AVIAN PLUMAGES AND MOLTS

DEAN AMADON

FUNCTIONS OF FEATHERS AND PLUMAGE

The primary function of feathers is flight, but they also insulate and protect the body from the physical environment. The reptilian scales from which they evolved have this as their principal function. Perhaps a reptile that was becoming warm blooded evolved frayed scales to provide better insulation and these in turn proved to be preadapted for flight. In birds that long ago lost the ability to fly such as the kiwis (*Apteryx*) the vaned structure of the feathers of flying birds has deteriorated.

Feathers are collectively called plumage, just as the hairs of a mammal make up its pelage or fur. The term is also used for particular "ensembles" of feathers such as "downy plumage" and "male breeding plumage." Recently Humphrey and Parkes (1959) have proposed a new usage for the word "plumage," and the entire concept of plumages is discussed at greater length later in this paper.

If all birds had uniformly black feathers like a crow and if selection for flight and insulation were the only influencing factors, what direction would the study of feathers take? The adaptations, especially of the wing and tail feathers, for flight would be of paramount interest: first, the general adaptations and then such specialization as notched outer primaries and forked tails, which aid aerial stability or maneuverability. Then one would turn to the original function of feathers and other epidermal structures, that of protecting the animal from the environment. This function has been retained in feathers, and, as suggested, may have preadapted them for flight.

But not all birds are black. Feathers often have complex patterns, culminating in such amazing structures as the vanes of the peacock (*Pavo*), which are, as Darwin noted, one of the problems posed by nature to the theory of natural selection. This variety in color pattern extends to different parts of the bird's body and to the individual bird at different ages and seasons. That the shape and texture of feathers is as adaptable as their color scheme is shown by the extravagantly modified plumes of egrets and birds of paradise. Even the normal structure of the feather may be lost, as in the celluloid-like head feathers of the Curl-crested Araçari (*Pteroglossus beauharnaesii*) or the plumes of the King of Saxony's Bird of Paradise (*Pteridophora alberti*). Feathers basically adapted for flight maneuverability such as a forked tail may secondarily be modified for display, as in the Greater Racket-tailed Drongo (*Dicrurus paradiseus*). In several instances, for example the tail feathers of snipe (*Gallinago*), feathers have become modified for producing sounds used in sexual display.

It is clear, then, that feathers and plumage are extremely responsive to selection. What are the secondary functions they have acquired, over and above the primary ones of flight and insulation?

Camouflage. Streaked grassland birds, sand-colored desert birds, and white arctic birds are well-known examples of concealing coloration. Sometimes the camouflage is heightened by behavior as when a bittern (*Botaurus*) stretches head and neck skyward, thus blending with the marsh vegetation. The dark hues of forest birds (Gloger's Rule), the white of arctic birds, and the sandy hues of desert birds are probably primarily adaptations for concealment.

Display. The important relation of feathers to display cannot be overemphasized. (a) Displays related to reproduction. We do not need to outline the formal classifica-

tion of such displays, for in all types plumage is usually important, and often all-important. Among the functions of such displays are attraction of a mate or mates; species recognition; maintenance of pair bonds; sexual stimulation; and threat toward conspecifics of the same sex (usually males) and others. (b) Warning displays. These are not common among birds, but the ear tufts of "horned" owls, in conjunction with glaring yellow eyes, may scare off some enemies. Cott (1947) believes that the conspicuous black and white plumage of wheatears (*Oenanthe*) may serve notice that they are, if not inedible, at least unpalatable.

Signal marks. The white outer tail feathers of such birds as juncos (*Junco*) and meadowlarks (*Sturnella*), which are conspicuous in flight but not otherwise, are examples of signal marks. The flashing white plumage of terns (Sterninae) may serve as a signal to attract others of the species to a school of fish; alternatively it may be less frightening to the fish. Selection may even produce convergent coloration in a number of species that profit by associating together (Moynihan, 1960, 1962; Dixon, 1963).

It is hardly necessary to say that several functions may be served by the plumage, or parts of it, simultaneously. A meadowlark is streaked and camouflaged dorsally, and has a yellow breast set off by a black crescent, which is used in sexual display, and white outer tail feathers that serve as a signal in flight or when the tail is flicked. Thus the plumage, like the entire organism, represents a compromise among various selective pressures. Even a peacock retains the power of flight. Furthermore, the plumage may change periodically to serve specific functions, notably in seasonal breeding plumages.

Most species of birds and often the sexes and the immatures as well can be identified from plumage alone with no other clues, except sometimes size and proportions. This should be sufficient indication of the biological importance to birds of recognizing each other by sight. The well-known fact that birds react to even crudely stuffed specimens is further evidence of this. Avian systematics at the racial, specific, and, to a considerable extent, generic level is based on the fact that each taxon, with very few exceptions, is separable from its closest relatives in terms of plumage. Usually this is the most evident morphological difference. Further, as the result of the work of such ethologists as Lorenz, as well as of geneticists, we now take it for granted that every special feature of a bird's plumage, whether the rosy underwing coverts of a Rose-breasted Grosbeak (*Pheucticus ludovicianus*) or the nasal bristles of a crow, are functional and adaptive.

