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MOLT AND PLUMAGE TERMINOLOGY OF HOWELL ET AL. (2003) STILL MAY NOT REFLECT HOMOLOGIES

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Abstract. Forty-five years ago Humphrey and Parkes (1959) introduced their system of nomenclature for molts and plumages (the H-P system). They claimed that their biologically neutral terminology, independent of the bird's life cycle events, could accurately reflect homologies of molts and plumages across a wide range of avian taxa. Soon, however, several investigators reported trouble adapting the terminology to unusual sequences of molts and plumages, and others expressed doubts that it could accurately reflect true phylogenetic homologies. Howell et al. (2003) reviewed these problems and proposed a modification of the original H-P system that identifies the juvenal plumage as the first basic plumage, and any postjuvenal plumages that are not repeated in later plumage cycles as formative plumages. By doing this, they solved the problem of adapting the original H-P system to plumages of the first year of life in many species. However, they have not overcome the arguments of Stresemann (1963) and Amadon (1966) that patterns of molting and plumage are so variable, and so subject to natural selection, that there is doubt that the H-P terminology can reveal phylogenetic homologies even among closely related species. Molting and plumage sequences within a clade comprising four species of the genus *Carduelis* confirm that within this limited grouping, molting and plumages are highly variable, and apparent homologies are not revealed in the H-P terminology as modified by Howell et al.

Key words: Carduelis, *carduelines, homology, molt, plumage.*

La Terminología de la Muda y el Plumaje de Howell et al. (2003) Podría no Reflejar Aún las Homologías

Resumen. Hace cuarenta y cinco años, Humphrey y Parkes (1959) introdujeron su sistema de nomenclatura para la muda y el plumaje (el sistema H-P). Ellos sugirieron que su terminología biológicamente neutra, independiente de los eventos del ciclo de vida de las aves, podría reflejar con exactitud las homologías de la muda y el plumaje a través de un amplio espectro de taxa. Sin embargo, poco después varios investigadores notaron problemas al adaptar la terminología a secuencias inusuales de muda y plumajes, y otros expresaron dudas en cuanto a si podría reflejar con exactitud las verdaderas homologías filogenéticas. Howell et al. (2003) revisaron estos problemas y propusieron una modificación del sistema H-P original que identifica el plumaje juvenil como el primer plumaje básico, y cualquier plumaje post-juvenil que no se repita en ciclos posteriores del plumaje como plumaje formativo. Haciendo esto, solucionaron el problema de adaptar el sistema H-P original a plumajes del primer año de vida de muchas especies. Sin embargo, no lograron resolver las críticas de Stresemann (1963) y Amadon (1966) de que los patrones de muda y plumaje son tan variables y tan propensos a ser afectados por selección natural, que es dudoso que la terminología H-P pueda revelar homologías filogenéticas, aún entre especies estrechamente relacionadas. Las secuencias de muda y plumaje al interior de un clado formado por cuatro especies del género *Carduelis* confirman que dentro de este limitado grupo, la muda y el plumaje son áltamente variables y que algunas homologías aparentes no son reveladas por la terminología H-P con las modificaciones de Howell et al.

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Soon after Humphrey and Parkes (1959) proposed their system of naming molts and plumages (the H-P system), some investigators had trouble applying it and expressed doubts about the claim of Humphrey and Parkes that it reveals homologies of molts and plumages across a wide variety of avian taxa (Miller 1961, Stresemann 1963, Amadon 1966). Nevertheless, American ornithologists soon adopted the H-P system (e.g., Palmer 1962), and it replaced the older system invented by Dwight (1900). The H-P system has superceded the Dwight terminology in America to such an extent that a recent ornithology textbook does not mention the latter in its treatment of molting and plumages (Gill 1995), despite the fact that the Dwight system is still the preferred one in Europe (e.g., Jenni and Winkler 1994).

Now a group of investigators has presented a useful review of problems with the H-P system, and proposed a way to resolve some old questions about that system's ability to reveal homology of molts and plumages (Howell et al. 2003). Here I review these problems and evaluate how well Howell et al. have solved them. I argue that the H-P system cannot reliably reveal phylogenetic homologies of molt and plumage, either in its original form or as modified by Howell et al. The H-P system therefore provides no advantage over the older, life-history-dependent nomenclature initiated by Dwight (1900). Dwight's nomenclature is more useful because it, unlike the H-P system, incorporates information about ecological and physiological factors affecting the bird's life cycle.

