) The barred and spotted breast shield of the Wigeon. This is a not uncommon variant in drake European Wigeon Anas penelope Linnaeus and the same markings are constant in the Chiloë Wigeon Anas sibilatrix Poeppig (Harrisons 1957 A).
- (b) The barred underparts of the Northern Shoveler. Three of a series of 33 drake Northern Shoveler Anas clypeata Linneaus had dark barring covering the whole of the underparts, a character found in the Cape Shoveler Anas smithi (Hartert) and the Australasian Shovelers Anas rhynchotis Latham. (Harrisons 1959 B).
- (c) The pale facial crescent of the Northern Shoveler. This is a transient character only shown particularly by first year drakes in moult and is beautifully illustrated by Peter Scott in Delacour (1956). This character is constant in adult drakes of the Australasian species A. rhynchotis (Harrisons 1959 B).
- (d) The white facial band of Tufted Duck. This is a frequent variant in female Tufted Duck Aythya fuligula Linnaeus and it is occasionally as extensive as in female Greater Scaup Aythya marila Linnaeus; Lesser Scaup Aythya affinis Eyton and New Zealand Scaup Aythya novaeseelandiae Gmelin. (Harrison, J. G. 1954 A). It is illustrated by Peter Scott in Delacour (1959).
- (e) The dark flecking on the under parts of Tufted Duck and Greater Scaup. This is a rare variant in the winter plumage of these two species (Harrisons 1961 A: 1962 A), but constant and striking in the New Zealand Scaup.
- (f) The white under tail-coverts of the Red-crested Pochard. We have one duck Red-crested Pochard Netta rufina (Pallas) in our collection with this character and Mr. Eric Gillham (verbatim) has seen others in St. James' Park, London. It is a constant feature of the Rosy-bill Netta peposaca (Vieillot).
- (g) The white under tail-coverts of the Tufted Duck. This is a common variant in female Tufted Duck and is illustrated by Peter Scott in Delacour (1959). It is a constant feature in the Ferruginous Duck Aythya nyroca (Güldenstädt), Australian White-eye Aythya australis Eyton, Madagascar White-eye Aythya innotata (Salvadori) and Baer's Pochard Aythya baeri (Radde).
- (h) The pink breast of the Smew. One example of an adult drake Smew Mergus albellus Linnaeus with a patch of pink on the upper breast is on record (Harrison, J. G. 1954 A). The tint was the same colour as on the breast of the drake Red-breasted Merganser Mergus serrator Linnaeus.
- (i) The black flecking on the belly of the Grey Lag and Pink-footed Goose. Black flecking, almost amounting to small bars, is a common

variant in the Grey Lag Goose Anser anser (Linnaeus) and we have one Pink-footed Goose Anser fabalis brachyrhynchus (Baillon), in which it is present as a minimal expression. It is constant and striking in the White-fronted Goose Anser albifrons (Scopoli) and Lesser White-fronted Goose Anser erythropus (Linnaeus).

(j) The white facial band in the Grey Lag and Bean Goose. Narrow facial bands of white are not uncommon in the Grey Lag Goose and the races of the Bean Goose Anser fabilis (Latham), including the Pink-footed Goose. This character is highly developed in the White-fronted and Lesser White-fronted Goose. It is also frequently seen in the domestic grey goose, when it may be much broader.

3. VARIANTS PRESENTING CHARACTERS WHICH ARE MORE WIDESPREAD WITHIN THE ANATIDAE.

Certain other well-marked variations have been described, which

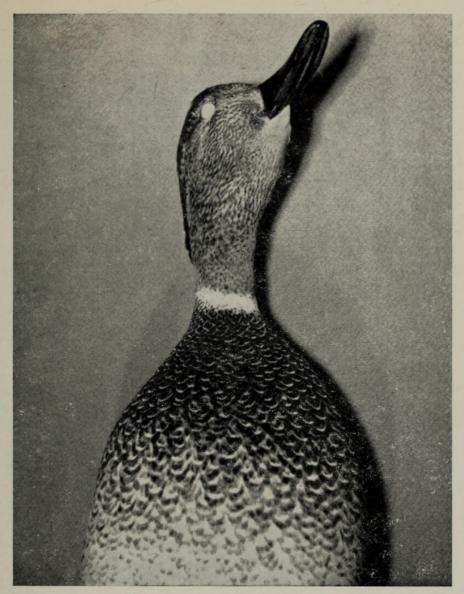
probably also indicate degrees of affinity.

