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SIGNIFICANCE OF WHITE MARKINGS
IN
BIRDS OF THE ORDER PASSERIFORMES

BY

HENRY CHESTER TRACY

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INTRODUCTION.

The present investigation was undertaken for the purpose of testing the validity of one of the earliest recognized categories of coloration, that of "Directive Markings," in a single order of birds. The term directive is used in the sense given it by Todd (1888) and not that of later writers (Marshall, 1902), who have used the word as expressing a different function of white markings in butterflies' wings—protective through drawing the enemy's attack away from vital parts. As here used it resembles the term recognition markings, and might be regarded as a

* The present paper is the result of work carried on in the Department of Zoology of the University of California as partial fulfillment of the requirements for the master's degree, under the direction of Professor Charles A. Kofoid, to whom the writer is indebted for advice and criticism. He is also under many obligations to Mr. Joseph Grinnell, Director of the Museum of Vertebrate Zoology, for much information placed at his disposal. The author also had access to the large collections in the Museum, and was allowed free use of these and of such data on file there as proved pertinent to the problem in hand.

synonym were there not good reasons for believing that the white markings exposed in flight serve rather as a clue to the *direction* taken by disappearing forms of birds, than as an aid to recognition of the species.

The investigation of the theory of directive markings in birds is hampered by the impracticability of carrying on field experiments such as those of Professor Reighard (1908) in pursuance of a similar inquiry in regarding warning coloration in fishes. Obviously it is out of the question to capture and liberate large numbers of birds with a view of detecting natural reactions under such artificial conditions. Field observations can, however, be offered, but these, in the nature of the case, do not afford evidence which is experimentally precise. Much depends upon the individual in the field—the personal equation. This source of error cannot be set aside by recourse to photographs, for the reason that the crux of the problem of directive markings, in so far as it concerns actual perception, is the effect of the *moving* white of the wings or other parts of the flying birds. Photographic plates show but the fixed effect of motionless patterns, and tell us nothing as to their efficacy in attracting visual attention to those patterns in motion.

I have, therefore, narrowed the field to a discussion of the *revealing* properties of flight-exposed white markings, and a study of the occurrence of such markings throughout the order Passeriformes, deducing from such occurrence a very suggestive correspondence of coloration with habit and feeding range. I have no direct evidence to offer as to the origin and mode of evolution of the white markings in birds. It may not be amiss, however, before proceeding further, to call attention to the limitations of explanations based on intrinsic factors alone.

INTRINSIC FACTORS IN THE EVOLUTION OF COLOR.

Riddle(1908) has proved that the melanin deposited in barbules varies with nutrition. He has also shown that fundamental bars in feathers may have their origin in rhythms of blood pressure. He thus establishes a presumption in favor of a continuously acting cause, apart from heredity, governing the degree of pigment deposited in birds' feathers. He is perhaps

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right in asserting that further evolutionary studies of bird coloration should take their departure from this point. Nevertheless, if this be true, the gap between fundamental bars in feathers and the varied patterns in which white appears in every conceivable combination, often accompanied by intensification of pigment deposits in adjacent plumage, is one which can only be filled by difficult, expensive, and long continued research. In the meantime the discoveries of Thayer (1909) have greatly simplified the explanation from the selective standpoint, while those of Reighard point to an intrinsic tendency toward variety of pattern, needing only immunity such as that afforded by a coral reef, to develop colors and contrast that are neither adaptive nor due to sexual selection, and for which the physiological elements of nutrition, temperature, etc., do not account. Thus it is probable that the production of bars and stripes in feathers, and the rate of pigment deposit, are but secondary processes in a larger scheme. They may themselves be dependent on selective agencies which, if they exist at all, operate upon the whole organism.

If we were concerned here with the problem of bird coloration in general, we might linger upon examples of an apparent physiological basis for dark coloration, such as that of most species of *Corvidae*; these are largely omnivorous feeders, active and of exuberant vigor. But we should certainly be wrong if we failed to take account of the great degree of immunity which these birds enjoy from the attacks of raptorial birds, because of their size and aggressiveness. It is doubtful whether a seed-eating bird of delicate flesh and harmless disposition could have been permitted to develop such a black plumage as that of the raven, even had the physiological excuse for pigment excretion been as great in its case. Some other way would have been found, we may reasonably say, for the excretion of melanin, or else that type of bird would have become extinct for lack of protective coloration.

Similar difficulties involve such special varieties of the physiological explanation of color patterns as are connected with color distribution on the breast, crown, rump, etc., of birds, regarded as centers of high or of deficient circulation. A study

of any series of birds ranging through half a dozen families will give quite contradictory results. The crown will be found white on some, black on others; the breast usually light colored, but sometimes with a spot or chain of spots, or the throat spotted and the breast plain; and the rump white in some, heavily pigmented in others. Only patient ingenuity could long persist in seeking evidence for the correlation of pigmented areas with regions of fuller circulation; and the seeker for such evidence must shut his eyes to the patent fact that to produce a monochrome plumage such as that of the Leconte thrasher the dermal circulation must be uniform over the entire surface of the body; the existence of the theory would seem to demand the denial of such a condition.

Cunningham's suggestion (1900, p. 109) of a local stimulus incident to the elevation of plumes, etc., in courtship, is useful in accounting for the special development of certain epidermal features, but it sheds no light on the cause of intensification of color in the breeding male, in the plumage as a whole. The *vigor* theory attempts to do this, but leaves untouched a large number of instances in which there exists no sexual dimorphism in coloration, and still others in which the female takes over not only the color character, but also the courting antics of the male, leaving him the responsibility for incubation, as is the case in the knot (*Tringa canutus*).

The other class of intrinsic factors in color evolution grouped under the general term heredity, is one which this paper will merely recognize as existing, a potent but little understood influence. If it can be shown that white markings do not occur indiscriminately on birds of all habits and environments, but are associated with similar habits and ranges among birds not otherwise closely allied, it will be clear that they cannot be regarded solely as evidences of the manifestation of hereditary tendencies, but may fairly be attributed, at least in part, to selective influences.

