of Upland Plovers there. Thus does man's activities play havoc with the finest natural homes of certain species of birds. The colony of Ravens, formerly located in the romantic Rocky Gap, six miles east of Cumberland, was also no more. As if to mitigate this disappointment, however, I found on July 9, a family of Blue Grosbeaks (Guiraca c. caerulea) on Knobley Mountain, making at least one species, and that an interesting one, to be added to the birds of western Maryland.

Oak Park, Illinois.

# PATTERN DEVELOPMENT IN TEAL.

#### BY GLOVER M. ALLEN

An article by Mr. Frederic H. Kennard in 'The Auk' for October 1919, describing and naming the Southern Blue-winged Teal as a distinct subspecies, brings out a point of considerable evolutionary interest, which it seems to me is worth emphasizing. The chief mark of the newly recognized race is the presence of a white superciliary stripe continuing the white crescent between the eye and bill, characteristic of the common Blue-winged Teal, and the two stripes, one on each side, meet at the back of the head and are continued medially to form a white nuchal patch of varying extent. This unusual extension of the white crescentic mark is found in the adult males only and is characteristic of the completely developed nuptial plumage in the Southern birds. A similar, though often irregular line, is sometimes seen in partially white domestic pigeons and ducks.

The formation of a definite pattern of pigmented (i. e., colored) and pigmentless (i. e., white) areas, particularly in birds and mammals, is a subject which has greatly interested me, and in an article in the American Naturalist (vol. 48, p. 385–412, 467–484, 550–566, 1914) I have endeavored to establish that in these two classes of vertebrates, white markings when present tend to occur in certain definite places. This is due to the fact that the surface

of the body may be divided into some eleven areas from whose individual centers the tendency to produce pigment in the epidermal structures (hair or feathers) tends to become less and less as the periphery of the particular area is reached. These areas may bear some as yet unrecognized relation to the distribution of nerves. The borders of contiguous areas may overlap, and the details of their topography in different mammals and birds may vary, but in general their outlines are fairly definable as follows:

(1) a median crown patch, in birds pigmenting the top of the head from base of beak to occiput above the eyes; (2) an ear patch on each side covering the side of the head and upper throat from the level of the eye to the median line above and below; (3) a neck patch on each side pigmenting the area from the upper throat to the shoulders; (4) a shoulder patch on each side pigmenting the feathers of the wing and a narrow area at its base from center of back to center of breast; (5) a side patch on each side of the body which includes the area from shoulder to rump; and (6) a rump patch on each side which pigments the posterior end of the body, the tail, and most or all of the hind leg. These patches are outlined in the accompanying diagram (Fig. 1). I have called these color areas primary patches. They may break up further to form complex patterns.

The definition of these patches is sometimes complicated by two (or three?) other types of pigmentation which in some species co-exist with this centripetal type—namely, a diffuse pigmentation from many small independent centers, producing the spotted effect seen for example in the Dalmatian Coach Dog, and a centrifugal type, which produces black "points" at tips of nose, ears, limbs or tail in certain species. A black median area on the spine is perhaps a manifestation of this same type. These three types of pigmentation behave differently in heredity and have been studied lately by several geneticists. It is likely that the median crown patch, very small in mammals, may really consist of two bilateral centers, here in close juxtaposition for in birds it is frequently divided by a white median line, though in the few mammals where I have seen it (e. g., dogs) it is not so divided.