(a) White neck spots and rings. This character when seen in its minimal form takes the shape of a white triangular spot anteriorly at the base of the neck. In its complete form it is a ring as in the drake Mallard. This is a widespread and not uncommon variant in drake European Green-winged Teal Anas crecca crecca Linnaeus (Kuroda 1937; Harrisons 1962 B) and has been recorded in a Yellow-billed Teal Anas flavirostris flavirostris Linnaeus (Harrisons 1958 B). The frequency of this variant and the known relationship of the Green-winged Teals to the Mallard make it probable that these examples could have been included in our second group. Similarly, the present variant Gadwall we believe indicates a relationship to the Falcated Teal, although the Mallard and the Falcated Teal are two more distantly related species of dabbling duck, in which the white neck ring has been strongly developed.

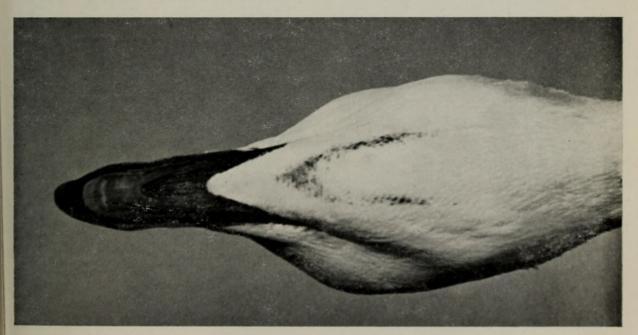
The drake Northern Shoveler commonly shows a white neck ring as a transient character during moult (Harrisons 1959 B) and a white neck ring is revealed in a hybrid between an Argentine Red Shoveler Anas platalea Vieillot and a Northern Shoveler (Harrisons 1963 A). Both of these characters we believe support Delacour's views (1956) that the "Blue-winged Duck" are evolved from Mallard. Peter Scott has also informed us (in litt.) that some drake Northern Pintail Anas acuta acuta also show transient white neck rings during the eclipse moult. This species is also close to the Mallard and when in this plumage shows a strong resemblance to the bright type of drake Kerguelen Pintail A. a. eatoni Sharpe, as is illustrated by Peter Scott in Delacour (1956). This is therefore a third example of a variant within the species (Group I), as already described for Mallard and Eider Duck.

At the same time it should be noted that white neck rings are widespread in the Anatidae, occurring in some races of the Canada Goose Branta canadensis (Linnaeus), in the Australian Shelduck Tadorna tadornoides (Jardine and Selby), the New Zealand Brown Teal Anas aucklandica nesiotis (Fleming) and possibly the Harlequin Duck Histrionicus histrionicus (Linnaeus). We do not think that this makes any difference to our conclusions on Teal and Shoveler variants.

In addition, white neck spots occur as part of an albinistic pattern revealed by inbreeding in the Mandarin Aix galericulata (Linnaeus) and



Gadwall drake with white neck ring variant.



Drake Eider, showing well-marked black V on chin. Hatched from Icelandic egg and died in March 1961 when three years old.

in Salvadori's Duck *Anas waigiuensis* (Rothschild and Hartert), probably from the same cause; while the white ring of the Mallard under these conditions enlarges to produce a pattern similar to the Northern Shoveler (Harrisons 1961 B).

- (b) White chin spots. These occur as common variant features in drake Red-crested Pochard, European Pochard and Tufted Duck and are constant in the Ring-necked Duck Aythya collaris (Donovan) and the Ferruginous Duck. A white chin spot has been recorded as a feature in an inbred Mallard population and in the Mandarin and Salvadori's Duck (Harrisons 1961 B). It is a prominent character in some Pochard X Carolina Aix sponsa (Linnaeus) hybrids and in Pochard X Tufted Duck.
- (c) Bimaculated facial pattern. This is one of the most difficult characters to evaluate and is seen in its extreme form as a normal character in drake Baikal Teal Anas formosa Georgi, as well as some ducks of the species, (Harrison, J. M. 1958 A), but is also present to a lesser degree, as pointed out by C. J. O. Harrison (1963), in both sexes of the Chiloe Wigeon, duck Velvet Scoter Melanitta fusca (Linnaeus), duck Scaup (summer plumage only) and duck Harlequin Histrionicus histrionicus. În our paper on plumage sequences in Northern Shoveler (1959 B) we stated that we thought the pale facial crescent of the Australasian and Northern Shoveler is homologous with the anterior half of the bimaculated facial pattern, a view which C. J. O. Harrison supports. This, therefore, brings into this group the Blue-winged Teal Anas discors Linnaeus, the Australasian Shoveler, the Bronze-winged Duck Anas specularis King, the drake Harlequin and Barrow's Goldeneye Bucephala islandica (Gmelin). This then links with the loral spot of the Goldeneye Bucephala clangula (Linnaeus) and the White-backed Duck Thalassornis leuconotus Eyton.

