COMMENTS ON THE STUDY OF PLUMAGE SUCCESSION

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PUBLICATION of the A.O.U. *Handbook of North American birds*, Vol. 1, has stimulated new interest in molts and plumages, particularly with respect to problems of nomenclature. The concepts and terminology adopted by the *Handbook* were, with minor modifications, those originally proposed by us (1959). Most recently, Professor Erwin Stresemann (1963) has published a stimulating critique of our 1959 paper; his thoughtful analysis provides us with a welcome opportunity to review our own concepts.

TERMINOLOGY OF MOLTS AND PLUMAGES

Professor Stresemann is the leading proponent of that school of thought which holds that the terminology of molts and plumages must be a functional one, i.e., must be linked inextricably with other features of a bird's life cycle, for example, with courtship ("epigamic"), nesting ("nuptial"), development ("immature" and "subadult"), etc. Although we have never questioned the obvious desirability of studying the molts and plumages of a species in a total biological context, we showed (1959) that a "dependent" plumage terminology may actually hamper rather than aid such a study. This is especially true when the biology of a species is poorly known, so that the "dependent" terminology implies a relationship which has not actually been determined.

Some of the major tenets of Professor Stresemann's approach to the study of molts and plumages, as expressed in his recent paper (1963), are herewith quoted as follows (not necessarily in their original order):

". . . there is no . . . fundamental pattern of plumage succession which can be traced almost throughout the class Aves" (pp. 6–7). "The only marks in the life of any bird which can be trusted are growing up and courtship . . ." (p. 4). ". . . 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" (p. 4). "[Professor Stresemann] strongly advocate[s] 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 . . ." (p. 7).

The concept of the complete molt as a landmark in the plumage cycle of a species dates back—not to Humphrey and Parkes (1959)—but to Dwight himself who wrote (1902: 249): "From time immemorial, the adult plumage of the breeding season has been accepted as the one most typical of the species, and the moult by which it is entirely swept away forms a fixed point in every plumage-cycle." What we (1959: 2) characterized as "the prevalence of [an] apparently consistent pattern" of molts and plumages among most birds was also anticipated by Dwight (1900:

130), who stated: "The only invariable moult is the postnuptial which, except in a very few rare cases, is absolutely complete and takes place in all species at the close of or soon after the breeding season peculiar to each." Thus we see that Dwight's plumage terminology, which Professor Stresemann advocates, is founded upon two concepts, the landmark molt, and the existence of a fundamental molt pattern among most birds, which Professor Stresemann denies.

We have earlier discussed at length (1959: 11–14) many of the shortcomings of a "dependent" terminology of molts and plumages. Our considered view, which we still hold, was summarized in our statement (p. 14) that:

> . . . currently used terminologies for molts and plumages have a sufficient number of serious drawbacks to warrant a thorough revision. We have no argument with the findings of modern workers regarding the nature and pattern of plumage succession of birds as it may be related to seasonal rhythms, reproductive cycle, ontogeny, and various other environmental and endocrinal phenomena. We do contend, however, that these phenomena may be related in different ways in different groups of birds, and that these relationships can only be obscured by making the nomenclature of plumages and molts contingent on states of any other cycle or developmental process. . . .
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> We are fully aware of the vast amount of work yet to be done, particularly on the more aberrant groups of birds, before anything like a full understanding of the biology of molts and plumages can be achieved. . . .

For birds of many parts of the world, as we have previously stated, the use of a "dependent" terminology of molts and plumages necessarily involves making unwarranted assumptions about the biology of poorly-known species.

Let us consider for a moment one of the many species of birds from such areas as Amazonia or New Guinea about which nothing is known except what may be deduced from museum skins and their labels. From examination of a series of such skins, the existence of molts can be demonstrated. But in the absence of any knowledge of other biological cycles of the species, how can the use of a "dependent" terminology for these molts be justified? It is perhaps well to remember that Dwight developed his concepts and terminologies using exclusively north temperate examples, for which certain broad assumptions about breeding seasons can be made. As has been demonstrated by many recent authors, these assumptions are not applicable to large areas of the world. Provision of appropriate terms for dependent terminologies applicable to each area of the world would result in a confusing proliferation of terms and could not in any case be done until the biology of each species was understood. The "semantically neutral" terminology which we advocate does not encounter this difficulty. In discussing our terminology, Professor Stresemann

(1963: 2) says: "Not a single one of their . . . names is derived from seasonal, reproductive, developmental, or other biological phenomena." To reiterate once more, our selection of an independent terminology *was* deliberate. Its conceptual basis, however, *is* a "biological phenomenon," one which was not touched upon by Professor Stresemann in his critique.