Whatever the original cause of pigmentation or absence of pigment and its replacement by structural colors, and whatever the mode of evolution of such colors and combinations, the assumption of a principle of natural selection everywhere efficient

though sometimes *passive*, is justified by the facts as to the distribution of white patterns in passeriform birds of the United States.

WHITE MARKINGS AS VISUAL CLUES.

Coloration in birds, whatever its cause or the mechanism of its production, is conceded to be adaptive; it responds to their needs, forms a part of their life adjustments.

Concealment from its enemies is not the only need in a bird's life, not the only adjustment that affects color-patterns. The bird also needs to be made known to other individuals of its kind, and to other species associated with it; and this need has certainly been met. Just how it has been met depends upon the bird's manner of life, and upon its chosen habitat; this much we know. Without entering upon any disputed phase of the subject, we may state at the outset that the need exists and has been met, if not by special provision in coloration, at least by peculiarities of form and manner, or by qualities of voice.

The vital importance to a bird of seeing and being seen by its companions, hardly finds a parallel among the lower vertebrates; certainly not among most fishes, though a school of fishes bears a superficial resemblance to a flock of birds. Neither in organization nor in instinct does the one approach the high development of the other. A comparison of the brain of a perch with that of a pigeon shows the remarkable superiority of the latter in respect to cerebral development. The phenomena of the associations of a bird's life, the well-known facts of mutual independence in feeding, nesting and migration among nearly all of the class *Aves*, indicate the degree to which individualism has been subordinated, and coöperation of a certain kind developed.

There are, however, great differences within the class. If we are to make any comparison between these and the lower vertebrates, let it be between gregarious sea-birds and fishes, not between oscines and herring. Delicate life-adjustments are to be found among the higher genera of the perching birds that are missing from the more primitive divers or long-winged swimmers, as well as from fishes. The number and variety of perils

that daily surround our smaller land-birds, and the extent to which these may be diminished by the birds' keeping in touch with one another, point to the need of something more than concealing coloration, and admit of special adaptations that shall act in harmony with it and yet serve to reveal the bird to its kind.

Notwithstanding this distinction there will be some who fail to find in the life-relations of the Passeriformes anything to occasion the development of marks whose main function shall be that of revealing the birds to each other. Thayer (1900), exposing the weakness of the "banner-mark theory," indirectly implicates all theories of directive coloration, as well as that of warning colors, and has since made them the object of special attack (A. H. Thayer, 1909). The ground for his criticism—and it is a good one—is that birds, in order to profit by such aids as signs and signals, or at least to need them, must be less acute than human observers, who easily recognize species of birds by slight hints, such as are afforded by silhouette, by mode of flight, by mannerisms of one sort or another, rather than by special marks. This is so true that it must and does discredit the crude interpretations such as the title "banner-mark" suggests. We must distinguish between hypothetical functions, the creation of fancy, and a series of well-defined stripes, bars, or checks, which may be interpreted by any one of at least three categories, of which that of "concealing coloration" is only one.

Starting out with a presumption in favor of some form of revealing clues among the higher land-birds, and eliminating a terminology which has been misleading, it remains for us to determine, if possible, what these clues are, and whether color features form a part of them; if so, how this harmonizes with the function of the same or similar color features as concealing.

How do the birds of our woods and fields actually keep track of one another? Obviously to a great extent by vocal sounds which they utter frequently when moving about in the foliage, or in unison when leaving a feeding ground as a flock; by call-notes, when moving in pairs or companies; by location notes, when separated and seeking to come together. No one doubts the existence of such vocal clues or their vital necessity to birds belonging to the order under discussion.

There are birds that appear to depend almost entirely upon directive calls for keeping together; they have become habituated to feeding in close and uninterrupted cover where they see other birds only at close range, or very seldom at any great distance. Obviously they must keep within hearing, or be lost to their companions. Sound-clues are sufficient in their case. This is true of the bush-tit (*Psaltriparus minimus californicus*), some warblers, and nearly all the wrens. These are birds of plain colors, for the most part, and *without white patterns of any sort.*

Among arboreal birds of open feeding range that are constantly exposed to view, different conditions obtain. Call-notes are used, but glimpses of other birds in flight may be just as useful for purposes of direction, since such glimpses are frequently to be had. Sight plays a part of corresponding importance in the economy of bird-movement—to some extent replaces sound as a means of recognition.

As there is in the *general* coloration of open-ranging birds no response to the need of some rapid and easy means of recognition, and as the special color patterns that have heretofore been regarded as serving that purpose are now being claimed as a part of "concealing coloration" (A. H. Thayer, 1909), it might appear that the category of directive markings is soon to lose its status altogether. But general coloration is seen to be normally protective, for birds that need protection; and as for the special patterns, even a satisfactory demonstration of their "obliterative" effect does not warrant the conclusion that such is solely or mainly their effect in all cases.

For a discussion of the "disruptive effect of color patterns" the reader is referred to G. H. Thayer, 1909, pp. 77-79, and to A. H. Thayer, 1909, pp. 562 et seq. The evidence here offered of their value as *revealing characters*, must not be regarded as contradicting anything but the application of the "concealing" principle to *birds in flight.*

During the month of February the writer had under observation a flock of fifteen meadowlarks (*Sturnella neglecta*), which foraged in vacant lots and fields within the city limits of Berkeley. They were well spaced while feeding, and when disturbed some

would fly across a road into the neighboring field, where they would presently be followed by others. Their white tail-borders were often conspicuous during the entire flight of the birds, the tail remaining partly spread. As the meadowlarks on being flushed rose to the height of a man's head or higher, they must have seen the retreating forms from a similar view-point, *i.e.*, against a dark background. They would not commonly see them against the sky. For the birds themselves, white tail-borders would serve no purpose if not a directive one. Common observation does not seem to be at fault here, nor the term "white guides" ill-chosen.