TROUBLE WITH TERMINOLOGY

An early attempt to employ the H-P system, in a careful study of molting in the Japanese Quail (*Coturnix japonica*), revealed problems in designating plumages that develop in a bird's first 23 weeks after hatching (Lyon 1962). Young quail that hatched in April and July grew a juvenal plumage beginning the day of hatching. Two to three weeks later they began another molt that replaced all flight feathers and most body

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feathers. These feathers were all replaced again beginning in late September to October, after which young birds were in fully adult, nonbreeding plumage. Thereafter, adults molted twice a year, alternating between a breeding plumage and a nonbreeding plumage (Lyon 1962). Lyon had difficulty deciding how these two complete postjuvenal plumages in the birds' first summer should be named according to the H-P system.

The H-P system dictates that the replacement of the juvenal plumage is always accomplished by a Prebasic 1 molt, producing a Basic 1 plumage (Humphrey and Parkes 1959:15). Therefore, the first molt of pennaceous plumage, involving body and flight feathers, which the birds start when a mere two or three weeks old, must be called the Prebasic 1 molt, into the Basic 1 plumage in which birds may breed in their first summer. What should the second complete postjuvenal molt of the young birds be called? Humphrey and Parkes (1959:20, figure 4) indicate that this would be called the Prealternate 1 molt. This puts the bird into an Alternate 1 plumage worn during its first winter, and, by a partial prebasic 2 molt in spring into a Basic 2 plumage in which it breeds in its second year. This alternation of plumages is thus 180 degrees out of phase with the conventional pattern seen in the Northern Bobwhite (*Colinus virginianus*; Lyon 1962) and many other birds, and generates a definitive basic plumage with an incomplete molt, which is contrary to the rule that the prebasic molt is always a complete one (Humphrey and Parkes 1959:15). Therefore, to bring the definitive cycle of the Japanese Quail into register with that of the Northern Bobwhite, Lyon (1962) hypothesized that as an adaptation for breeding in its first summer, the Japanese Quail has suppressed the ancestral Prebasic 1 molt, so that its first postjuvenal molt is now the Prealternate 1 molt, producing the Alternate 1 plumage in which it can breed. The next molt then becomes the Prebasic 2 molt into the Basic 2 plumage of its first winter. Thus, the sequence of plumages according to Lyon's interpretation is Juvenal—Alternate 1—Basic 2—Alternate 2—etc. This stunning deviation from the H-P system showed that Humphrey and Parkes may have been too sanguine in their estimation of its practicality.

Stresemann (1963) described a similar problem in naming the plumages of the Red-backed Shrike (*Lanius collurio*), in which an extra immature plumage falls between the juvenal and what seems to be the Basic 1. The H-P system includes no terms to describe such extra plumages, which are never repeated in subsequent cycles. In their response to Stresemann's (1963) critique, Humphrey and Parkes (1963) did not address this issue, nor did they propose any way to adapt their terminology in cases where a molt appears to have been suppressed.

Now Howell et al. offer a valuable review of the difficulties that many subsequent investigators have had in naming such added plumages in a bird's first year of life. They propose the ingenious solution of considering the Juvenal plumage as the Basic 1, and naming the added plumages *formative.* We can now see that the Japanese Quail fits their Simple Alternate Strategy (SAS), and the Red-backed Shrike fits their Complex Basic Strategy (CBS). However, the question is still open on what to do in cases in which an ancestral molt may have been completely suppressed.

TROUBLE WITH HOMOLOGY

Humphrey and Parkes (1959) argued that the primary benefit of their system is in revealing homologies of molts and plumages across a wide range of avian taxa throughout the world. Thus, all plumages named Basic 1 are to be considered homologous in the usual phylogenetic sense. Several investigators immediately pointed out examples that posed problems for this concept of plumage homology.