PLUMAGE SUCCESSION AS A BIOLOGICAL PROCESS

Certain attributes of feathers vary in ways which can be described and studied comparatively. Among these are variations in structure (both gross and microscopical), pigmentation, distribution (pterylosis), and details of development (morphogenesis). It should be noted that the study of each of these characteristics of feathers has its own techniques and vocabulary.

Still another attribute of feathers is their periodic development and replacement throughout the life of an individual bird. This is a complex, energy-consuming biological process which can be considered in several ways. Among these are the following.

1. The relative timing of initiation of feather growth in each area of the bird's body (molt centers, molt gradients, etc.).

2. The physiological and morphogenetic events involved in the development and ultimate replacement of each individual feather.

3. The cyclic nature of feather replacement (sequence of molts and plumages).

Feather replacement is thus one of a number of biological processes, the variations of which may be described and classified using an appropriate specialized vocabulary.

One of the major points of our 1959 paper is that molt is a growth phenomenon resulting in a new generation of feathers; loss of the previous generation of feathers is a relatively unimportant by-product of this process when considered from the point of view of energy expenditure. For this reason we advocated naming molts for the incoming rather than the outgoing generation of feathers (thus "prebasic" rather than "postnuptial" molt). This concept has since received additional and unexpected support from the work of Watson (1963), which shows that, at least in many birds, the mechanism of feather replacement from one definitive plumage generation to another is the same as that from natal down to juvenal plumage, that is, molt, rather than being a "two-part process entailing the passive loss of old feathers (ecdysis) and the subsequent growth of new feathers (endysis)" is in fact "a single growth process actively concerned only with the production of feathers of the new generation. The new growth causes the passive loss of the old feathers."

Thus it is evident that our newly proposed terminology is not simply a

substitution of our names for those of Dwight, but reflects a fundamental change of concept. Many of Dwight's conclusions about molts and plumages remain valid and have formed the basis for much of our own thinking. We prefer, however, a nomenclature which more closely reflects molt as a biological phenomenon and is more accurately applicable to birds of all parts of the world.

CONSISTENCY IN PATTERNS OF PLUMAGE SUCCESSION

Professor Stresemann specifically rejects our suggestion that there "appears to be a fundamental pattern of plumage succession which can be traced almost throughout the class Aves" (Humphrey and Parkes, 1959: 2). We went on to point out, however, that "such a pattern has been noted and utilized by students of this subject for over a century."

Patterns of plumage succession in birds show remarkable similarities that are inescapably apparent when the plumages and molts of representatives of diverse orders are studied in detail. Take, for example, the following sequence of molts: [juvenal plumage]—partial first prebasic molt —partial first prealternate molt—complete second prebasic molt—partial second prealternate molt—[etc.]. This sequence is shared by species of such taxonomic and ecological diversity as: Horned Grebe (*Podiceps auritus*), Double-crested Cormorant (*Phalacrocorax auritus*), Great Blue Heron (*Ardea herodias*), Sora (*Porzana carolina*), Purple Sandpiper (*Erolia maritima*), Herring Gull (*Larus argentatus*), Common Murre (*Uria aalge*), European Kingfisher (*Alcedo atthis*), Water Pipit (*Anthus spinoletta*), Wheatear (*Oenanthe oenanthe*), Myrtle Warbler (*Dendroica coronata*), and American Goldfinch (*Spinus tristis*).

Professor Stresemann and others have seriously questioned the applicability of the homology concept to the study of molts and plumages. Nevertheless, homology is implicit in any comparative study of feather replacement, as for example, the use of modes of primary molt as evidence for taxonomic relationships (Stresemann, 1958, 1959; Stresemann and Stresemann, 1960, 1961; Verheyen, 1958, 1962).