It will be seen that the common assumption to the effect that white upon an object makes it conspicuous is well grounded in this case, for the reason that there is nothing corresponding to it in the usual background; further, because it does not in the least efface the outlines of the bird's contour, and finally because the bird is in motion at the time when the marking is displayed. We take note, therefore, of the distinction between a flight-exposed marking and one that appears at its full value when the bird is at rest. The former acquires added conspicuousness from the fact that a moving object fixes and holds the attention, indeed a white object moving across a dull background is the best mechanism that can well be devised for signalling at long distances.

Mr. A. H. Thayer, in the article to which we have just referred, indicates a supposed correlation between white rear-markings and the habit of nesting on the ground and flying from the nest when disturbed, stating that the markings are absent from birds that habitually run from it to escape a furred enemy. This would point to an obliterative function in the rear-mark, which shows white against the sky as seen from the level of a quadruped. This statement and conclusion seem to have been hastily made, for they apply only in the case of water birds such as rails, coots and gallinules which the author of the statement had in mind. The horned lark (*Otocoris alpestris*, all subspecies), the meadowlark (*Sturnella magna* and *S. neglecta*), and the vesper sparrow (*Pooecetes gramineus*), are among the

rear-marked birds that run from the nest, habitually, when disturbed.

In the foregoing paragraphs, the evidence for the revealing function of white rear-markings exposed in flight has been given as common observation, supplemented by psychological analysis of the facts; and the supposed instance of a concealing function in the case of certain birds has been shown to be quite inconclusive as regards perching birds. These considerations alone would point strongly to the other interpretation of the markings as advanced by Todd (1888), and rather generally accepted since. They are not, however, the only ones bearing on the question.

In giving recognition to the theory of directive markings of this type Wallace (1889, p. 222) alluded to their prevalent occurrence among flocking birds, as strengthening the theory, since it was just here that they would be of the greatest use. He did not, however, test the facts regarding such occurrence, or inquire into the question of a significant absence of white markings among non-flocking birds; nor has anyone else done so, heretofore. It is a test that is easily made by segregating all the birds bearing the white rear-marks, and making an inventory of those that remain. In order to judge of the significance of the resulting division it is necessary to know to what extent the birds thus arbitrarily separated differ in habits, especially as regards flocking; and this is not as easy as might be supposed, among the perching birds.

The accompanying list gives all the species of open-ground passeriform birds native to North America. Although the white tail-borders occur also on a few arboreal birds, these may be regarded as coming in the class of "top-patterns," which will be taken up in connection with birds of the forests and thickets.

PASSERIFORM BIRDS OF THE OPEN.

WITH CONCEALED WHITE.

ICTERIDAE	<i>Junco hyemalis</i> , all subsp.
<i>Sturnella magna</i>	<i>Junco aikeni</i>
<i>Sturnella neglecta</i>	<i>Junco phaeonotus</i> , 3 subsp.
ALAUDIDAE	<i>Junco bairdi</i>
<i>Otocoris alpestris</i> , all subsp.	<i>Junco insularis</i>
<i>Alauda arvensis</i>	MOTACILLADAE
FRINGILLIDAE	<i>Anthus pratensis</i>
<i>Calcarius lapponicus</i>	<i>Anthus spraguei</i>
<i>Calcarius pictus</i>	<i>Anthus cervinus</i>
<i>Calcarius ornatus</i>	<i>Anthus - rubescens</i>
<i>Rhyncophanes mccowni</i>	<i>Budytes flavus alascensis</i>
<i>Plectrophenax nivalis</i> , all subsp.	<i>Motacilla alba</i>
<i>Plectrophenax hyperboreus</i>	<i>Motacilla ocularis</i>
<i>Calamospiza melanocorys</i>	TROGLODYTIDAE
<i>Chondestes grammacus</i> subsp.	<i>Heleodytes brunneicapillus</i>
<i>Poocetes gramineus</i> , 2 subsp.	<i>Oroscoptes montanus</i>

WITHOUT CONCEALED WHITE.

FRINGILLIDAE	<i>Passerherbulus caudacutus</i>
<i>Leucosticte atrata</i>	<i>Passerherbulus nelsoni</i>
<i>Leucosticte australis</i>	<i>Passerherbulus maritimus</i> ,
<i>Leucosticte tephrocotis</i>	2 subsp.
<i>Leucosticte griseonucha</i>	<i>Peucaea aestivalis botterii</i>
<i>Passerculus bairdi</i>	<i>Peucaea mexicana</i>
<i>Passerculus princeps</i>	<i>Peucaea cassini</i>
<i>Passerculus sandwichensis</i> ,	<i>Aimophila ruficeps</i> , and subsp.
3 subsp.	<i>Aimophila carpalis</i>
<i>Passerculus beldingi</i>	<i>Spizella passerina</i>
<i>Passerculus rostratus</i>	<i>Spizella p. arizonae</i>
<i>Ammodramus savannarum australis</i>	<i>Spizella breweri</i>
<i>Ammodramus s. bimaculatus</i>	<i>Spizella pallida</i>
<i>Passerherbulus henslowi</i>	<i>Spizella atrogularis</i>
<i>Passerherbulus lecontei</i>	<i>Spizella pusilla</i> , and subsp.

WITH WHITE IN NUPTIAL PLUMAGE.

ICTERIDAE
<i>Dolichonyx orizivorus</i>

FAINTLY MARKED WITH WHITE.

<i>Amphispiza bilineata</i>
<i>Amphispiza belli</i>
<i>Amphispiza nevadensis</i>

THE PROBLEM DISCUSSED FOR BIRDS OF THE OPEN.