In equatorial Colombia, the Rufous-collared Sparrow (*Zonotrichia capensis*) has two complete cycles of molting and breeding per year (Miller 1959, 1961). Young birds fledge with a dull, streaked, juvenal plumage typical of the other species of the genus, but they molt out of this into a brightly patterned adult breeding plumage, similar to the alternate plumages of North American species of the genus. This molt involves all the body feathers, but not the flight feathers. Thereafter, they have a complete molt every six months into a brightly patterned plumage in which they breed (Miller 1961). Thus, the Rufous-collared Sparrow has an H-P plumage sequence of Juvenal—Basic 1—Basic 2—etc. However, comparing the coloration of the plumages of this and the other species, Miller (1961: 160) concluded that ''the postjuvenal, highly patterned plumages of *capensis* worn during nuptial activities are the obvious homologs of the 'alternate' plumage of the other *Zonotrichias.*'' Thus Miller argued that the basic plumage of the H-P system could well be the newly evolved character, and the brightly patterned alternate plumage represents the original ancestral condition. Certainly this is a reasonable competing hypothesis for which there is physical evidence that can be further studied.

Admitting that it may be impossible to be certain that plumage sequences that appear to be homologous are indeed so in the phylogenetic sense, Humphrey and Parkes (1959:2) argued that apparent equivalence should provisionally be considered true homology unless further studies revealed otherwise. Thus, the homologies implied in the H-P system are to be considered hypothetical, subject to future verification.

Stresemann (1963) pointed out that some species molt their remiges twice per cycle. The remiges are therefore parts of both basic and alternate plumages despite being identical in form and function. By the H-P terminology, the set of remiges in the basic plumage cannot be considered homologous with the set of remiges in the alternate plumage. Stresemann considered this to be a misapplication of the homology concept.

Commenting further on the H-P system, Amadon (1966) argued that there is no necessary equivalence of homology between a molt and the resulting plumage. Natural selection can act upon the timing and extent of molting independently of the structure and coloration of the plumage, which can in turn be subjected to entirely different selective factors. Molting is simply a mechanism of replacing feathers, and can be highly variable even within a single species. As he put it in the days before all-season radial tires, ''the fact that a

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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'' (Amadon 1966:274).

Howell et al. (2003) seem appropriately hesitant to apply the concept of homology of molts and plumages too generally, for they state that it is reasonable to conclude that the only molt, and resultant plumage, that should be considered homologous across all species is the single complete or nearly complete molt per cycle that is typical of their Simple Basic Strategy. Furthermore, they state that juvenal plumages might not be homologous across all species, although it is useful to assume that they are for recognizing broad patterns of plumage development across all species. They also state that alternate, supplemental, and formative plumages need not be homologous among species. Nevertheless, they argue that we should assume that such molts and plumages are homologous unless they are shown not to be so. According to Howell et al., the key to accurately determining plumage homology is to count the Juvenal plumage as the Basic 1 plumage. Since this plumage is generated by a complete molt, and since Humphrey and Parkes (1959) defined all basic plumages as being generated by a complete molt, they have neatly solved the problem of having to view the old Prebasic 1 molt of many species as being split into two or more periods of molting, usually with the molt of the flight feathers offset to later periods (Palmer 1972). The Basic 1 plumage of the H-P system now becomes a new plumage, the Formative 1, not homologous with any basic plumage.

But what of the idea that homologies implied by the nomenclature are to be considered as provisional hypotheses pending further verification? Howell et al. argue that color patterns of plumages cannot be used to determine molt homologies, and that misuse of the H-P system has resulted in part from ''failure to divorce plumage color and pattern from an evaluation of homologies'' (p. 637). Therefore neither the homology of molts, nor the homology of the plumages produced by those molts, can be verified any way other than by examining the underlying history of molting during the bird's lifetime. Thus Howell et al. eliminate all means of independently testing and potentially falsifying the provisional hypotheses of homologies suggested by a sequence of molts. This is not a scientific approach to the problem.