KINDS OF PLUMAGES

Plumages peculiar to the young bird. No bird when it hatches has a fully adult plumage, and in most cases its immature plumage is very distinct. Or the chick may be stark naked! In such cases some down appears later, although in one genus of swifts the "down" consists of modified feathers of the subsequent pennaceous plumage (Collins, 1963). Young megapodes (Megapodiidae) that can fly on their first day of life are the only approach to an exception, but even their plumage is far from identical with that of the adult. Most birds have one or more downy (neosoptile) plumages. In addition, most species have one or more pennaceous (teleoptile) immature plumages. There are a few species in which all the plumages except the downy are identical or virtually so, and yet the bird does not breed until several years old. The Common Shearwater (*Puffinus puffinus*), which apparently does not breed until it is five years old, is an example.

At the other extreme, some birds breed either sporadically or regularly while in immature plumage. Heinz Meng (personal communication) reports that at perhaps one nest in eight of the Cooper's Hawk (*Accipiter cooperii*) one, apparently never both, of the pair will be in immature plumage and hence a bird hatched the preceding year. The same occurs in various other hawks and falcons. A few small songbirds, especially in the male sex, do not, at least in all individuals, acquire the breeding plumage by the time they are a year old. Nevertheless they are in full song and ready to nest. The Purple Finch (*Carpodacus purpureus*) and the Redstart (*Setophaga ruticilla*) are familiar examples. Still, one can spend a lifetime of field study and never meet with more than a handful of birds breeding in immature plumage.

Whether such breeding as does occur is as successful as that by fully adult birds (as shown by adult plumage) is debatable. Certainly in many cases it is not. There is ample evidence that in some birds that do not breed until two or more years of age such as the Great Cormorant (*Phalacrocorax carbo*) and various penguins, certain sexual manifestations occur earlier (Kortlandt, 1942).

In some insular birds, as noted later in considering sexual dimorphism, the plumages are not fully stabilized. Thus the immature males of several species of Galápagos finches (Geospizinae) are streaked and grayish, the adults black. Some individuals, however, breed in the streaked plumage; in fact, some never go beyond it to the black plumage, or at least not in captivity. Perhaps these finches are evolving a black adult plumage, perhaps they are losing it (both positions have been upheld). But at any rate the plumages are in a state of selective flux. The same is true of some other insular groups, such as the complicated ones discussed by Mayr (1933). In some such cases plumages that were adapted to mainland conditions are nonadaptive or anachronistic under insular conditions. The result is great variability, which may persist indefinitely or until a new norm is reached.

Most classifications of plumages, including the one adopted in this report, are "functional" to the extent of recognizing immature and adult plumages as such. Yet reproduction would seem to be an unassailable proof of maturity, and birds that breed in immature plumage provide a severe test of such a classification. Some of the considerations making this seem less perplexing have already been given. They may be recapitulated and amplified as follows. Relatively few birds breed in "immature" plumage, and in most species it never occurs. When it does, we usually lack proof that it is successful, or as successful as in older birds; the partner is usually a fully adult bird; in many of the instances where such breeding occurs, the selective background is in a state of flux and the plumage no longer properly called "immature." We cannot expect biological processes to be always clear cut, and this is particularly true of those associated with maturing. Plumages are often associated with definite molts. If we plucked a feather from a Cooper's Hawk nesting in immature plumage, it would be replaced, presumably, by an adult feather. The bird is physiologically adult but will not acquire adult plumage until the midsummer molt two or three months later.

Some groups of birds, such as many hawks, have two downy plumages. They are usually similar, but the second down may be longer or "woolier," and of a different shade of color. Usually or always the first set of down grows from the same follicles as the pennaceous feathers. When the latter appear they push the down out, and it adheres to their tips. The second down grows from other follicles and is the down retained, though less copiously, beneath the contour feathers of later plumages.

The bird's first plumage of "normal," vaned or pennaceous feathers is usually

called the "juvenal plumage," and the bird at this stage is best called a juvenal (Eisenmann, 1965).

Sutton (1935, 1936, 1941) and others have shown that the juvenal plumage in various fringillids, among others, is reduced or "telescoped" and never achieves full development. By the time the bob-tailed young is leaving the nest, this juvenal plumage is giving way, at least in some feather tracts, to the ensuing plumage, which may be variously an immature or an adult plumage. In species that develop more slowly, such as the American Robin (*Turdus migratorius*), the juvenal plumage is not quite so ephemeral.

One can scarcely consider the telescoped juvenal plumage as only a transitional stage between the down and the following plumage. One must call it a separate plumage but recognize that it is never fully developed. It does have the function of providing a plumage during a relatively brief period while the bird is still growing. In some cases it serves as a camouflage during this critically exposed, flightless stage of life.

As already noted, most birds have no more than two pennaceous immature plumages (including the juvenal), many only one, some none at all. That is to say, the latter species molt directly from the down into a plumage that is to all intents and purposes inseparable from that of the adult. Even when one finds a series of annual immature plumages, each in succession slightly more like the adult plumage, the final change to the adult breeding plumage may be relatively abrupt as in the Bald Eagle (Crandall, 1941).

