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

Author: Ernest J. Willoughby
Source: The Condor, 106(1) : 191-196
Published By: American Ornithological Society
URL: https://doi.org/10.1650/7439
MOLT AND PLUMAGE TERMINOLOGY
OF HOWELL ET AL. (2003) STILL MAY
NOT REFLECT HOMOLOGIES

ERNEST J. WILLOUGHBY

Department of Biology, St. Mary’s College of
Maryland, St. Mary’s City, MD 20686-3001

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 accu-
ратely 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 oth-
ers expressed doubts that it could accurately reflect
true phylogenetic homologies. Howell et al. (2003) re-
viewed these problems and proposed a modification of
the original H-P system that identifies the juvénal
plumage as the first basic plumage, and any postju-
venal 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.

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 plum-
ages 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 plum-
ages (Howell et al. 2003). Here I review these prob-
lems and evaluate how well Howell et al. have solved
them. I argue that the H-P system cannot reliably re-
veal 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, incor-
porates 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 care-
ful 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
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 juvenile plumage is always accomplished by a Prebasic 1 molt, producing a Basic 1 plumage (Humphrey and Parkes 1959:15). Therefore, the first molt of penaceous 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).

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, Juvelan 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 other species, Miller (1961:160) concluded that “the postjuvenile, 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
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 juvenile 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 Juvenile 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 (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 CARDUELINES

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
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 synapomorphy 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—Alternate 2—etc., and the Howell et al. sequence Juvenal (= Basic 1)—Formative 1—Alternate 1—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

### 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.

<table>
<thead>
<tr>
<th>Species</th>
<th>Year 1</th>
<th>Year 2</th>
<th>Year 3</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pine Siskin</td>
<td>PB1</td>
<td>PB2</td>
<td>PB3</td>
</tr>
<tr>
<td>Lawrence’s Goldfinch</td>
<td>PF1</td>
<td>PB2</td>
<td>PB3</td>
</tr>
<tr>
<td>Lesser Goldfinch (West Coast)</td>
<td>PB1</td>
<td>PA1</td>
<td>PB2</td>
</tr>
<tr>
<td>Lesser Goldfinch (Interior)</td>
<td>PB1</td>
<td>PA1</td>
<td>PA2</td>
</tr>
<tr>
<td>American Goldfinch</td>
<td>PB1</td>
<td>PB2</td>
<td>PB3</td>
</tr>
</tbody>
</table>

- Juvenile-like plumage color
- Bright male plumage color
- Bright male and female plumage color

Downloaded From: https://bioone.org/journals/The-Condor on 29 May 2019
Terms of Use: https://bioone.org/terms-of-use
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 flavigans) 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 pre-breeding 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 re-inforces 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.

I thank J. Jordan Price for helpful criticism of an earlier draft.

**LITERATURE CITED**


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

Manuscript received 8 September 2003; accepted 24 September 2003.

1 E-mail: theunis@nioz.nl
La aparición de individuos, con interesantes excepciones, cambia principalmente a lo largo del crecimiento de nuevas plumas y su sucesiva pérdida. Aunque en general es el aspecto más llamativo, la mutación plumular es uno de los muchos casos de cambios genéticos mostrados por las aves en un año (en particular, Murton y Westwood 1977, Gwinner 1986). Una comprensión de la evolución del aspecto variable de plumas de aves requiere considerar los aspectos cíclicos de la vida aviar (Jacobson y Wingfield 2000), con atención debido a lo que podría ser el entorno apropiado. En un esfuerzo así, el estudio de plumas parece un lugar obvio para comenzar, pero los problemas de herencia y homología proporcionan un obstáculo para el progreso (Rohwer et al. 1992, Thompson y Leu 1994, Chu 1994, Jukema y Piersma 2000). El sistema nomenclatural diseñado por Humphrey y Parkes (1959; el H-P System) estaba en el camino de este tiempo y mucho más tarde, especialmente en el Viejo Mundo. Un resurgimiento de los estudios de la variabilidad anual de plumas (por ejemplo, Piersma y Drent 2003) ahora parece estar en el camino, así como el desarrollo inicial por Howell et al. (2003) del sistema H-P en torno a la comparación de homologías. En el curso del año, el tamaño del gástrulo aviar (mayor en las playas de cría, más pequeño en verano), y estos cambios de tamaño pueden ser interpretados como resultado de las diferencias entre la capacidad para el trabajo digestivo, la calidad de la dieta, las necesidades energéticas, y el ahorro de mantenimiento y transportes (Van Gils et al. 2003). Estas variaciones pueden ser el resultado de una demanda de procesos de suministro, pero esfuerzos reducidos en el organismo digestivo antes del vuelo largo (Piersma 1998, Piersma y Gill 1998, Piersma, Gudmundsson y Lilliendahl 1999, Landys-Ciannelli et al. 2003) y el mantenimiento de tamaño durante un largo vuelo (Battle et al. 2000) más bien sugieren que la preparación de organismo de tamaño endocrino durante las migraciones (Landys-Ciannelli et al. 2002) también está en juego.

En general, parece que el alterar muy lejos de la isla de los detecciones de homologías en las plumas y plumas de aves. Pero nuestro punto es: para una comprensión de la variabilidad del tipo de organismo de todos, y especialmente en los estudios de la evolución de plumas de plumas variables, necesitamos un sistema "template," un desarrollo profundo e básico de homología (Wagner 2001) que es más fácil de describir y adecuado para las comparaciones intraspecíficas e interspecíficas. Las plumas de aves cambian de tal manera que nos proporcionan con tal una relación (Wingfield y Jacobs 1999), pero para datar comparaciones descriptivas de estudios de plumas durante ciclos anuales (Tabla 1), inducirán un surgimiento de comparaciones detalladas de plumas y plumas. No estoy tan seguro de que los estudios de plumas y plumas y plumas y plumas de plumas de plumas sean supeditados por el hecho de una resistencia y de manera evolutiva sensible. En 1959, Humphrey y Parkes proporcionaron un marco adecuado. La esperanza es que Howell et al.'s alteración del sistema H-P para facilitar la exploración de homologías, así como su primer catarización de estrategias de plumas basadas en el ciclo anual (sus tabla 1), inducirán un surgimiento de comparaciones de plumas y plumas. No estoy tan seguro de que los homólogos interesados en otros aspectos del flexible, y en el endocrino y la neuro interpretación de esta flexibilidad, será crucial para desarrollar estas. Esto/membería el estudio de plumas y plumas de plumas y plumas a la fase centenaria de la biología aviar.
LITERATURE CITED