The list shows five families that carry white markings, as against two families that do not. Of the twenty-six species or subspecies that carry them, all but three are to be classed as flocking birds; and even these are unquestionably gregarious to a marked extent. They may follow each other serially from place to place, as the cactus wren (*Heleodytes brunneicapillus*) and the sage thrasher (*Oroscoptes montanus*), or they may flock for a limited season, as the vesper sparrow (*Pooecetes gramineus*). The list contains the most perfect types of flocking birds in the whole order, such as the meadow pipits of the genus *Anthus*, and the horned larks (*Otocoris alpestris*), the lark sparrows (*Chondestes grammacus*), and all the juncos. Taken as a whole the white-marked group is unquestionably a flocking series. The bearing of this on the problem of white markings in birds is made clear by a comparison with the second list in which all but the species of two genera, *Leucosticte* and *Dolichonyx*, are seen to be of a non-flocking, skulking type, exemplified by the grasshopper and Savannah sparrows. Of these two exceptional genera the leucostictes are birds of the Boreal Zone exclusively, feeding on wind-blown insects at high altitudes; themselves conspicuous through their dark coloration and, by virtue of their Alpine-Arctic habitat, escaping most of the birds of prey. In short, they are of an environment altogether different from that commonly referred to as "open ground" in the sense of prairie and plains, and may be eliminated from the comparison. *Dolichonyx*, the bobolink, on the other hand, is a bird in its southern habitats palustrine, and only in its breeding range a bird of the meadows, where it displays the qualities of the second group, and is, in the case of the female, like them unmarked. The coloration of the male in breeding plumage evidently corresponds to that of the marsh blackbirds, to which it is closely allied. Our second list, then, if it be found to contain no flocking birds but the two just mentioned, is a striking proof of the absence of white markings in birds of the open ground that do not flock.

For an interesting exhibition of correspondence between habit and coloration, we turn to the grasshopper and Sandwich spar-

rows (*Ammodramus*, *Passerculus*). To quote a pertinent description: "Among the many inconspicuous, plain, little striped-backed sparrows of the Western United States, *alaudinus* is one of the commonest, plainest, and most inconspicuous. Anywhere in the meadows, prairie grass or weed patches, one may dart out from under your feet, zig-zag over the grass tops for a little way, and drop into the grass, hopelessly lost until he is again forced to take wing. At a distance you see and hear the birds giving their plain little song from the top of a tall weed or fence stake, but on nearer approach they drop into the grass and are lost." This characteristic is here emphasized because in all of the species mentioned as unmarked birds we shall find this or similar traits having a like bearing on our problem, while in all of them the typical flocking habit is lacking. The latter may be replaced by what might be termed a spurious form of flocking. As an instance: the rufous-crowned sparrow (*Aimophila ruficeps*), common on the Berkeley hills, may be surprised feeding in open patches when it at once takes to brushy cover far from which it does not stray; and when traveling moves in loose bunches of scattered individuals flitting from bush to bush unostentatiously.

Field ornithologists will observe, however, that others of the birds here mentioned are in some sense gregarious and gather at certain seasons for migratory or other movements. We have, however, evidence to the effect that such movements are sometimes, if not always, essentially different from typical flocking. Two western sparrows from the arid region are frequently seen in considerable numbers moving from their southerly winter range to a summer habitat to the northward. To the casual observer they might appear to be "flocking birds." A quotation from a memorandum made by Mr. Grinnell during the recent Museum Expedition to the region along the Colorado River, will show the error of such conclusions.

"Both *Spizella breweri* and *S. socialis* are now abundant on the desert in migrating flocks, not flocks, however, in the sense that pipits flock, but scattering companies. Each individual in a company moves wholly independently of any other; and they do not move en masse when alarmed, but helter-skelter in different

directions around and through bushes without call-notes. The helter-skelter disappearance of the flock certainly puzzles me and leaves me wondering where any one of the birds may be relocated. The eye gets no single permanent impression."

The behavior here cited is found when analyzed to be the exact opposite of what occurs in a typical foraging flock of birds having white rear-markings. In a flock of pipits the birds do not move independently, as a rule, in changing feeding grounds; they move in a body when alarmed, in one general direction, with great uniformity; not through bushes, always with call-notes, thus using every reasonable means of keeping the flock together. Under stress of alarm, growing darkness, or accidental scattering through considerable distance, the bright moving rear-marks must at least be of appreciable value to the bird in keeping others of the flock in sight. Whether or not that is the main reason for their existence is, of course, open to question.

THE PROBLEM DISCUSSED FOR ARBOREAL SPECIES.

We have been considering up to this point only the white markings characteristic of birds of the open. Among arboreal species the problem becomes more complicated both as to variety and distribution of the patterns and their possible significance. A form of "top-white" which can be shown to have the effect of making the wearer conspicuous is the basal patch of white upon flight feathers, usually the bird's primaries. It need not have this effect, however, when regarded as a fixed pattern against a foliage background. The latter gives it a disruptive value, as Thayer (1909) has shown for similar designs. In order to test the concealing values of this particular wing marking I mounted the green-backed goldfinch (*Astragalinus psaltria hesperophilus*) and the black-headed grosbeak (*Zamelodia melanocephala*) with spread wings and photographed them against sunlit foliage and backgrounds of leaves with spaces of sky showing through them. The birds were difficult to find in the resulting prints. Undoubtedly the photographs by their lack of relief exaggerated the concealing effect; yet that there is such an effect, in general, it is safe to admit.

When, however, the bird takes wing a wholly different principle comes into play. Suppose it be the goldfinch that has left its perch. What we actually see is a pair of wings opened and closed, alternately revealing and concealing a pattern which finds no background to blend with, because it consists of intermittent flashes of white, not haphazard like the ruffling of leaves, but rhythmical, emphasizing the essential features of the flying bird. This is not speculation but a description of facts—it is what one sees in the field. Those who are unfamiliar with the bird named may recall a similar flight-effect in the black-throated blue warbler (*Dendroica caerulescens*), and even more striking patterns in the common shrike (*Lanius ludovicianus*), the mocking-bird (*Mimus polyglottos*) and the “black mocker” (*Phainopepla nitens*). Concealed wing patterns are not the only ones that become conspicuous in flight. Obviously any white pattern located on primaries, secondaries, tertiaries, or wing coverts, will be expanded to the greatest extent during the motions of flight. It happens that even the comparatively obscure wing bars of the lazuli bunting (*Passerina amoena*) are easily distinguished as white bands on the flying bird. The white of scapular feathers, as in the magpie, is emphasized in the same way. Tail blotches on some warblers reveal their whereabouts as they flit from twig to twig, rather than conceal them. I have not, therefore, attempted to distinguish various classes of top markings among arboreal birds with a view to finding special functions for each. It is precisely such attempts that have discredited theories of the functions of these markings. Arbitrary distinctions do not occur in nature.