One or two further examples of variability in immature plumages may be given. The race of *Zonotrichia capensis* living in Colombia near the equator molts directly from the juvenal to the adult plumage. In North American species of the same genus the plumage following the juvenal is an immature "first winter" plumage (Miller, 1961). In a species of African thrush, *Pogonocichla stellata*, some subspecies have a pennaceous immature plumage, some do not (Friedmann and Stager, 1964).

A suggested terminology for the molts and plumages of young birds is given in tabular form later.

Adult plumages. A great many birds have only one adult plumage. A Great Horned Owl (*Bubo virginianus*), for example, looks the same when a year old as when age 25, nor are there seasonal variations.

Many species, on the other hand, have two distinct adult plumages. With scarcely an exception, it is correct to refer to these as the breeding and the nonbreeding plumage. In the vast majority of birds that have two adult plumages, each is worn for part of the year. In the Ascension Island colony of Sooty Terns (*Sterna fuscata*), which is on a roughly 10-month breeding cycle, the breeding and nonbreeding plumages would also be adjusted to this nonannual cycle. (In this species the nonbreeding plumage differs only by having a few white feathers on the lores and crown.)

In each of the above two categories one finds some species in which the plumages of the sexes are the same, some in which they are different. In the group with a single adult plumage there are many in which the sexes are the same. The group in which the sexes are different is also large, especially in the tropics, but includes familiar birds of the temperate zone, such as the Belted Kingfisher (*Megaceryle alcyon*).

In the group having two adult plumages, a breeding and a nonbreeding, in only a few of the species (for examples, loons, most grebes, and egrets) do the sexes have the same two plumages.

The group in which the sexes are not the same includes such birds as the Scarlet Tanager. In many such species the distinctive plumages are limited to the male sex, and the female is nearly or quite the same the year around. The nonbreeding plumage of the male is then often very like that of the female. In certain birds, such as some of the wood warblers of the genus *Dendroica,* the females do have a nonbreeding plumage that is less colorful than the breeding plumage, although the contrast is not as great as in the male sex. In still others the sexes are more or less different in breeding plumage but identical in nonbreeding dress. Various shorebirds will serve as examples. In some of the latter, notably the phalaropes, the female is the more colorful sex. As is well known, this is correlated with a reversal in sexual display and parental behavior; it again demonstrates the plasticity of plumage.

At this point we may summarize the classification of adult plumages just proposed: I. One adult plumage: A. Sexes alike, B. Sexes different; II. Two adult plumages—a breeding and a nonbreeding: A. Sexes alike, B. Sexes different; III. Three or more adult plumages (rare).

There are other ways in which the plumages of adult birds could be arranged, but the above classes are the only ones that seem to be generally applicable and useful. It would not be very helpful, for example, to group plumages into those in which the feathers contain turacin pigment (family Musophagidae) and those lacking it (all other birds). A classification into species with metallic coloration and those lacking it would divide male and female of many species.

Another method of classifying plumage, although impractical for general use, is that based on genetic and hormonal control. Here selection has produced functionally similar plumages in a variety of ways. Thus after gonadectomy in the female Mallard (*Anas platyrhynchos*), the bird acquires a male type plumage at the next molt. This plumage is genetically determined and is normally inhibited in the female by sex hormones.

In the fowl (*Gallus gallus*) the situation is reversed. Gonadectomy produces no change in the female, but the male at his next molt loses the male secondary sexual plumes and hackles and reverts to a female-type plumage. Hence the latter is genetically determined in this species, and the male secondary sexual features are produced by male sex hormones.

Finally, in the House Sparrow (*Passer domesticus*) gonadectomy produces no plumage change in either sex. The distinct male and female plumages are apparently under separate genetic control, or at least are not influenced by the sex hormones. In addition to such major distinctions, a recent writer (Johns, 1964:449) states that "previous studies have shown that a wide variety of hormones may be responsible for the differences between male and female plumage in different species of birds." The function of the plumage seems to be the important thing. How the "required" plumage is produced in terms of physiology, genetics, or molt is of secondary importance.

At the same time it must be emphasized that the classification suggested above, although convenient, is not of any profound significance from the standpoint of phylogeny. Species in the same genus may fall into different categories. In the Troupial (*Icterus icterus*) the sexes are alike; in the the Orchard Oriole (*Icterus spurius*) they are unlike. Even within species or superspecies such differences may exist.

Exceptions. There are very few species with more than two regularly recurring adult

plumages. The ptarmigans (*Lagopus*), to whose molts and plumages Salomonsen (1939) devoted an entire volume, have three plumages. There may be a few others.

Are there any species with two adult plumages that cannot properly be called "breeding" and "nonbreeding"? Again the number of exceptions seems to be very small, and again the ptarmigan may be among the few. The winter and summer plumages of these birds may both be cryptic (as in an ermine or a varying hare), and hence neither of them really breeding plumage as such. The plumages of the Old Squaw Duck (*Clangula hyemalis*) are also very complicated. The possible selective basis for this has been discussed by Sutton (1932), Humphrey and Parkes (1959), and others.