Like Miller, Stresemann, and Amadon, I am skeptical that there is a necessary equivalence of the homology of the timing and sequence of a molt with the homology of the plumage produced during the molt. Both molting and plumage characteristics are too variable and subject to independent selective forces to reveal universal underlying patterns. Even the sequences of molting of the remiges and rectrices have revealed few if any patterns useful for revealing phylogenetic relationships among avian orders, and vary even within orders (Stresemann and Stresemann 1966). In any case, the equivalence of the homology of a molt with the homology of the plumage it produces is hypothetical, and would have to be well tested to engender confidence that counting feather generations is a true key to determining plumage homologies. The alternative hypothesis is that selective pressures can add or subtract molts, alter the sequence of feather replacement, and change the characteristics of the plumage so often during evolution within a group of species that there is liable to be much analogy by convergence, but little true homology.

DETERMINING HOMOLOGIES IN SOME CARDUELINE FINCHES

A recent cladistic analysis of the 126 extant species of cardueline finches, based on molecular, karyotypic, paleontological, morphological, and behavioral characters indicated that the Pine Siskin (*Carduelis pinus*), Lesser Goldfinch (*C. psaltria*), Lawrence's Goldfinch (*C. lawrencei*), and American Goldfinch (*C. tristis*) make up a single clade within the genus (Badyaev 1997). In my studies of these species I have found remarkable variability in their molting and plumages, despite their apparently very close phylogenetic relationships. This group provides an instructive test of how well the H-P system and the modifications proposed by Howell et al. reveal hypothetical homologies of molts and plumages.

OVERVIEW OF PLUMAGES AND MOLTING IN FOUR *CARDUELIS* SPECIES

The Pine Siskin lacks sexual dichromatism, and adults closely resemble the juvenile in coloration (Dawson 1997). There is a partial postjuvenal molt, and one complete molt per year thereafter (Dawson 1997; Fig. 1).

Lawrence's Goldfinch has marked sexual dichromatism, males being generally yellower and having black on the crown and throat that is lacking in females. The adult female differs from the juvenile by having an orange-yellow breast patch similar to that of the male, but smaller and duller (Willoughby et al. 2002). There is a postjuvenal molt that renews all the body feathers and usually some or all remiges and rectrices, so young birds become indistinguishable from older birds in their first winter. Thereafter, there is a single complete molt per year, although male plumage brightens and becomes more sexually dichromatic for breeding by the action of plumage abrasion (Willoughby et al. 2002; Fig. 1).

The Lesser Goldfinch has marked sexual dichromatism, females being plain and juvenile-like in appearance, males having bright-yellow underparts, black crown, and more boldly marked black and white wings and tail. The sexual dichromatism is acquired in the postjuvenal molt, which involves the body and a variable number of remiges and rectrices (Watt and Willoughby 1999). Birds of the Pacific coastal United States and Baja California usually have only a single, postbreeding molt per year, but a few also have a very limited prebreeding body molt. Birds of the interior United States and Mexico have two complete molts per year, but there is no seasonal color change (Watt and Willoughby 1999; EJW, unpubl. data; Fig. 1).

The American Goldfinch has marked sexual and seasonal dichromatism. In winter, both males and females resemble the juvenile coloration, but in summer, the males become bright yellow with contrasting black crown, black wings, and tail, while females remain

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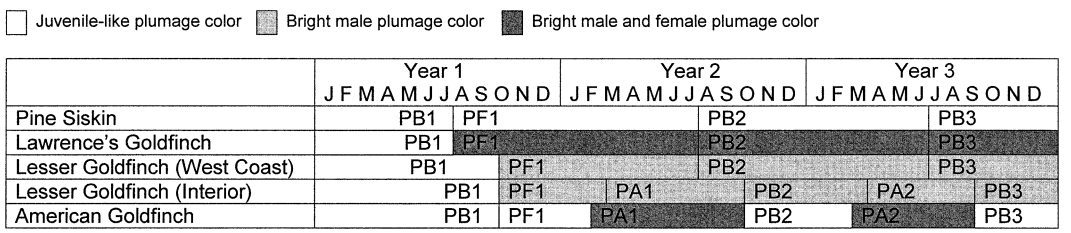


