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THE NOMENCLATURE OF PLUMAGES AND MOLTS*

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IN *The Auk* of 1959 (76: 1–31) there appeared an article by P. S. Humphrey and K. C. Parkes entitled "An approach to the study of molts and plumages," which will be the subject of this paper. Some readers may not be familiar with Humphrey and Parkes's paper and therefore would welcome a summary of the principal points discussed by these authors. Feeling unhappy with the terminology of molts and plumages as proposed (in 1900) by Dwight, and which has been, to use their words, the foundation of most, if not all, subsequent work, they decided to replace it with an almost completely new nomenclature. In their opinion (p. 14) "there is clearly a need for a semantically 'clean,' independent, uniform, and practical terminology applicable to plumages and molts of all birds," and therefore they endeavored to introduce a nomenclature which might assist in clarifying homologies of molts and plumages.

With that aim in mind, they do not spare a single one of the expressions which are in current use, except the term juvenal plumage. They do away with adult, subadult, immature, annual (or perennial) plumage, nuptial plumage, off-season or non-breeding plumage, and so with Dwight's whole system of molt nomenclature, because they believe that molts should be named in terms of the incoming, and not of the replaced, generation of feathers. They introduce the new term basic plumage to designate what we used to call annual or, following Lynes (1930: 38), perennial, plumage. The molts by which this basic plumage, as well as the juvenal plumage, are replaced should henceforth both be called prebasic molts, no longer the annual and the postjuvenal molt, respectively. In birds which have as adults two plumages per cycle, as, for instance, the Scarlet Tanager (*Piranga olivacea*), the complete molt is, in their

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terminology, again the prebasic molt (not the postnuptial molt), producing the dull-colored basic plumage (not the off-season, or winter, plumage). The basic plumage in such birds is succeeded by another, brighter plumage, which the authors call the alternate plumage (not the nuptial plumage). The intervening molt gets the name prealternate molt (no longer the prenuptial molt).

May I now be allowed to state that, when reading this article, I felt just as uneasy about the new terminology as the authors seem to have felt about the terminology of Dwight. Fifty years of experience with problems of molt and plumage may justify my intervening in the discussion. This case concerns not only American ornithologists, but those working in other countries as well.

One of my main objections is directed against the attempt of the authors to replace a nomenclature based on, and connected with, the biological cycle by a sterilized and homogenized terminology. Not a single one of their few names is derived from seasonal, reproductive, developmental, or other biological phenomena. I base this objection on the following facts.

Throughout the class Aves the principle can be traced that the male sex looks most conspicuous and ornate during the mating time. In the Holarctic Region this effect is frequently attained by abrasion of the fringes of the contour feathers which had grown in late summer, a process which may result in a drastic change of appearance by the time of pair formation. In other cases a similar and usually even more fundamental change is brought about because of the insertion of another generation of body feathers, the dull-looking off-season plumage, between the plumages worn during courtship. If one wants to compare biologically, one will have to equate the brilliant spring plumage of the Starling (*Sturnus vulgaris*), brought about by abrasion of the feather tips, with the bright red plumage of the Scarlet Tanager, obtained by molt of all body feathers in late winter. Our authors, however, hold a different view; they believe that the greenish yellow, off-season plumage of the male Scarlet Tanager is homologous with the perennial plumage of the Starling, and therefore call them both the basic plumage. This I consider a mistake, gravely affecting their whole outlook. I shall now try to support my view by arguments.

May I start with the mode shown by most species of Passeriformes that live in the equatorial rain forest? They molt from a short-lived juvenal plumage directly into their first perennial dress, in which they are at once ready to reproduce. Many populations of this equatorial habitat consist of a mixture of breeding, non-breeding, and molting individuals in perennial dress.

At both sides of this equatorial belt, which ends, roughly speaking, at a distance from the equator of about 8°, the periodicity of day length begins to become clearly effective. By the direct or indirect influence of this periodicity the gonads of all individuals of a given population stay in extreme regression for a certain period. The length of this rest period is subject to some individual variation. Therefore, periodically changing signals of the external appearance, chiefly plumage characters, may become significant in intraspecific competition, if coupled with the stage of gonadal development. A complication of the pattern of molting may therefore produce an epigamic advantage.

Such complication has evolved in a number of species belonging to more than 14 families of the songbirds. Instead of going from one perennial dress into the next one by a succession of complete annual molts, the males of these species undergo within 12 months a postnuptial and a prenuptial molt. By the postnuptial molt the off-season dress is produced, a rather exact recapitulation of the juvenal or the immature plumage, while the prenuptial molt leads to the nuptial dress.