From a study of pied individuals of species which normally have complete pigmentation, it is found that the white markings

tend to occur at the peripheries of the pigment centers as above defined, and result from the failure of pigment to develop at the edges of these centers. The more the pigmentation is restricted, the greater is the amount of white between the respective centers. If each patch or center were to be slightly reduced, a series of five pigment spots on each side, and one on the crown would result, bounded by white lines—a median white line from the occiput to tail, and cross stripes separating the five patches of each side. A much greater but regular restriction of each patch would result in reducing the pattern to a series of five small spots on each side with a single median one on the crown; and still further reduction brings about a pure white condition with black eyes—(possibly

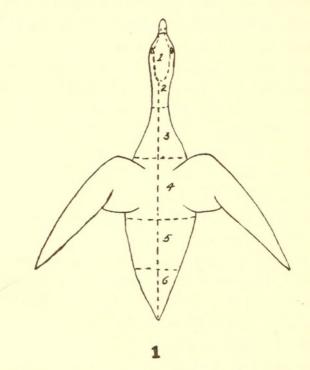


Figure 1.—Diagram showing chief pigment areas of a bird's body, from above.

the eyes being in part of ectodermal origin, should themselves be regarded as an additional pair of pigment centers). Such white animals with black eyes occur as artificial breeds in a number of species, and on account of their possessing a potential pigmentation, act as pigmented individuals in crosses with true albinos which do really lack the pigment-producing factor. Actually there is great variation in the amount of reduction, for not only

does each spotted individual differ in the extent of its pigmented areas, but corresponding areas of opposite sides vary in the amount of reduction in the same individual, so that often the contiguous patches of one side may show a white break between them, while those of the opposite side retain contact.

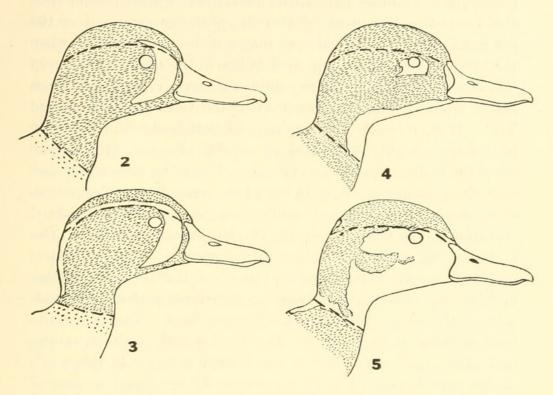


Figure 2.—Head of Blue-winged Teal, to show pattern. In this and the other heads, the approximate outline of crown patch and the boundary between ear and neck patches, are shown by a heavier dotted line.

Figure 3.—Head of Southern Teal, showing extension of white pattern through restriction of ear patch dorsally and posteriorly.

Figure 4.—Andaman Teal (*Polionetta albigularis*) showing slight reduction of ear patch.

Figure 5.—White-cheeked Andaman Teal (P. a. leucopareus) showing incomplete formation of a white collar by failure of ear patch to meet the upper end of neck patch.

But to return to the Teal, the point of interest is that the white crescentic mark of the normal bird is due according to this view, to a restriction of the ear patch (whose ultimate center is the aural region) at its front end, so that a pigmentless area is left at the base of the bill (Fig. 2). The head pattern of the common Blue-

winged Teal has developed no further. In the Southern Teal, however, (Fig. 3) a further restriction of the ear patch has taken place, producing a complete line of separation between it and the crown patch, so that a white superciliary line results from the failure of these two patches to develop pigment at their common border; and in those individuals that show a white nuchal area, this restriction has involved also the posterior extension of the ear patches of opposite sides so that a white streak results when they fail to meet along the median line of the neck. this condition, with its more complex pattern, represents a more highly evolved plumage than that of the Common Blue-winged Teal. It is, therefore, not unexpected that it should occur only in the most highly developed or nuptial plumage, at the time when the bodily vigor is most intense. It may be well to add here that the presence of albinistic or white areas does not imply, as many suppose, an impaired bodily vigor, but merely a specialized condition of the factor producing pigment in the epidermis. fact that the amount of white in the pattern of many natural species is very variable, indicates, I presume, that its areal development has not come under a strong selective force so that the boundaries of the white areas have not become fixed. That the white head-marking of the Southern Teal is of a fairly definite nature, may show, conversely, that it has become a factor in this bird's welfare and is tending to be symmetrically developed as part of a definite pattern. For this reason the extension of the usual white area is of value as a diagnostic mark of the more southerly breeding Teal.