The establishment of a uniform terminology applicable to all birds (which, after all, is what Dwight attempted) carries with it at least an implication of homology. Whether the similar patterns of plumage succession in distantly related birds are indeed phylogenetically homologous is of little significance when weighed against the practical convenience of an easily applied uniform terminology. Such a terminology is a vital prerequisite for the study of plumage succession as a biological phenomenon, especially when approached from the comparative viewpoint.

The value of homology-oriented thinking in comparative studies of plumage succession is dramatically illustrated when the existence of hith-

erto undescribed molts and plumages can be predicted and then confirmed by the examination of specimens. As an example, Palmer, in preparing the description of the plumage sequence of *Ardea herodias* for the *Handbook of North American birds* (Palmer, 1962: 392–393), had difficulty in translating the account by Bent (1926: 107–108) into a definite sequence of molts and plumages. Comparison with the account of *A. cinerea* by Witherby *et al.* (1939: 131–133) made it plain that Bent had overlooked the first prebasic molt, confusing the juvenal and first basic plumages. There was still, however, a discrepancy in the sequence, as Witherby *et al.* listed the molt *following* the first prebasic molt as *complete*, beginning rarely in May, usually in June or July. Adult birds, as indicated by Witherby, have a partial prealternate molt in late winter or early spring, replacing feathers assumed at the prebasic molt in the previous fall. No such prealternate molt, however, had been described for the first year of life. A sequence in which the prealternate molt is wholly skipped the first year, to be assumed as part of the normal molt cycle in later life, would be most exceptional. At Palmer's request, Parkes examined specimens and found that there is, indeed, a partial first prealternate molt of limited extent, in December and January, occupying the place in the cycle where it "ought" to be.

As we have previously stated (1959), the great majority of species whose plumage successions have been thoroughly studied conform to our system without "forcing the facts to a Procrustean bed." We feel, therefore, that the most useful constructive criticism would not emphasize the poorly known species or those few with apparently aberrant patterns of plumage succession. Rather, perhaps, it would be well to test our system against the numerous birds whose patterns of plumage succession are already known, or for which ample specimens are available for study. Partly hypothetical cases (for example, *Cyanerpes cyaneus*; cf. Stresemann, 1963: 5) are surely not suitable as a basis for criticism. Specimens in the Carnegie Museum clearly demonstrate the existence of a grayish-green juvenal plumage in both sexes of *Cyanerpes cyaneus* preceding the yellowish-green first basic plumage. Thus Stresemann's doubts about the existence of two green plumages are without foundation. We think that the plumage succession of no species is so hopelessly impossible of interpretation as to justify the complete abandonment of any plumage terminology, as suggested by Professor Stresemann for the Little Blue Heron (*Florida caerulea*).

We made full allowance in our 1959 paper for the fact that "a few groups of birds [which were specified later in the paper] present exceptionally difficult problems of interpretation when attempts are made to fit them into the system of homologies here proposed." That these diffi-

cult groups comprise a small minority is suggested by the fact that Dwight (1900), in studying 152 species of passerine birds of New York, belonging to 20 families, found most species to be readily placed in one of a limited series of patterns of plumage succession essentially similar to those outlined by us (1959: 24); Dwight's chief difficulty arose from uncertainty about the presence and extent of the prealternate molt, which is hardly surprising in view of the limited material available to him.

Many birds other than the north temperate passerines studied by Dwight (1900), including waterfowl and birds from the Philippines (tropical) and Argentina (south temperate), have been shown in our own studies to have patterns of plumage succession compatible with our system.