Now comes our point. The intercalation of the off-season dress is obviously a secondary acquisition. The development of two seasonal dresses, one of which has an epigamic signal effect, depends on the evolution of an influence of hormonal periodicity on plumage characters. Only after this evolutionary stage has been reached will the postnuptial molt produce, by the action of a hormonal check, the masculine off-season dress. In non-migratory species this is worn almost exclusively during the period of gonadal regression, which in some weavers and sunbirds lasts no longer than about 8 to 10 weeks.

Within the equatorial belt, however, most of the sunbirds and weaver birds in question wear a perennial dress (Ticehurst, 1935; Chapin, 1954: 188–584; Moreau, 1960: 319–321), which probably is due to the permanent absence of the same hormonal brake that developed beyond this belt. Their perennial dress is colored exactly like the nuptial dress of their non-tropical relatives, for this is the genetically fixed dress, which can be toned down, but not intensified, in the physiological experiment (Stresemann, 1940).

It seems to depend on the biological requirements of a given species, by which of the two seasonal molts the wing feathers are renewed. I do not agree at all with the following generalizing statement of our authors (p. 15): "In birds which have, as 'adults,' two plumages per cycle . . . the complete molt is . . . the prebasic [i.e., the postnuptial] molt, followed by the basic [i.e., the off-season] plumage." I can think of many exceptions based on my own personal observations. A few examples follow. Most loons and the weaver finch *Amandava* molt the wing when

going from off-season dress into nuptial dress. Some of the sunbirds, for instance *Cinnyris asiatica*, start molting the primaries while still in full nuptial dress; this goes on in off-season plumage, and the bird is almost in full nuptial dress *again* when the last old primary is shed. How to classify this mode of molting? Is the postnuptial molt to be considered the complete one, or the prenuptial? In other cases the postnuptial molt as well as the prenuptial molt is confined to the body, while the wings are molted separately in between, for instance in the phalaropes (Phalaropodidae), in Sabine's Gull (*Xema sabini*), in the puffin (*Fratercula*), and others. The grebes drop all wing feathers while still in full nuptial plumage, shortly before going into off-season plumage. Franklin's Gull (*Larus pipixcan*) and certain terns (Sterninae) change all their remiges twice a year while in off-season plumage. Would our authors assert that these two sets of wings are not homologous with each other? That would mean, I think, misapplying the homology concept.

All this may have sufficiently shown that it was a mistake to choose all the many various cases of complete wing molt as the directive event, and to call every plumage produced by it the basic plumage. Such arbitrary procedure would either be inapplicable to many cases, or it would lead to amusing consequences. In *Nectarinia takazze* as well as in some other sunbirds the remarkable fact exists that some populations have a perennial bright dress acquired by complete postnuptial molt, other populations a dull dress acquired by complete postnuptial molt and a bright dress acquired by partial prenuptial molt, in succession (personal observation). One would therefore be obliged to name the bright plumage, if worn by the double-plumaged Ethiopian population of this sunbird, the alternate plumage, but if worn by the single-plumaged Kenya population, the basic plumage. I could multiply such examples *ad libitum* (see Lynes, 1930: 38–42, etc., on *Cisticola*; Moreau, 1960, on *Ploceus*; Chapin, 1954: 188–282, on African sunbirds; Ticehurst and Whistler, 1939: 762, on *Franklinia*).

Thus one cannot rely on the hints given by the complete molt. The only marks in the life of any bird which can be trusted are growing up and courtship, thus exactly those points which have been discarded by our authors as being of no use for clarifying plumage homologies.

Still another complication in the sequence of molts must be considered here. Some resident species which customarily move amidst harsh grass or dense cover have two identical or almost identical plumages per annum, separated by two complete molts; their number may be larger than we know at present. This double molt is of no epigamic advantage, and merely caused by the need to replace the worn plumage after about six months instead of twelve. In such cases there is no change of coloration

involved, and one would therefore miss the point by homologizing this second semiannual dress with the semiannually worn nuptial plumage of the former category.

On long-distance migration too, and not only in dense cover, the plumage, including the wings, becomes abraded, often to a considerable degree. This is the cause of the phenomenon of double molt in many small songbirds with long migration routes, for instance, in European warblers. In the resident species of the genera *Sylvia* and *Phylloscopus* the whole plumage is molted only once a year; they wear a perennial dress. Those species which migrate to a moderately distant winter area have a second molt in winter, confined to the body. Those with very long migration routes, as *Sylvia borin* and *S. communis*, or *Phylloscopus trochilus* and *P. sibilatrix*, renew even the wings twice a year (Witherby *et al.*, 1938: 11, 17, 78, 85; Ticehurst, 1938). Such a diversity of cases could hardly be expressed reasonably in the simple language of the new nomenclature, in which the first feather generation per cycle is consistently called the basic, the second generation the alternate, and the third (wherever such exists) the supplemental, no matter what their biological meaning may be. Counting feather generations seems to me an objectionable method of determining plumage homologies.