Many species, such as bitterns, have a single cryptic plumage the year around. In others only the male is brightly colored. This sex, especially in polygynous species, is more or less expendable. Finally, in the mazes of the tropical jungle, many species in which both sexes are brilliantly colored throughout the year are able to survive.

As just noted, many species of birds with a single adult plumage are very dully and cryptically colored. It might be argued that this somber dress is not the breeding plumage. But since these birds do, in fact, breed in it, it must considered as such. One may note that many species having dull plumage do display it. The male of the cuckoo (*Tapera naevia*), for example, raises its short crest every time it calls.

Finally, it may be noted, there are a few birds in which the adult plumage changes slightly with age. A male Wandering Albatross (*Diomedea exulans*) may be a little whiter at age 25 than 10, but can hardly be said to have a different plumage.

PHYLOGENY OF PLUMAGES

It is logical and probably correct to believe that the elaborate male breeding plumage of peacocks or birds of paradise evolved from a simpler dress and has always been limited to the male. This is especially true in those birds in which the male has a simpler, female-like, nonbreeding plumage. It does not follow that colorful breeding garb has always evolved from simpler antecedents and that the duller plumages are necessarily more primitive. In some tropical tanagers and New World orioles both sexes are brightly colored. In close relatives of these that have recently penetrated the temperate zone, the female has acquired a dull plumage worn the year around, and the male of some of them now has a dull nonbreeding plumage. Species that have colonized islands where they no longer are surrounded by closely related species and hence no longer require plumage-isolating mechanisms often become dull colored. The Laysan Teal (*Anas laysanensis*) is an example. Barely a trace remains of the brilliant green head of its Mallard ancestor. Gilliard (1956) believed that some dull-colored bowerbirds are secondarily so; they have substituted colorful bower ornaments for bright plumage.

Nor are the plumages of the immature or of the female necessarily more "primitive" than those of the male. In the African starlings of the genus *Onychognathus* and in the cuckoos of the genus *Eudynamys*, the immature females are more or less like the adult males and only later acquire the distinctive female plumage. In some woodpeckers and also in the Bornean Bristlehead, *Pityriasis*, the young have more red in the plumage than the adult. In the jay *Cyanocorax dickeyi*, the young has a bright-blue patch on each side of the head; these are white in the adult. Some reptiles are brightly colored, and the artists who have portrayed *Archaeopteryx* as a gaudy creature may well be right.

The above remarks are not meant to deny the possibilty of useful studies of plumage phylogeny within closely knit monophyletic groups. Indeed some of the groups mentioned above such as the orioles of the genus *Icterus* provide subjects for such analysis.

MOLT

Although seemingly fragile, feathers are quite tough. Yet they do wear out. They are replaced by a process known as molt, carried over with some modifications from the reptilian ancestors of birds. One might expect each feather to be replaced individually as needed. This is more or less, perhaps, what does occur in some tropical birds, for example *Colius* (Moreau *et al.*, 1946:350) and in some species of large size. In most, however, molt occurs during a relatively restricted portion of the year. The feathers in the young bird grow in rapidly over a relatively short period so they may wear out and need replacing more or less simultaneously. Flight is of such vital importance to birds that the plumage must be kept in good condition. Feathers are dead structures. Their condition, good or bad, has no physiological effects. It is better to replace them too soon than too late.

Molting takes energy and must be fitted into a cycle, usually annual, in which there are other demanding periods, notably reproduction and often migration. Molt does not as a rule take place during reproduction or migration or when food is scarce as during winter or a long dry season, when mere survival may require all of the bird's resources. Even if the feathers require replacement no oftener than every 17 months, for example, there may be compelling selective reasons that bring molt into an annual cycle. In most temperate-zone birds reproduction is followed by molting, which occurs during the late summer when food is still plentiful. Indeed in the Steller Jays (*Cyanocitta stelleri*) of Queen Charlotte Island, Pitelka (1958) found evidence that molt takes precedence over reproduction and occurs when food is most plentiful. In the humid tropics where pressures may be less and seasons poorly differentiated, considerable molt may occur during the period of reproduction.

Thus molt is just as sensitive to selection as are the colors and patterns of feathers. In the flycatchers of the genus *Empidonax*, although the species are very similar, Johnson (1963a, 1963b) found the molt sequences and schedules to be scarcely the same in any two species. Sometimes such differences can be correlated with the life cycle. In a species that migrates early, the molt may be delayed until the winter quarters are reached. A resident, tropical population of a species may have a different molt schedule than a northern migratory one. Some birds living in harsh grass have two complete molts each year. In condors and large eagles the big wing quills grow so slowly that molt cannot be completed in a year without interfering with flight. It seems to be unknown whether in these birds, especially tropical species, the molt is correlated with the calendar year at all. In accipiters the female that stays at the nest while incubating and caring for the young begins to molt at this time, but her hunting mate does not.