FIGURE 1. Example of inconsistency within the modified H-P terminology of Howell et al. (2003), as applied to four *Carduelis* species considered by Badyaev (1997) to form a single clade. Dull juvenile-like adult plumage, a presumed plesiomorphy, is indicated by lack of shading, and colorful, sexually dichromatic plumage, a presumed synapomorphy, is indicated by shading. Darker shading means both sexes are unlike the juvenile, light shading means only the male is unlike the juvenile. According to Howell et al., plumages of different species produced by molts of the same name should be considered homologous. However, the shading indicating shared plumage color characters fails to reveal a corresponding pattern, with bright plumages variously identified as formative, basic, and alternate, whereas their physical characteristics suggest they should be considered homologous. Abbreviations identify molts: PB = prebasic; PF = preformative; PA = prealternate.

duller and plainer than males, but become greener (Middleton 1993). A postjuvenal molt replaces all body feathers, but not wings and tail. An extensive prebreeding molt of body feathers but not remiges and rectrices produces the sexually dichromatic plumage of summer, and a complete postbreeding molt produces the juvenile-like winter plumage of both sexes (Middleton 1977, 1993).

APPARENT HOMOLOGIES IN *CARDUELIS*

Pine Siskin. This species fits the molting and plumage pattern that Humphrey and Parkes (1959:24) considered most likely to be the primitive condition for all birds. Lack of sexual dichromatism is rare within the genus, with only eight of the 31 species lacking sexual dichromatism, and only one other, *C. atrata*, having adult coloration similar to the juvenile (Sibley and Monroe 1990, Clement et al. 1993). This suggests that these may be recently evolved traits in the Pine Siskin. Nevertheless, let us assume that it is the primitive condition hypothesized by Humphrey and Parkes, to see how homologies are traceable in the other, more typical members of its clade.

The Pine Siskin has the H-P plumage sequence of Juvenal—Basic 1—Basic 2—etc., and the Howell et al. sequence of Juvenal (= Basic 1)—Formative 1—Basic 2—etc., with a CBS pattern. If this species truly reflects the primitive condition in its clade, deviations from this pattern must be more recently evolved character states.

Lawrence's Goldfinch. The sexual dichromatism and molt cycle of this species resemble the majority of carduelines. It shows the H-P sequence of Juvenal—Basic 1—Basic 2—etc., and the Howell et al. sequence of Juvenal (= Basic 1)—Formative 1—Basic 2—etc., with a CBS pattern. If the Pine Siskin shows the primitive condition, sexual dichromatism is synapomorphic with the rest of its clade. What is odd, and suggests this is a recently evolved plumage, is the way the sexual dichromatism intensifies in spring by plumage abrasion. The yellow breast feathers of the male (but not the female) are structurally modified to resist wear so the orange-yellow breast patch remains bright and expands in area, while the dorsal body feathers lose special brown edges to make a yellower back and greater contrast between the black crown and surrounding head feathers (Willoughby et al. 2002). No other member of this clade has these special traits (EJW, unpubl. data).

Lesser Goldfinch. The birds from the Pacific coastal regions show a typical cardueline pattern of molts and plumages (Newton 1972). The Humphrey-Parkes sequence of plumages is Juvenal—Basic 1—Basic 2—etc., and the Howell et al. sequence is Juvenal (= Basic 1)—Formative 1—Basic 2—etc., with a CBS pattern (Fig. 1). Assuming the Pine Siskin is primitive, the sexual dichromatism shown by the male is a newly evolved character, meaning that the basic plumage is not entirely homologous with that of the Pine Siskin, although the juvenile-like coloration of the female might be considered to be so.

Lesser Goldfinches of the interior states and Mexico differ markedly in molt cycle, but not in plumage, from the Pacific coastal birds. The complete prebreeding molt is clearly a recently evolved trait, unreported for any other cardueline. It resembles the complete postbreeding molt in timing and sequence of plumage renewal, and produces no change of coloration (Watt and Willoughby 1999; EJW, unpubl. data). Therefore, both molts and plumages appear in all respects to be homologous. However, since the birds appear to breed only once per year, the H-P system designates the plumage sequence Juvenal—Basic 1—Alternate 1—Basic 2—Alternate 2—etc., and the Howell et al. sequence Juvenal (= Basic 1)—Formative 1—Alternate 1—Basic 2—Alternate 2—etc., a CAS pattern (Fig. 1). Thus the Pacific coastal birds always breed in a basic plumage and the interior birds always breed in an alternate plumage, even though the resulting plumages are indistinguishable, and would thereby otherwise be considered to be homologous.