Let me add another objection. To apply the new terms consistently according to their definition, one has to trace the sequence of plumages down to the juvenal plumage, because this is chosen by Humphrey and Parkes as the starting point of the succession of their plumage names, the one succeeding the juvenal always being called the first basic plumage. But what to do if there are doubts about the existence of an alleged juvenal plumage? The green dress preceding the blue-and-black nuptial dress of the male Blue Honeycreeper (*Cyanerpes cyaneus*) has been considered to represent an immature postjuvenal dress, following an earlier, loosely structured, first juvenal dress (Dickey and Van Rossem, 1938: 479–480; Skutch, 1954: 401, 1962: 111). But nobody seems to have distinguished between these (hypothetically two) green dresses, and I doubt that two exist. What will happen if the blue-and-black dress should be shown to succeed the juvenal dress? The application of the terms basic and alternate will have to be reversed, the first blue-and-black plumage becoming the first basic plumage, afterwards periodically replaced by the female-like definitive basic plumage and the blue-and-black alternate plumage.

In many of the larger birds the process of ripening is a slow one. The drake of the Mallard (*Anas platyrhynchos*), for instance, molts from juvenal plumage directly into his first nuptial plumage, which can rightly be named the adult nuptial plumage, but its pattern is not definitive,

since in the next summer the markings of its flank feathers will become a bit more subtle, and minor changes seem to go on like this for years (Stresemann, 1940). All we may safely say in such cases is that the bird is in adult plumage, and it would be incorrect to call this plumage definitive, as our authors have proposed.

The change from juvenal to adult plumage is frequently not such a sudden one as in the Mallard and other Holarctic ducks. It can be very gradual, either by a succession of immature plumages, as in the Gannet *Sula bassana*, or by a very prolonged molt which slowly leads from one developmental stage to the next. Such transitional flow defies every effort to divide it into separate plumages. The Little Blue Heron (*Florida caerulea*), for instance, when young, belongs to this category. It takes it the first eight months of its second year to molt gradually from juvenal plumage into a plumage approaching that of the adult bird in color and structure; at the end of this period it has exchanged even the last one of its white juvenal quills for black ones, and in the late autumn of this, its second year, it molts into adult off-season plumage, looking henceforth like its parents. In the new *Handbook of North American birds* (Palmer, 1962: 428), however, the attempt has been made to adapt this state of affairs to the nomenclature of our authors by cutting up the transitional continuity. The following sequence of plumages is given: juvenal, basic I, alternate I, basic II, alternate II, basic III (definitive). Might it not have been preferable to study and to describe what is going on instead of being consistent in plumage nomenclature by forcing the facts to a Procrustean bed?

Allow me to quote a last example. *Lanius collurio*, the European Red-backed Shrike, has a second juvenal plumage differing from the first one only by its more durable structure. It is worn during migration from Europe to tropical Africa where it is replaced in December and January, thus after about four months, by the sexually dimorphic (and in the male quite differently colored) perennial plumage of the adult bird. Its only reason for existence is that it is far better fit for long distance travel than the first juvenal plumage would be. The intentionally inarticulate language of Humphrey and Parkes has no equivalent for the term second juvenal plumage or even immature plumage. This dress of *Lanius collurio* would have to be named first basic plumage, succeeded by a series of definitive basic plumages. Such nomenclature, however, would be quite misleading. Two plumages of fundamentally different relation to function would equally be termed basic, and the ideal aim of the new nomenclature, to assist in clarifying homologies, would once more be completely missed.

To sum up: there is no such thing as a fundamental pattern of

plumage succession which can be traced almost throughout the class Aves. The initiators and the promoters of the new nomenclature were far too optimistic when they thought that descriptive and comparative plumage studies would proceed in a more orderly fashion if they were conducted in the light of their homology concept. In my opinion the result is an artificial, man-made order, incompatible with the facts. The more one learns about plumages and molts, the deeper one enters into this rich field of research, the more one wonders at the diversity of modes which have been produced by yielding to various kinds of selective pressure or by other factors. To do justice to the facts and to transmit them accurately we need an articulate, and not an oversimplified, language.

I therefore strongly advocate the further use of the widely accepted terminology of Dwight, with those few alterations or complements that have since been proposed by Hubert Lynes, Alden Miller, and others who have, like these two outstanding ornithologists, made plumage sequence their special field of research. Why not use, as was done for half a century, the terms immature, subadult, adult, annual (or preferably perennial) plumage, off-season plumage, nuptial plumage, postjuvenal molt, annual molt, prenuptial molt, and postnuptial molt? They make due allowance for the great diversity of cases and do not lead us upon the treacherous ground of unwarranted homologization. Those who dislike the term nuptial plumage could call this the epigamic plumage, as opposed to the apogamic plumage in the sense of Julian Huxley.

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