Ashmole (1963) has found that in the Line and Phoenix islands there are two breeding seasons in the Sooty Tern each year, occurring at six-month intervals. If a pair is successful in one breeding season, the two birds probably do not nest in the following one, but if unsuccessful they do. "These populations have apparently evolved a uniquely flexible molt program, such that under certain circumstances (perhaps the successful rearing of a chick) breeding is followed by a complete molt, but often molt stops and the bird breeds again before all of the primaries and sec-

ondaries have been replaced. It is suggested that because of this flexibility in the molt, individuals are sometimes able to take part in successive breeding periods only six months apart."

These are only a few of the examples that might be cited to show the extreme sensitivity of molt to selection. Most birds, it is true, have one complete molt a year; but this, one must conclude, is only because they happen to live on a planet where most areas have climatic seasons that impose regular annual variations in food supply. Even so, whenever some other molt schedule is superior, it has evolved.

Secondary function of molt. As noted above, all birds have different plumages when very young than when adult, and hundreds if not thousands of species have two alternating adult plumages, a breeding and a nonbreeding. In the overwhelming majority of cases the only way in which the transition from one plumage to the other can be accomplished is by molt. For example, at the beginning of the reproductive season egrets grow special display plumes; after the reproductive season they molt them. Were molt not so highly modifiable by selection, all such changes in plumage could scarcely have evolved.

In general, one may assume that the energy demands of molt keep the plumage changes to the minimum. Thus the male Scarlet Tanager would be no more striking, perhaps less so, if the black tail and wing feathers were also replaced by scarlet ones. So it is not surprising to find that these large feathers are replaced only once each year.

HOMOLOGY IN ADULT PLUMAGES AND MOLTS

Enough has been said, perhaps, to show the impossibility of establishing convincing homologies among plumages and molts, at least in adult birds. The feathers of a bird all grow from similar feather papillae in a similar way. They all molt and are replaced in the same way. They are all homologous as feathers; but to try to establish other homologies is an uncertain endeavor. It is the plumage and its function in the daily life of the bird that are important. Molt is merely a means of replacing worn feathers or of changing them if a different plumage is to follow.

If one considers feathers that are repeatedly plucked and then replaced, either as a result of abnormal behavior or perhaps to line a nest, can it be maintained that the tenth "generation" of feathers to grow from such a frequently plucked feather tract or individual feather papilla is homologous with the tenth "generation" to grow on some other part of the body, an event that may not occur until years later, if at all? In the formation of brood patches feathers are shed out of phase with the rest of the plumage.

This does not mean that molt is not of interest in itself as providing numerous examples of adaptation and for other reasons. And despite the variabilities, its patterns are of value in phylogeny, especially in the remiges and rectrices, which, because of their vital importance in flight, are conservative. Stresemann (1963b) has shown that the usual number of 10 primary wing feathers dates back to *Archaeopteryx* itself, and he (1963c) has written prolifically on the taxonomic significance of molt patterns. Humphrey and Parkes (1963:499) state that "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." To say, however, that both a Condor (*Vultur gryphus*) and a Kestrel (*Falco sparverius*) have 10 primaries that are apparently homologous and follow certain molt patterns is not to say that the plumages following a complete molt in these or other birds are homologous.

The breeding plumages of all birds are functionally homologous, excepting perhaps in the case of the few individuals that breed in immature plumage. All provide the main element in the bird's external appearance at this season at least, and appearance in these visually oriented creatures is of great biological significance in reproduction. This is true even in plain-colored species, in which vocalizations are very important. In some birds, of course, the eyes, bill, wattles, legs, and appendages are brilliantly colored and help make up the total visual image. But in such cases, if we wish to stretch a point only slightly, these unfeathered parts may be considered a part of or at least a backdrop for the breeding plumage, both as regards biological function and as a matter of convenience. Sometimes, as in the bright bill sheath of the puffins, even these horny parts of the "plumage" are molted. Seasonal changes in color, as in the legs of herons, are not infrequent.

Nonbreeding adult plumages, on the other hand, are probably not always functionally homologous. In the vast majority of cases, however, they are cryptic plumages, which lessen the impact of predators.

THE CONCEPT OF "PLUMAGE"

As noted above, the word "plumage" is generally, as in this report, used as a collective term for a bird's feathers. We limit the practice of naming different plumages to those that are stable for an appreciable length of time and that are distinctive in appearance and function. Thus the male Scarlet Tanager has two plumages that qualify in all of these respects, a breeding and a nonbreeding plumage. When molting from one to the other, the bird is for a time in an intermediate mottled condition. This is purely transitional, and we do not regard it as a separate plumage. If, however, it were to become stabilized for a period of some weeks, for example while the bird was migrating through mottled autumn foliage that blended with this coloration, we would consider it a distinct and separate plumage.

If a bird's feathering looks different and has a distinct function, then it is biologically a separate plumage regardless of how extensive or minor the changes. We have already mentioned the Sooty Tern, in which the nonbreeding plumage differs only in having the lores and forehead flecked with white (other terns have similar but more extensive changes). In egrets the breeding plumage differs only in the acquisition of elaborate plumes, which do not differ in color from the entirely white nonbreeding plumage.