If Mexican birds were found to breed in the autumn after the prebasic molt, as happens occasionally with the California birds (Watt and Willoughby 1999), we could not distinguish these plumages in the H-P system, for we would have to reckon a plumage cycle of six months duration, like that of the Rufous-collared

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Sparrow studied by Miller (1961). This is because although it is intended to reveal homologies by naming molts and plumages independently of seasonal, reproductive, or developmental phenomena, the H-P system ironically defines the plumage cycle by the duration of the breeding cycle, whether that be 6, 10, 12, 14, or 18 months long (Humphrey and Parkes 1959:11).

Howell et al. explicitly forbid considering breeding and plumage coloration to determine plumage homologies in all cases in which basic and alternate plumages are indistinguishable in origin and coloration (Howell et al. 2003:638). As an example of this, they cite the Black-chested Prinia (*Prinia flavicans*) in Botswana, in which birds under certain environmental conditions alternate between a bright summer breeding plumage and a duller winter plumage, both acquired by complete molt. In other environmental conditions, however, these same birds molt from the summer plumage into an identical winter plumage in which they breed again in the autumn (Herremans 1999). Howell et al. argue nevertheless that the Black-chested Prinia always alternates between a basic plumage in winter and an alternate plumage in summer. But consider what we would have to conclude if environmental conditions were perpetually favorable for breeding in both summer and winter: Black-chested Prinias would have a single plumage per cycle, and what we now call the alternate plumage would become the basic plumage! Thus the homology suggested by the H-P system and advocated by Howell et al. is an artificial construct, based solely on whether or not the species wears the plumage during a breeding season!

American Goldfinch. This species is unique among cardueline finches in alternating between a juvenile-like nonbreeding coloration and a bright, sexually dichromatic breeding coloration, produced in the prebreeding body molt (Middleton 1977, 1993). Its H-P plumage sequence is Juvenal—Basic 1—Alternate 1—Basic 2—Alternate 2—etc., and its Howell et al. sequence is Juvenal (= Basic 1)—Formative 1—Alternate 1—Basic 2—etc. (Fig. 1). Although it conforms to the CAS of Howell et al. its alternate plumage is so similar to the basic plumages of Lesser and Lawrence's Goldfinches that all appear to be homologous. Part of the sexual dichromatism persists in the form of the bright-yellow median, lesser, and marginal coverts of the mature nonbreeding males. These feathers are acquired in the definitive prebasic molt (Middleton 1993). Its nonbreeding (basic) plumage is otherwise like the juvenal plumage, but this seems to be the newly evolved character state, which is made possible by the addition of the extensive prebreeding body molt that restores the dichromatic coloration for breeding. Thus we see that the American Goldfinch's alternate plumage appears homologous in coloration with the definitive basic plumages of the Lesser and Lawrence's Goldfinches, while its unique basic plumage coloration is almost certainly a newly evolved condition.

SUMMARY

Collectively, these four close relatives show both of the common sequences of molting and plumages designated by Howell et al. as the Complex Basic and Complex Alternate Strategies. The Lesser Goldfinch shows both patterns in different parts of its range. Definitive basic plumages resemble the juvenal in two species (Pine Siskin, American Goldfinch), but is highly sexually dichromatic and unlike the juvenal in two others (Lesser and Lawrence's Goldfinches). In the Lesser Goldfinch, basic and alternate plumages are indistinguishable in coloration and in the characteristics of the molts that produce them. In the American Goldfinch, the alternate plumage resembles the basic plumage of the Lesser and Lawrence's Goldfinches, but can be distinguished from them by being produced in a partial molt. There is, therefore, no obvious underlying pattern to suggest that the H-P system can really reveal true homologies in this group. In fact, this group reinforces the views of Stresemann (1963) and Amadon (1966) that molting and plumages are so variable and subject to natural selection that there can be no fundamental pattern of plumage succession that can reliably reveal molt and plumage homologies. At best, plumage sequences may suggest possible homologies, but like any presumed homology, they are hypothetical, and must be subjected to testing by reference to various other observable differences and similarities between characters (Wiley 1975). Astonishingly, however, Howell et al. explicitly forbid using any character other than the sequence of molts themselves to test these hypotheses.