On my expressing to Mr. Kennard an interest in this bird, he has kindly called my attention to an observation of Mr. Stanley C. Arthur (since published in 'The Auk') who has for three years past kept in confinement in the flying cage of the Audubon Park, New Orleans, one of these Southern Teal, showing the characteristic "necktie" marking. In the spring following its capture, this drake molted into the nuptial plumage, but the white superciliary line and nape patch seemed less definitely white than Mr. Arthur's recollection of them the year before. In the next year, however, when the bird again assumed its spring plumage, neither the white line nor the white nape patch was apparent. The bird's

death occurred shortly after, in April of that year. This interesting case only serves to emphasize still further that this "necktie" pattern is a newly acquired character in the phylogeny of the race, and in the growth of the individual is assumed at the time of its highest physiological development. The fact that the captive bird finally lost this marking may have been due to impaired vigor, either as a result of old age or as a result of the abnormal conditions of captivity, which as is well known, nearly always result in interrupting the usual course of physiological processes. If due to senescence, it is paralleled by numerous other cases in both vertebrates and invertebrates. A familiar one is the "going back" of deer antlers in old males.

The Southern Teal is not the only duck that might be cited as a case of formation of a distinct geographical race through the differential development of white areas in the plumage by restriction of pigmentation. Mr. Outram Bangs has called my attention to the case of the Teals of the Andaman Islands, Polionetta albigularis, in which (Fig. 4) the ventral side of the throat and a spot just below the eve are white, showing thus only a slight restriction of the ear patches ventrally and about the eye. In one of two specimens from the same locality, however, white feathers appear at the base of the bill, and the white mark below the eye is much larger than in the other, indicating that the pattern is still in an unstabilized condition. The development of white areas thus begun, is carried still further in the race P. a. leucopareus from North Reef Island, in the same group, in which the restriction of the ear patches is so extensive (Fig. 5) that the upper throat and side of head to the level of the eve are white as far back as the ear opening, and a white collar has resulted through failure of the ear patch to reach the upper edge of the neck patch. Behind the ear, the crown patch is still united with the ear patch except at the occiput, where a very small white spot occurs in one of the two specimens seen. One might conceive of a further stage in evolution of this pattern, whereby the crown patch would persist intact, but the ear patches dwindle perhaps to a very small spot over the ear opening. Such a pattern is found in the Old-squaw female in winter. A subsequent loss of the crown patch would then leave a head pattern similar to the adult male Old-squaw.

Dr. John C. Phillips tells me that the Congo Teal shows very beautifully in a series of specimens from the same general region, a variation in the degree of restriction of the individual pigment centers. The common Mallard as I have shown in the article above cited (Am. Nat., 1914, vol. 48, p. 483) frequently shows under domestication, the development of white superciliary lines that correspond in position with white areas which have in other species become a permanent part of the pattern. The normal male Mallard has in the fully developed plumage, a white collar at a point bounding the upper limit of the wine-colored neck. is merely the development of a white area at the point of contact between the ear patches covering the sides of head and upper throat, and the neck patches pigmenting the lower throat. the two sets of patches are of different colors.) In the domesticated Black Mallard this white ring is often absent, on account of the complete development of the two sets of pigment patches. I have also seen a female Mallard in which a white half-ring was present as an albinistic spot in just the place where it is completely developed in the male, showing that this is one of the contact points between two pigment centers, a place of least color formation, where, if restriction of pigment areas takes place, a white mark will first result. Indeed the Anatidae seem especially favorable for a more intensive study of this method of pattern formation, and well merit special investigation as to the development and transmission of partial pigmentation. Already careful studies of rats, mice, guinea-pigs and rabbits have been made by geneticists on these lines, and it is to be hoped that comparative studies on birds will follow.

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