Professor Stresemann has shown that within certain genera such as *Sylvia* and *Phylloscopus* there is marked diversity in patterns of plumage succession. As he suggests, this diversity is apparently of adaptive origin. He believes that such adaptive diversity precludes the use of a single terminology applicable to all species of such a genus. We contend, however, that just as adaptation allowed the changes in size, color, proportions, wing formula, etc., to result in evolution of the extant species of *Phylloscopus* from an ancestral leaf-warbler, so must the present variation in molt sequence within the genus have evolved from an ancestral type. Only by studying comparatively the sequence in the extant species can we deduce the course or courses of evolution within the genus. Such comparisons cannot be made without certain postulated homologies being accepted for molts and plumages, just as they are for organs and behavior patterns. We cannot believe that a sequence of molts and plumages was created anew for each species of *Phylloscopus*.

MISCELLANEOUS NOTES

In reading Professor Stresemann's paper (1963) we noted several statements which deserve specific comment. Because of space limitations, we confine our commentary to three of the more significant points.

1. "The drake of the Mallard (*Anas platyrhynchos*) . . . molts from juvenal plumage directly into his first nuptial plumage . . ." (p. 5). However, as Witherby *et al.* (1939: 238–239) and Schiøler (1921, 1925) have shown, the first basic plumage conspicuous in such ducks as the Shoveler (*Anas clypeata*) still exists in reduced form in the Mallard between the juvenal and first alternate ("first nuptial") plumages.

2. "Throughout the class Aves the principle can be traced that the male sex looks most conspicuous and ornate during the mating time" (p. 2). In point of fact, sexual dimorphism of the type in which males "are most conspicuous and ornate" during a single season only ("the mating time") is found in a relatively small number of species. It is, for example, absent

in such groups as the tube-noses, geese, grebes, loons, gulls, terns, auks, hawks, owls, parrots, pigeons, goatsuckers, swifts, most coraciiform birds, most piciform birds, and many passeriform birds.

3. "The intercalation of the off-season dress [in males of "a number of species belonging to more than 14 families of the songbirds"] is obviously a secondary acquisition" (p. 3). Although possibly true of some groups of birds such as certain sunbirds and weavers, this generalization does not "obviously" apply to the majority of the seasonally dimorphic birds.

The "off-season" plumage of males, because of its frequent resemblance to the plumage of females and juvenals, has long been considered to be more "primitive" than the bright plumage of the breeding season. If this assumption is correct, the bright plumage of the male must be a secondary acquisition. For a more detailed discussion of this and related points, see Humphrey and Parkes (1959: 24–25).

SUMMARY AND CONCLUSIONS

In summary, we feel we can do no better than to quote from our 1959 paper certain statements which seem to have been overlooked in subsequent discussions of molts and plumages (pp. 1–2, 17):

> In spite of the vast progress made by many workers in recent decades in understanding some of the factors which affect the physiology of molt (genetic control, hormonal balance, photoperiod, temperature, diet, etc.), it must be remembered that such information is available for but a small fraction of the species of birds of the world. We believe that it is greatly desirable to have a system available whereby variations in the patterns of plumage succession may be described, compared, and contrasted among different groups of birds, whether or not the physiological mechanisms have been worked out for the groups in question. . . . It is, of course, impossible to be certain that plumage sequences which appear to be exactly equivalent in various groups of birds are truly homologous in the phylogenetic sense; however, we believe it is not only useful but even necessary to treat such equivalence provisionally as homology in studies of the type we have mentioned. . . .
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> We are well aware that difficulties will be encountered in applying this terminology to certain groups of birds. In some cases this will prove to be due to incomplete knowledge of the molts and plumages of that group, and further study will show that such birds conform to the pattern of homology outlined above, with, of course, their own specialized modifications of the pattern. Other cases may well show that parts of our fundamental thesis need to be altered or broadened. We feel, however, than an understanding of the most prevalent patterns of plumage and molt and their homologies is a necessary prerequisite to the study of groups which may seem to depart from those patterns, and we believe the system outlined above will aid materially in gaining such an understanding.

In conclusion, we address ourselves to those who have carefully studied our proposals and find them unsatisfactory for their intended descriptive and comparative purposes. We believe we have made a good case for the

existence of major shortcomings in the many variations of the Dwightian terminologies. Nothing is gained by rejecting our proposals merely to avoid abandoning that which is familiar. We ask that critics provide for us and for other students of plumage succession an improved conceptual and terminological framework within which we may all continue productive research in this promising and important field of ornithology.

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