Certainly the H-P system in both the original and Howell et al. forms may reflect molt and plumage analogies. But Humphrey and Parkes found fault with the Dwight system because it could not certainly reflect homologies in its terminology, only analogies. Unlike the Dwight system, though, the H-P system holds no information about molt timing or the plumage functions in the life cycle of the bird. We are left with nothing more than an artificial formula for assigning biologically neutral names to molts and plumages, claiming to be independent of the developmental and cyclic events of a bird's life (Humphrey and Parkes 1959), while ironically anchoring the plumage cycle to the juvenal plumage and the breeding cycle. I prefer the Dwight system.

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UNDERSTANDING EVOLUTION OF PLUMAGES AND OTHER CYCLIC AVIAN LIFE-HISTORY PHENOMENA: ROLE FOR AN IMPROVED MOLT TERMINOLOGY

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Abstract. Birds show quite distinct changes in both external and internal appearance. An evolutionary interpretation of these cyclic life-history phenomena would benefit from a system of description aimed at mapping shared ancestries of arguably the ''easiest'' of traits: the molts and seasonal plumage changes. By 1959, Humphrey and Parkes had already provided the basis of such a system, but its development and application, especially with regard to the confusing first plumage cycle, by Howell et al. (2003), adds considerably to its power. I hope this leads to an upsurge of evolutionary studies of molt and plumage cycles that in turn provide the basis for analyses of other aspects of the flexible phenotype of birds. With such an increase, the study of molts and plumages could once again be at center stage of avian biology.

Key words: annual cycles, life-cycle stages, molt, phenotype, phenotypic flexibility, seasonality.

Entendiendo la Evolución de los Plumajes y Otros Fenómenos Cíclicos de las Historias de Vida de las Aves: El Papel de una Terminología Mejorada para la Muda

Resumen. Las aves muestran cambios bastante marcados en su apariencia externa e interna. Una interpretación evolutiva de estos fenómenos cíclicos de las historias de vida se beneficiaría de un sistema de descripción dirigido a mapear formas ancestrales compartidas de lo que se podría decir son los caracteres más ''fáciles'': las mudas y los cambios estacionales del plumaje. Hacia 1959, Humphrey y Parkes ya habían establecido la base de un sistema de este tipo, pero su desarrollo y aplicación, especialmente con respecto al confuso primer ciclo del plumaje, por parte de Howell et al. (2003) incrementan considerablemente su poder. Espero que esto lleve a un rápido incremento de estudios evolutivos de la muda y los ciclos del plumaje que a su vez provean la base para analizar otros aspectos del flexible fenotipo de las aves. Con un incremento tal, el estudio de la muda y el plumaje

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podría una vez más ocupar un lugar central en la ornitología.

The appearance of individual birds, with interesting exceptions, changes mainly through the growth of new feathers and their subsequent wear. Although it is the most eye-catching aspect, a changing plumage is only one of the many phenotypic changes shown by most birds in the course of a year (e.g., Murton and Westwood 1977, Gwinner 1986). A comprehensive understanding of the evolution of the highly variable plumages of birds therefore needs consideration of other cyclical aspects of avian life histories (Jacobs and Wingfield 2000), with due attention to the appropriate environmental context. In such an endeavor, the study of plumages seem an obvious place to start, but issues of shared ancestries and homologies provide a real obstacle for progress (Rohwer et al. 1992, Thompson and Leu 1994, Chu 1994, Jukema and Piersma 2000). The nomenclatural system designed by Humphrey and Parkes (1959; the H-P system) was ahead of its time and much underused, especially in the Old World. A revival of studies of the seasonally changing phenotype (e.g., Piersma and Drent 2003) now seems to be under way, so the critical development by Howell et al. (2003) of the H-P system aimed at mapping homologies comes at a good time. Being quite happy with the way in which the H-P system was developed and applied by Howell et al. (2003), I would like to widen the scope of their contribution and discuss how evolutionary studies of plumage variation can provide the basis for comprehensive assessments of the evolution of all cyclical aspects of avian life histories.