In order to give the reader an opportunity to review the entire series of white-patterned birds and to compare it with the complete series of those that lack top-white, I have prepared the accompanying lists. One family, the Mniotiltidae, has been reserved for more detailed study, and is given in a separate list. The ground-frequenting birds of the open have already been given. These lists, therefore, are fully representative of arboreal perching birds of the temperate zone, and include all species of the order Passeriformes regularly found in the United States.

PASSERIFORM BIRDS OF ARBOREAL HABIT.

A. BIRDS WITH WHITE WING OR TAIL MARKINGS.

FRINGILLIDAE

Hesperiphona vespertina
Pinicola enucleator leucura
Loxia leucoptera
Astragalinus tristis
Astragalinus psaltria
Astragalinus psaltria hesperophilus
Zamelodia melanocephala
Zamelodia ludoviciana
Passerina amoena
Sporophila moreletti sharpei
Spizella monticola
Pipilo erythrophthalmus
Pipilo maculatus

LANIIDAE

Lanius borealis
Lanius ludovicianus

VIREONIDAE

Lanivireo solitarius
Vireo belli
Vireo huttoni

ICTERIDAE

Icterus nelsoni
Icterus melanocephalus auduboni
Icterus cucullatus sennetti
Icterus bullocki
Icterus parisorum
Xanthocephalus xanthocephalus

TROGLODYTIDAE

Mimus polyglottos

TURDIDAE

Myadestes townsendi
Planesticus migratorius
Planesticus confinis

SITTIDAE

Sitta canadensis
Sitta pygmaea

CORVIDAE

Nucifraga columbiana
Pica pica hudsonia
Pica nuttalli
Cyanocitta cristata

TYRANNIDAE

Muscivora forficata
Tyrannus tyrannus
Tyrannus verticalis
Myiarchus cinerascens
Myiarchus magister
Sayornis nigricans

SYLVIIDAE

Polioptila caerulea
Polioptila californica
Polioptila plumbea

HIRUNDINIDAE

Hirundo erythrogaster
Tachycineta thalassina

BOMBYCILLIDAE

Bombycilla garrula
Phainopepla nitens

PARIDAE

Penthestes atricapillus

B. BIRDS WITHOUT WHITE WING OR TAIL MARKINGS.

TURDIDAE

Icterus naevius
Hylocichla mustelina
Hylocichla fuscescens
Hylocichla guttata
Hylocichla ustulata
Hylocichla aliciae
Sialia sialis
Sialia mexicana

Sialia currucoides

Cyanosylvia suecica robusta

CINCLIDAE

Cinclus mexicanus unicolor

SYLVIIDAE

Acanthopneuste borealis
Regulus calendula
Regulus satrapa

CHAMAEIDAE

*Chamaea fasciata**Piranga erythromelas**Piranga hepatica**Piranga rubra*

PARIDAE

*Baeolophus bicolor**Baeolophus inornatus**Baeolophus atricristatus**Baeolophus wollweberi**Penthestes atricapillus**Penthestes carolinensis**Penthestes sclateri**Penthestes gambeli**Penthestes rufescens**Penthestes hudsonicus**Penthestes cinctus alascensis**Psaltriparus minimus**Psaltriparus melanotis lloydi**Auriparus flaviceps*

ICTERIDAE

*Molothrus ater**Tangavius aeneus involucratus**Agelaius phoeniceus**Agelaius gubernator californicus**Agelaius tricolor**Euphagus carolinus**Quiscalus quiscula**Quiscalus major macrourus*

CORVIDAE

*Cyanocitta stelleri**Aphelocoma woodhousei**Aphelocoma cyanotis**Aphelocoma californica**Aphelocoma texana**Aphelocoma sieberi**Aphelocoma insularis**Xanthoura luxuosa glaucescens**Perisoreus canadensis**Perisoreus obscurus**Corvus corax**Corvus cryptoleucus**Corvus brachyrhynchos*

TYRANNIDAE

*Tyrannus melancholicus couchi**Tyrannus vociferans**Pitangus sulphuratus derbianus**Myiodynastes luteiventris**Myiarchus crinitus**Myiarchus lawrencei olivascens**Sayornis phoebe**Sayornis saya**Nuttallornis borealis**Myiochanes pertinax pallidiventris**Myiochanes virens**Myiochanes richardsoni**Thryomanes bewicki**Thryomanes leucophrys**Thryomanes brevicauda**Troglodytes aedon**Troglodytes parkmani**Nannus hiemalis**Telmatodytes palustris**Cistothorus stellaris*

SITTIDAE

Sitta carolinensis

CERTHIIDAE

Certhia familiaris

TROGLODYTIDAE

*Dumetella carolinensis**Toxostoma bendirei**Toxostoma redivivum**Toxostoma lecontei**Toxostoma crissale**Toxostoma cinereum**Toxostoma longirostre**Toxostoma rufum**Toxostoma curvirostre**Salpinctes obsoletus**Salpinctes guadalupensis**Catherpes mexicanus**Thryothorus ludovicianus**Spiza americana**Arremonops rufivirgata**Guiraca caerulea**Passerina cyanea**Passerina versicolor**Passerina ciris**Pyrrhuloxia sinuata**Pipilo fuscus**Pipilo crissalis senicula**Oreospiza chlorura*

TANGARIDAE

Piranga ludoviciana

FRINGILLIDAE

Pyrrhula cassini
Carpodacus purpureus
Carpodacus cassini
Carpodacus mexicanus frontalis,
 and other subsp.
Carpodacus amplus
Loxia curvirostra
Acanthis linaria
Acanthis hornemanni
Spinus pinus
Astragalinus lawrencei
Cardinalis cardinalis
Melospiza melodia
Melospiza georgiana
Melospiza lincolni
Zonotrichia albicollis
Zonotrichia leucophrys
Zonotrichia coronata
Zonotrichia querula
Passerella iliaca
Empidonax difficilis
Empidonax flaviventris
Empidonax trailli
Empidonax minimus