The lability of molt has made possible the very extensive occurrence of breeding and nonbreeding plumages. There are, however, a few cases in which differential feather wear takes its place. The Snow Bunting (*Plectrophenax nivalis*) is mottled with brown in nonbreeding plumage. Late in the winter these brown edges break off, leaving a sharply black and white breeding garb, which is just as definitely a distinct plumage as one produced by molt. (There is a slight molt in this species around the base of the bill, but this does not affect the conclusion.) This process is not ordinary feather wear. The paler borders of the feathers break off "as neatly as if they had been snipped with scissors" (Coues). Sometimes a line of demarcation develops along the inner edge of the portion of the feather that is to be lost. The process is sometimes caused or facilitated by an arrangement in which the pale border of each feather is exposed and the dark portion covered by the feather above. This method of plumage change is, therefore, a specific adaptation, comparable, for example, with the process whereby certain portions of the long tail feathers of a motmot develop structural weaknesses and are lost to produce the racket-tips. The Starling

(*Sturnus vulgaris*) is often cited as a species in which the change to the glossy, unspotted summer plumage is by such a process, although in this case it has also been maintained that the change is the result of ordinary wear resulting from entering and leaving nesting cavities. The fact remains that the species looks quite different in spring and that this is probably adaptive.

In the male Pennant-winged Nightjar (*Macrodipteryx vexillarius*) the long "pennants," one on each wing, snap off after the breeding season. This may be regarded as the change from a breeding to a nonbreeding plumage, although the process is seldom so simple.

Some, perhaps all, birds that are exposed to extremes of seasonal temperature, for example resident northern chickadees, grow extra feathers in winter (Wetmore, 1936:164). Since these feathers are the same color as the others and merely "fill out" the plumage without noticeably changing its appearance, I would not regard such species as having separate winter and summer plumage. In winter Ruffed Grouse (*Bonasa umbellus*) grow bristles along the edges of the toes that function as "snowshoes." Technically, I suppose, this should be regarded as a distinct winter plumage.

Speaking broadly, it is now taken for granted that, unless proved otherwise, all characters and processes of living things are adaptive. If a bird has one plumage in the breeding season and another in the nonbreeding season, we assume that this has arisen through selection and that the plumages are adaptive. Likewise, in each and every case in which the sexes of a bird differ in color, however slightly, it is to be assumed that this is adaptive for there is no likely method by which such distinctions can be maintained other than by selection. The only, or at least the chief, exceptions are temporary situations in which the selective milieu has changed and the plumage has not yet fully responded. There may in such situations be a time lag in losing formerly adaptive characters.

Color phases, on the other hand, are generally to be regarded as nonadaptive manifestations of balanced polymorphism. It does not matter whether a screech owl is rufous or gray. Phases are not to be regarded as distinct plumages but rather as a special type of individual variation in a single plumage.

Geographical variation in plumage presents no particular difficulties of interpretation. In some cases (*e.g.*, pale desert birds) the variation is directly selective. The frequent geographical variation in plumage features associated with display is, on the other hand, usually not linked with the physical environment. It merely reflects multiple adaptive pathways or interspecific adjustments.

Thus we believe that plumage should continue to be used as a collective term for a bird's feathers. This ensemble is what the bird sees; this is what we see. If a feathering of changed appearance and function is acquired, it is a different plumage. Such a definition of plumage is morphological in that two plumages must be visibly different and functional in that distinctions would not have evolved if they were not adaptive.

Humphrey and Parkes (1959) use the word "plumage" for a single generation of feathers, tacitly assuming it is possible to keep the various generations separate. Under this system many (nonmolting) birds would have parts of two plumages. Thus the male Scarlet Tanager in breeding condition has wing and tail quills of one plumage and body feathers of another. For what is called "plumage" in the present paper they coin the word "aspect" or, if the feathers are analyzed by molt,

"feather coat." They acknowledge, however, that in some connotations "plumage" will continue to be used in a broadly descriptive sense.

Admittedly, in a study of molt it is necessary to know when the various feathers and feather tracts are replaced. Numerous intensive studies of molt have shown that to do this it is not necessary to change the usual definition of plumage. To define plumage as a "generation of feathers" means that an exact knowledge of the molting schedule of a species is needed before one can analyze its plumages. In some species there is no very exact schedule of molt, and almost every individual would have to be treated independently. Selander and Giller (1960), for example, found that only 2 per cent of first-year Brown-headed Cowbirds (*Molothrus ater*) have a complete postjuvenal molt. In other icterids studied by them the percentage varies, but is as high as 28 per cent in female Red-winged Blackbirds (*Agelaius phoeniceus*). They have suggested a selective basis for this variation. The study of such molt phenomena can be accomplished without recourse to a system that obscures the fact that these species do in fact have a postjuvenal molt into another plumage. That most individuals retain some feathers from the preceding plumage should not becloud the issue.

SYSTEMS OF PLUMAGES AND MOLTS

The system of molts and plumages proposed by Dwight (1900) has, with some later modifications, been extensively used. Some of Dwight's terms such as "nuptial" plumage are scarcely acceptable today, and there are a few inconsistencies in his terminology. Nevertheless, Dwight's system is, in my opinion, correct in its main essentials. He was assured of a biologically viable system when he realized that "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."