Sooner or later any in-depth study of birds has to come to grips with seasonal variation in phenotype, whether external or internal. In my own study on the life histories of long-distance-migrant shorebirds I have come to the realization that almost all phenotypic aspects are seasonally variable, and that this seasonal variability may tell us much about the selection pressures molding the birds' life histories (Piersma 2002, Piersma and Drent 2003). For example, some of the Bar-tailed Godwits (*Limosa lapponica*) staging in the Netherlands during northward migration show a supplemental molt of rusty-red contour feathers belonging to what was interpreted to be the alternate plumage (Piersma and Jukema 1993). That only individuals with relatively high body masses, complete alternate plumages, and a smaller likelihood of tapeworm infestation (Piersma et al. 2001) showed this supplemental molt, strongly suggested that the rusty-red plumage carried from spring until autumn signaled individual quality and was the outcome of sexual selection on both sexes. In addition, in Bar-tailed Godwits, and also in Ruffs (*Philomachus pugnax*), sexual selection pressure apparently has been so strong that the extravagant plumage of the breeding season in fact represents a third feather generation counting from the prebasic molt (Jukema and Piersma 2000). The bright new replacement feathers grown by Bar-tailed Godwits on spring staging areas (Piersma and Jukema 1993) count as a fourth.

A less conspicuous, but no less dramatic, seasonal change in avian phenotype was discovered in a study of preen-wax composition of Red Knots (*Calidris canutus*; Piersma, Dekker, and Sinninghe Damsté 1999). Before northward migration, or just after arrival on the High Arctic breeding grounds, individual Red Knots shift from producing a mix of well-known types of monoester waxes to a novel category of diester waxes (Sinninghe Damsté et al. 2000). We initially interpreted the production of diester waxes as a sexually selected quality signal visible to conspecifics, but subsequent analysis has demonstrated the shift to occur in almost all studied shorebird species, with the tightest correlation (with respect to sexes) with the timing of incubation rather than display and ornamental plumages (Reneerkens et al. 2002). Thus, the production of diester waxes during the breeding season may reflect natural selection (e.g., providing olfactory crypsis) rather than sexual selection.

A final example concerns the strongly variable size of the digestive tract of the Red Knot, a molluscivore that ingests hard-shelled prey whole, crushes the shells in a relatively heavy muscular gizzard and evacuates the shell fragments through the intestine (Battley and Piersma 2004). In the course of the year gizzard size doubles (smallest on the tundra breeding grounds, largest in midwinter), and these size changes can be interpreted as resulting from trade-offs between the capacity for digestive work, diet quality, energy requirements, and savings on maintenance and transport costs (van Gils et al. 2003). These changes may be the outcome of direct demand-supply processes, but strategic reductions in digestive organ size before long-distance flights (Piersma 1998, Piersma and Gill 1998, Piersma, Gudmundsson, and Lilliendahl 1999, Landys-Ciannelli et al. 2003) and gizzard size retention during a long-distance flight (Battley et al. 2000) strongly suggest that seasonal orchestration of organ size by endocrine pathways (Landys-Ciannelli et al. 2002) is also at play.

I now seem to have ventured very far from the issue of detecting homologies in the molts and plumages of birds. But here is my point: for a comprehensive understanding of the variable phenotype of organisms of all kinds, and especially in studies of the evolution of seasonally variable phenotypes, we need a seasonal ''template,'' a developmentally deep and basic phenotypic trait (or character, see Wagner 2001) that is easy to describe and well suited for intra- and interspecific comparisons. The seasonally changing plumages of birds provide us with such a trait (Wingfield and Jacobs 1999), but to date comparative descriptive studies of molts and plumages have been hampered by the lack of a robust and evolutionarily sensible terminology. In 1959, Humphrey and Parkes provided a good framework. I hope that Howell et al.'s alteration of the H-P system to facilitate the discovery of homologies, as well as their first categorization of molt strategies of bird families based on annual cycles (their table 1), will induce an upsurge of comparative studies of molt and plumage cycles. I am confident that ornithologists interested in other aspects of the flexible phenotype, and in the endocrine and neural orchestration of this flexibility, will be keen to build on these analyses. This would bring the study of molts and plumages back to the center stage of avian biology.

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