Empidonax hammondi
Empidonax wrighti
Empidonax virescens
Empidonax griseus
Empidonax fulvifrons
Pyrocephalus rubineus mexi-
canus
Camptostoma imberbe

HIRUNDINIDAE

Progne chalybea
Progne subis
Progne cryptoleuca
Iridoprocne bicolor
Riparia riparia

BOMBYCILLIDAE

Bombycilla cedrorum

VIREONIDAE

Vireosylva olivacea
Vireosylva philadelphia
Vireosylva gilva
Lanivireo flavifrons
Vireo atricapillus
Vireo griseus
Vireo vicinior

The facts as to the distribution of white markings among birds of the various local associations may be gathered from a study of the first list. It also affords a basis for finding any agreement of physical or temperamental characters among birds so marked, or the occurrence of habits that may have a bearing on their coloration. A similar purpose is served by the second list—with this drawback: it includes a number of color features that may be of a value similar to that of white patterns, and even more *revealing*. Accordingly we need not be surprised if we find among species bearing such features, for example, nearly all the crows and blackbirds, the habits and distribution that are characteristic of white-marked birds.

There is, moreover, a correspondence, especially among the unmarked groups, that appears to be due primarily to intrinsic influences producing family characters; like all color characters these are too inconstant for the systematist to utilize. Still, in some cases they suggest a persistence of some ancestral type dominating extrinsic influences. Such a correspondence is seen

in the family of wrens which an amateur can usually recognize by noting the superficial color pattern. A similar tendency appears in the vireos and also in the flycatchers. If, therefore, we find white patterns conspicuously lacking among Troglodytidae, Vireonidae and Tyrannidae, we are bound to consider whether or not this may be partly due to the stability of a type (intrinsic influence) or to selective influences alone. The occurrence of a perfect adaptation at variance with the type in the bleached, sand-colored monochrome of the Leconte thrasher (*Toxostoma lecontei*) indicates that the Troglodytidae may not be exempt from the strict enforcement of the principles of adaptive coloration, where the conditions of their life demand it.

There are some relative differences among birds that might conceivably enter into the explanation of correspondences in color, but apparently do not to an appreciable extent. Size is one of these. The only way in which it appears to affect coloration is by affording immunity from enemies. Size combined with vigor and aggressiveness opens the way for conspicuous coloration. But the need of concealment on the part of the aggressor neutralizes the effect of this immunity in most cases. The raven is one of the exceptions within the order of perchers, and the condor, Egyptian vulture, and turkey buzzard, outside it. These are birds that need no concealment for aggression, but profit by a conspicuousness that makes them recognizable to each other at great distances.

As for warning coloration, there seems no reason for believing that it occurs among perching birds. Were the principle thoroughly established we might be justified in regarding the magpie as an instance; but since other functions may readily be assigned to the contrasts in its plumage, and since these are not necessarily utilitarian, as the bird is largely "immune," the whole hypothesis is negligible for the birds under discussion.

Temperamental differences form another set of elements to be considered. A search for correspondences in this direction shows at least a few well attested instances of boldness of disposition accompanying the supposed conspicuousness of plumage. Such are the kingbird (*Tyrannus tyrannus*), the scissor-tailed flycatcher (*Muscivora forficata*), the mockingbird (*Mimus poly-*

glottos), the magpie (*Pica hudsonia*), and the shrike (*Lanius borealis*). These are interesting cases, but little can be inferred from them as to the significance of white markings in the group at large.

It is in the correlation of special color features with special feeding and breeding ranges that we get the first clear indication of a large underlying principle determining which birds shall possess the white pattern and which shall not. The top-marked finches are seen to be birds of open woods mainly, largely of roving disposition and wide feeding range. Unmarked species of the family are mainly birds of low zones and narrower feeding beat. Only two of the first list are characteristically low rangers and given to covert-seeking: these are our eastern and western white-marked towhees (*Pipilo erythrophthalmus* and *P. maculatus*). On the other hand nearly all of the second list are either confined to close foliage of medium height, or belong to such associations as the rank growth of humid regions, the dark borders of shady swamps, or thickets of the chaparral belt. They are the thrushes, painted in monochrome above; warblers, lacking top-patterns; wrens with their finely barred color scheme; flycatchers with dull olivaceous or other uniform shadings. These are correspondences that surely have significance, and require for their interpretation something more than the older theories of coloration could offer.

Finding such good illustrations of the disruptive effect of white or bright patterns among animals and birds, the authors of "Concealing Coloration in the Animal Kingdom" (Gerald and A. H. Thayer, 1909), have come to believe that no other explanation is needed to account for the presence of top-white in birds that show themselves against the sky, than natural selection working through this means. Their belief accords with the conditions just cited. It does not, however, take account of the fact already mentioned that markings often become conspicuous during the flight of the bird, nor does it take note of the correlation that has been shown to exist among open-ground birds, of flight-revealed markings with the flocking habit—a condition which we shall also find largely present among the arboreal birds. In the use of these lists of birds to determine the latter point,

the very arbitrariness of the grouping tends to be misleading. A list of all perching birds that have color features tending to conspicuousness in flight (whether white or some other color), would correspond much more nearly to a complete list of the flocking birds. It would include the gregarious species of the family Icteridae which mainly lack white patterns. It would include the pine siskin (*Spinus pinus*) which has yellow wing markings instead of white. Yet, even as it stands, the list is very suggestive. When we consider the value to all birds ranging in the open foliage of instant recognition at a distance, and sight-clues for the purpose of keeping together, we shall not easily believe that wing and tail white are solely features of concealing coloration. Their revealing function during flight is entirely in harmony with their concealing functions when at rest.