Humphrey and Parkes (1959) presented a new system and terminology of molts and plumages, some aspects of which have already been considered. The alacrity with which their proposals have been adopted must give pause to the would-be critic. Their work was criticized by Stresemann (1963) and, in passing, by Miller (1961). Humphrey and Parkes (1963) replied to Stresemann's criticism. It is necessary, however, to examine the suggestions of Humphrey and Parkes a little more closely.

These authors regard the complete molt as the most important event in the cycle of molts and plumages. Because it takes more energy to grow feathers than to shed them, they conclude that molts should be named in terms of the plumage that follows. Actually, do we not by "molt" mean the entire process of losing one feather or coat of feathers and growing another? Or, if not so inclusive, we think of molt in terms of shedding feathers rather than of growing them. Thus we might say that a sick bird molted its feathers but failed to replace them. The first downy plumage of the young bird cannot be defined in terms of any preceding molt, since there is none. It would seem, therefore, that ideally the name of a molt should include both the preceding and following plumage. Since this is not feasible, it seems best, as did Dwight, to give the molt a convenient name, and then define it. If this is reasonable there should be no objection to a terminology that includes a postjuvenal and also a prenuptial molt.

More importantly, Humphrey and Parkes conclude that the plumage following a complete molt (of pennaceous feathers) is homologous in all birds, despite the fact

that in some birds this is the breeding, in some the nonbreeding, plumage (not to mention immature plumages). I have attempted to show above that molt is so variable and so subject to selection that it is futile to postulate homologies in the usual phylogenetic sense in either molts or plumages, downy plumages perhaps representing an exception. It is difficult to believe, for example, that the dull nonbreeding plumage of a grebe is homologous with the brilliant breeding plumage of a Scarlet Ibis (*Eudocimus ruber*); yet both follow a complete molt. Closely related species sometimes differ in this respect, and exceptionally even races of the same species differ, as in *Nectarinia takazze*, an African sunbird (Stresemann, 1963:4). One race of this bird has a dull nonbreeding plumage; another does not. Mayr (1942:50) gives another example. Beebe (1914) found that if male Scarlet Tanagers are kept on a fat-rich diet in a darkened room, the summer molt into the nonbreeding plumage is usually entirely inhibited. The following spring, these experimental birds, if restored to natural conditions, molt directly into breeding plumage again, bypassing the nonbreeding plumage completely.

Humphrey and Parkes call the plumage that follows the juvenal the "first basic," regardless of whether it is an adult or an immature plumage. Miller (1961) stressed the inadequacy of a system in which the "first basic" plumage in one species is an adult plumage, while in another species of the same genus (*Zonotrichia*) it is an immature plumage. But as we have seen, the same diversity may exceptionally be found even among races of a single species (*e.g., Pogonocichla stellata*).

The selective pressures responsible for this diversity are operating upon the plumages in some cases and the molts in others. That is to say, if there is a strong selection for seasonal display plumes, the appropriate molts to acquire and shed them will usually evolve concomitantly with the plumes themselves. On the other hand, if the plumage is subject to great wear, an extra molt is acquired with no change in the pattern or color.

By realizing that the physical reality, plumage, must take precedence over the process, molt, Dwight avoided the pitfall of considering plumages with completely different functions as homologous. To use a very crude analogy, the fact that a vehicle is equipped with snow tires in winter and normal tires in summer (each with a different function) is certainly more significant than the manner in which the tires are changed.

Even if the plumages to which Humphrey and Parkes apply the term "basic" were all homologous, it would still be unreasonable to adopt for general use a system that cuts so diametrically across the functions of plumages. But, as noted, there seem to be ample grounds for doubting the validity of their concept of plumage homology.

There is, however, one other aspect of the question that may be mentioned. The breeding plumage of many birds, for example, a Bluejay, is acquired at a single molt; that of others, such as the Scarlet Tanager, at two molts, the wing and tail quills at the postnuptial, the body feathers at the prenuptial molt, to use Dwight's terms. Humphrey and Parkes state that these two kinds of breeding plumages cannot, therefore, be homologous. Yet is it not possible that the tanager gets the wing and tail quills of its breeding plumage at the postnuptial molt, but postpones acquiring the scarlet body feathers because it is advantageous to have a dull body plumage during the winter? A species such as the sunbird *Nectarinia takazze* in which one race has a dull nonbreeding plumage (quite obviously of secondary origin) would suggest this possibility. If true, it would mean that the breeding plumages of the

TABLE 1

SUGGESTED CLASSIFICATION OF PLUMAGES AND MOLTS

Name of plumage	Name of subsequent molt
I. Young Birds	
A. Downy plumages	
Downy plumage	Postnatal molt
(or, when present)	
First downy plumage	First postnatal molt
Second downy plumage	Second postnatal molt
B. Pennaceous plumages	
Juvenal plumage (rarely absent)	Postjuvenal molt
Immature plumage (often absent)	Immature molt
(and, when present)	
Second immature plumage	Second immature molt
Third immature plumage	Third immature molt
etc.	etc.
II. Adult birds	
Adult plumage	Adult molt (or molts)
(or, if two occur)	
Breeding plumage	Postbreeding molt
(= "Nuptial Plumage")	(= "Prenuptial Molt")
Nonbreeding plumage	Prebreeding molt
(= "Winter Plumage," "Off-season Plumage," "Eclipse Plumage")	(= "Prenuptial Molt")

Bluejay and the Scarlet Tanager may be "homologous," even though the latter is acquired in two stages.