As a rare variant, a bimaculated facial pattern occurs in drake European Green-winged Teal (Harrison, J. M. 1954 B) and in albinistic Mallard (Harrison, J. M. 1959 C). In hybrids, a pattern remarkably similar to drake Baikal Teal is revealed in European Green-winged Teal X Mallard—the original "Bimaculated Duck" (Meyer 1857); X Shoveler (Payn, W. H. 1949; Harrison, J. M. 1954 B); X Pintail (Meinertzhagen 1930; Sage 1960): American Green-winged Teal Anas crecca carolinensis Gmelin X Pintail (Sage 1960): Wigeon X Shoveler (Harrison, J. M. 1959 D): Mallard X Grey Duck Anas supercilliosa Gmelin (Manson-Bahr 1953): Pintail X Red-crested Pochard and as a crescent only in Red Shoveler X Shoveler (Harrisons 1963 A). It is not revealed, however, in a hybrid Wigeon X European Green-winged Teal (Harrison, J. M. 1962 C). It was on these grounds that the Baikal Teal was presumed to show a primitive and basic pattern within the Anatidae (Harrison, J. M. 1953).

4. VARIANTS TOWARDS AN UNDIFFERENTIATED PLUMAGE Three species in which the drakes normally have white bellies, have been recorded with well-marked spotting. This includes Gadwall (Harrisons 1959 A); Teal and Pintail (Harrisons 1963 B).

5. VARIANTS IN OTHER GROUPS

These variants are not limited to wildfowl. Similar findings have been recorded in Great Spotted Woodpeckers *Dendrocopus major* (Linnaeus) and Jays *Garrulus glandarius* Linnaeus (Harrison, J. M. 1951). Several

examples of the Robin Erithacus rubecula Linnaeus have been obtained in Britain showing the lower part of the gorget as a broad dark greyish band as in Luscinia a. akahige (Temminck) from the Far East and similarly two Bullfinches Pyrrhula pyrrhula nesa Mathews and Iredale from Britain have been found with characteristics of the eastern Pyrrhula p. griseiventris Lafresnaye (Harrison, J. M. 1946; 1957 B).

Summary and Conclusion

- 1. The white neck ring variant in drake Gadwall is discussed and is shown to be linked with a pale chestnut ground colour on the throat, neck and cheek.
- 2. Other variants in the Anatidae are summarised. These fall into four groups:
 - 1. Variants within a species—in Mallard Pintail and Eider Duck, the former being a good example of a morphic cline.
 - 2. Variants resembling a closely-related species—eleven examples are given, which taken as a whole, provide further evidence of the relationships involved.
 - 3. Variants presenting characters which are more widespread within the Anatidae. This includes white neck spots and rings, white chin spots and the bimaculated facial pattern.
 - 4. Variants towards an undifferentiated plumage—three examples are given.

It is our opinion that all the variants in groups (1) and (2) provide indisputable evidence of an evolutionary relationship, as do many of those in group (3).

We see nothing against C. J. O. Harrison's view that certain "signal characters"—for example "bimaculation"—are patterns common to the Anatidae, which have become recessively dominant in some species, but remain latent in others. Nevertheless, as we have shown, if two closely related species are considered, in which a "signal character" is well developed in one, but absent in the other, there is a greater chance that variants of the latter will reveal "signal characters" of the former, rather than of some more distant species. This we regard as further evidence of a close phylogenetic and evolutionary affinity between the two. Such discontinuous variants can be very striking and precipitate.

C. J. O. Harrison has pointed out that within a family, the evolution of "signal characters" for species recognition is likely to be the same only in widely separated species and the closer the species, the greater the dissimilarity is likely to be. The evolution of the white neck ring in Mallard and Falcated Teal illustrate this. Their ranges overlap, but in the latter the ring is part of an elaborate pattern, in the former it is simple. Closely related to the former are the Green-winged Teal and to the latter, the Gadwall. None have white neck rings, but it is surely more than coincidence that these species should be the ones to reveal as variants both white neck spots and well-developed rings?

"Signal characters" have been quoted as being a safeguard against hybridisation. This is probably particularly true of the Anatidae of the Northern Hemisphere. It is curious therefore that certain hybrids should

so closely resemble another species and when one remembers that so many hybrids of the Anatidae are fertile, this would seem to favour the chances of further hybridisation.

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