An apt illustration of this harmony of functions is found in the following description of the western evening grosbeak (Bailey, 1902, p. 308):

“On a Sierra grade we have passed a flock busily gathering wild cherries in a bush beside the road, and when camped under the firs of Mt. Shasta have had wandering bands stop for a drink from the camp brook, delighting us by their striking yellow and white plumage. Although they are so highly colored and in flight their white wing patches make such prominent directive marks, this very yellow and white coloration often becomes positively protective. While watching the birds on Mt. Shasta one day, I was struck by the conspicuousness of one that flew across an open space. As it lit on a dead stub whose silvery branches were touched with yellow lichen, to my amazement it simply vanished. Its peculiar greenish yellow toned in perfectly with the greenish yellow of the lichen.”

It is of interest to note that the above observation was made before the disruptive effect of white patterns had been demonstrated by Thayer (1909), or the theory of their directive function seriously questioned. There could be no better instance than the one cited, of a double office performed by a single color feature—revealing in flight, concealing when in repose. Precisely this relation, I believe, exists through the group as a whole

SPECIAL STUDY OF THE MNIOTILTIDAE

For a more minute study of the relation of white color marks to a bird's habitual range I have chosen the American wood warblers. Not only are the members of this family very well distributed among the more or less well defined strata of local vegetation, but, unlike the Sylviidae or old world warblers, they show the highest degree of specialization both in regard to variety of pigments and to white patterns. It seemed worth while, therefore, to investigate the actual distribution of the species in the three categories of high or open foliage, medium, and low or close coverts. The results of such a study are embodied in the following table in which the mean height of the bird's occurrence has been compared with that of its average nesting site as recorded by numerous observers, and its feeding beat gauged with some accuracy. While it has not always been possible to distinguish clear lines of demarkation, on the whole there is a surprising agreement among writers who allude to the feeding levels of the warblers.

WARBLERS WITH WHITE WING OR TAIL MARKINGS.

OF HIGHEST RANGE.

	Level of Nest.		Level of Nest.
<i>Vermivora bachmani</i>	1'-3'	<i>Dendroica chrysoparia</i>	15' av.
<i>Compothlypis americana</i>	8' +	<i>Dendroica occidentalis</i>	2'-45'
<i>Compothlypis a. usneae</i>	8' +	<i>Dendroica caerulea</i>	40'-70'
<i>Compothlypis pityayumi nigrilora</i>	8' +	<i>Dendroica fusca</i> (Syn. <i>blackburniae</i>)	20'-84'
<i>Peucedramus olivaceus</i>	30'-50'	<i>Dendroica dominica</i>	20'-90'
<i>Dendroica magnolia</i>	3' +	<i>Dendroica graciae</i>	50'-60'
<i>Dendroica tigrina</i>	3' +	<i>Dendroica castanea</i>	15'-20'
<i>Dendroica auduboni</i>	4'-50'	<i>Dendroica striata</i>	1'-10'
<i>Dendroica nigrescens</i>	5'-52'	<i>Dendroica vigorsi</i>	8'-80'
<i>Dendroica virens</i>	3'-40'		

OF INTERMEDIATE RANGE.

<i>Mniotilta varia</i>	ground	<i>Dendroica kirtlandi</i>	ground
<i>Protonotaria citrea</i>	5'-25'	<i>Dendroica discolor</i>	1'-12'
<i>Vermivora chrysoptera</i>	ground	<i>Wilsonia citrina</i>	1'-5'
<i>Vermivora pinus</i>	ground	<i>Cardellina rubrifrons</i>	ground
<i>Dendroica coronata</i>	4'-20'	<i>Setophaga picta</i>	ground

OF LOWEST RANGE.

<i>Dendroica caerulescens</i>	1'-3'	<i>Dendroica palmarum</i>	ground
<i>Dendroica pensylvanica</i>	2' av.		

WARBLERS WITHOUT WHITE MARKINGS.

OF INTERMEDIATE RANGE.

	Level of Nest.		Level of Nest.
<i>Vermivora peregrina</i>	ground	<i>Oporornis tolmiei</i>	6"-4'
<i>Vermivora celata celata</i>	ground	<i>Wilsonia pusilla chryseola</i>	3'-5'
<i>Vermivora c. lutescens</i>	ground	<i>Wilsonia canadensis</i>	ground
<i>Vermivora c. sordida</i>	2'-8'	<i>Setophaga ruticilla</i>	2'-30'
<i>Vermivora rubricapilla</i>	ground	<i>Dendroica aestiva</i>	3'-25'
<i>Oporornis philadelphia</i>	6'-20'		

OF LOWEST RANGE.

<i>Helinaia swainsoni</i>	ground	<i>Oporornis formosa</i>	ground
<i>Helmitheros vermivorus</i>	ground	<i>Oporornis agilis</i>	ground
<i>Vermivora virginiae</i>	ground	<i>Geothlypis trichas</i>	ground
<i>Vermivora luciae</i>	2'-6'	<i>Geothlypis t. occidentalis</i>	6"-5'
<i>Seiurus aurocapillus</i>	ground	<i>Icteria virens</i>	1'-5'
<i>Seiurus motacilla</i>	ground	<i>Wilsonia pusilla</i>	ground
<i>Seiurus noveboracensis</i>	ground		

Of the fifty-seven warblers here treated, thirty-three have well-defined white top-patterns. Of these, twenty are high rangers, a number of them emphasizing their preference by choosing a nesting site at the extraordinary level of seventy, eighty, or even ninety feet from the ground.

It is a curious fact that a careful sifting of the recorded observations discovers no unmarked warbler belonging properly to the high feeding beats. A few, such as *Vermivora celata*, occur at variable heights and may be seen in the tops of trees; but these usually nest low, upon or near the ground, and are usually assigned an intermediate feeding beat. It seems to be true on the whole that the plain "protectively colored" warblers are unrepresented in the upper strata of our deciduous forests, that they are common at the medium levels, and, as shown in the table, belong mainly in the lower stratum, that of thickets, brush areas, tangles about marshy places. Briefly put, the situation among warblers seems to be: no plain plumages seen at the highest levels. But the converse—no marked plumages at lowest levels—is not strictly true. No arbitrary line is drawn. About the same number of the marked and unmarked occupy the intermediate feeding beats and nesting sites. It seems reasonable to infer, however, from the results shown by this tabulation that

top-patterns have decided utilitarian value to high-ranging warblers. That the value of white patterns is at a minimum for ground nesters and low feeders, seems to be as clearly demonstrated.