One may refer to Stresemann's critique of the Humphrey and Parkes proposals for amplification of some of the points made here. I close with a quotation from his paper: "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. . . ."

NOTES ON THE PRECEDING CLASSIFICATION (TABLE 1)

1. Of the plumages listed, the only ones that are invariable are one immature plumage of some nature and an adult plumage. The vast majority of species have at least two plumages before reaching adulthood: one downy and one pennaceous.

2. Sexual dimorphism may be indicated by simply placing the name of the sex before the plumage, thus "female adult plumage."

3. For the numerous species in which the adults wear the same plumage throughout the year (regardless of whether sexual dimorphism is present), I suggest simply "adult plumage." It will be understood that this is the adult breeding plumage. This has three advantages. In the first place, it implies that the species does not have a distinct breeding and nonbreeding plumage. Secondly, it seems a little more natural to speak of the "adult plumage" of a very plainly colored bird, such as a raven, than

it is to refer to its "adult breeding plumage." Finally, in those relatively few species that acquire the adult plumage long before they breed (for it does not seem reasonable to categorize formally an "immature plumage inseparable from adult plumage"), it again seems a little more natural to speak of it as simply "adult plumage" rather than "adult breeding plumage." Thus we would say that an albatross has acquired the "adult plumage" when a year old, even though we know it will not breed until six or more years of age.

4. As noted in earlier discussion, most of the molts listed are partial in at least some species. A handful of species have evolved a differential wear of patterned feathers whereby the transition from nonbreeding to breeding plumage is accomplished without molt playing a significant role.

5. The point has been made that molts are highly adaptive and that plumages cannot be defined in terms of the completeness or incompleteness of the molt that precedes or follows them. Some molts produce a change from one plumage to another; others simply replace the preceding plumage. For general purposes, only the broadest terminology can be used.

6. The very few species that are exceptional as to plumages must be handled on an individual basis. Thus perhaps the Old Squaw has a "prenesting breeding plumage," a "nesting breeding plumage," and a "nonbreeding plumage."

7. The alternative terms given in parentheses are regarded as less suitable than the ones used. In some cases, however, it may be worthwhile to retain these terms; for example, "eclipse plumage" for the special kind of nonbreeding plumage found in some waterfowl. In a very few cases there may be other plumages that will require special names as was noted for the Old Squaw.

SUMMARY

The most characteristic external feature of a bird, both biologically and visually, is its plumage. The feathers that comprise the plumage were derived from reptilian scales. The feathers not only propel the bird through the air. They retain and enhance the old functions of protecting the bird from the elements. In addition to these basic functions, feathers have acquired important secondary ones, among which may be mentioned species recognition, sexual display, and camouflage.

The great sensitivity of feathers and plumage to selection has permitted endless adaptations in these colorful and visually oriented animals. The young bird almost always has one or more downy plumages, and frequently one or more pennaceous plumages that differ from the adult plumage. There are frequently two adult plumages, a breeding and a nonbreeding, and rarely others. The sexes in the adult are very often different in color and frequently in the development of display plumes as well. Very few species are identical in plumage. A large part of ornithological research is currently concerned with various aspects of the ethological and evolutionary significance of plumage characters. This is because the behavior of the birds themselves reflects and is to a very considerable extent governed by the visual image—largely the plumage—of other birds.

Feathers when frayed are replaced by a process known as molt. The sensitivity of molt to selection has permitted the great range of adaptive variations in plumage just listed. Molts have evolved, for instance, to permit a change from nonbreeding to breeding plumage at times when the feathers would not otherwise need replacement. Speaking colloquially, one might say that molt is an adaptation to permit the bird to change its "clothes," either because they are worn out or because another ensemble

is needed for a different adaptive function. If feathers became perfected to the point of not wearing out during the adult bird's lifetime, there would be no further need for molt in species with a single adult plumage. Thus molt is biologically no more than a "necessary evil," as contrasted with plumage that serves numerous vital needs of the bird.

So great is the variability that any general classification of plumages and molts must deal only in broad generalities. The classification should reflect the functions served by plumages, for as noted it is these functions, molded by a long evolutionary history, that are responsible for the immense diversity that exists. This has, in fact, usually been done. One recalls such terms as "breeding plumage." The classification suggested in tabular form above presents no major changes from earlier ones, which were based to a considerable extent upon the work of Dwight. It is hoped, however, that a certain increase in simplicity and consistency has been achieved and that molt has been placed in a proper context.

The system of plumages and molts recently proposed by Humphrey and Parkes is considered. It is concluded that their system does not provide a satisfactory conceptual basis for understanding or, in the case of further research, for trying to determine what role plumage and molt play in the life of the bird. They have abandoned a functional classification for one based on supposed homologies. The latter cannot be demonstrated and are extremely dubious.

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