For those who find the arguments for the concealing functions of top-white conclusive, the table will primarily serve as evidence of the correctness of Mr. Thayer's interpretation. And such they are in so far as they corroborate the view that birds often seen against open foliage with sky-illuminated spaces should have and do have bright patches imitating these spaces. There may be no opposing view that can rob this one of its convincing power once it has been perceived. There is, however, a further consideration deserving attention.

High and open foliages involve more than a broken sky and leaf background with the need for imitating them. They involve wider spaces to travel; the ability to see companions at a greater distance; the need of seeing and keeping track of them by other means than call-notes; the long continued habit of so doing.

The warblers are among the most mutually dependent of birds, the least solitary, migrating in flocks and social during the daytime-portions of their travel. Among the least social the shyest and most retiring of the family are the plain or somber-hued species, including the so-called water thrushes (*Seiurus noveboracensis* and *S. motacilla*) and the Connecticut and mourning warblers (*Oporornis agilis* and *O. philadelphia*). The bolder, the most familiar, are in the *Dendroica* group (*Dendroica coronata*, *maculosa*, *auduboni*, etc.). This need not be a mere coincidence. We have noticed the same tendency in the order at large. With a preference for close, leafy coverts and secluded forest ways go the somberer tones, the monochrome coloration, and shy, furtive habits. With a preference for open woods and roving ways, greater distances and separations to be adjusted, have come the greatest variety of top-patterns among birds, many of them showing excellent devices for a revealing flight from the opening wing.

SEXUAL SELECTION AS AFFECTING WHITE PATTERNS.

It remains for us to touch on the question, does sexual selection enter into the problem of white patterns? For open-ground birds we can promptly answer that it does not. There are, however, many instances among arboreal birds where the white marking is intensified in the male. This very fact militates against the physiological contention that greater vigor in the male sex accounts for all color differences. White blotches or bars are caused by the absence of pigment. Were it not for the more intense coloration of other parts we might conclude on this basis that the white-marked male is deficient in vigor. It also argues against the view that white patches afford the best possible concealing pattern, for in that case the female should not have them obscured. Adherents of the directive theory may find support for their views in the fact that white wing bars do actually persist in the female in many cases, as in the pine grosbeak (*Pinicola enucleator*) and the white-winged crossbill (*Loxia leucoptera*) and others, so that it cannot be regarded as due solely to sexual selection. The analogy in the case of open-ground birds where both sexes are alike, as a rule, strengthens the directive interpretation. Further, if we are right in assuming that the male is the more vigorous and the leader of bird movements, then there is ground for believing that white markings, even though intensified in the male, are directive in some sense. That such a relation exists among warblers was the belief of Dr. Coues when he wrote the following paragraph descriptive of the warbler family.

“Some travel true to the meridian in hours of darkness, stopping at daybreak from their lofty flights to rest and recruit for the next stage of the journey. Others pass more leisurely from tree to tree in a ceaseless tide of migration, gleaning as they go. The hardier males in full song and plumage lead the way for the weaker females and yearlings.”

DIRECTIVE MARKINGS OUTSIDE THE ORDER
PASSERIFORMES.

An instance of revealing coloration outside the order Passeriformes seems worth citing since the very existence of a principle of directive coloration has been questioned (Thayer, 1900). The wings of the nighthawks, both eastern and western species, are, as is well known, marked with a single white spot in each. Far from tending to merge the bird's contour with anything in the background, these spots easily reveal and characterize the bird to observers. Even were there need for the nighthawks in their swift, crepuscular flights to be hidden from winged pursuers, it is hardly credible that the spots should serve this purpose. The Texas nighthawk (*Chordeiles acutipennis texensis*) is known to have a habit which gives revealing effect to the white throat-patch, as well as that on the wing. This throat patch is concealed as the bird takes its daytime rest in the open; but when surprised upon its nest it adopts the familiar wounded bird tactics to divert attention. After fluttering a short distance it faces the intruder, elevates and depresses its breast, thus appearing to make every effort to hold the attention of its enemy. Such a motion adds decidedly to the conspicuousness of the white patch. This effect of a pattern and corresponding behavior of the bird is perhaps unique, but it seems at least to establish a case of the revealing function of white.

CONCLUSION.

This paper has attempted to test the validity of the older interpretation of white markings in birds by analyzing their mode of occurrence in a single order, and to harmonize it, if valid, with a newer and apparently contradictory interpretation. It has shown that there is good ground for believing that flight-exposed markings, whatever their mode of evolution, are of actual utility to birds as sight-clues, whether occurring in the comparatively uniform rear markings of the open ground species, or the varied top patterns of the arboreal. It has called attention to a decided correlation of the markings with the habit of

flocking, as well as with that of open ranging. It has shown that sexual selection can only have operated in producing a more sharply defined pattern in the male, but cannot account for the existence of the pattern itself. Recent views as exemplified in Thayer (1909) as to the concealing effect of white markings have been regarded as greatly simplifying the problem and aiding our understanding of the possible meaning of the patterns. This newer view, however, is found to be in perfect accord with the older one known as the Theory of Directive Markings. It restricts the application of the latter, however, to patterns that can be shown to be conspicuous.

These considerations cannot be regarded as affording evidence in an ultimate sense. They lead at best to the provisional modification of an interpretation that was open to criticism, and tend to check over-emphasis upon the concealing principle in animal coloration. Doubtless they fall short of reaching the full meaning of the white or bright patterns of passeriform birds. Possibly the interpretation of diverse coloration as having developed under conditions of comparative immunity, from such sources of attack as those to which terrestrial animals are subject needs greater emphasis than has been given it.

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