THE FIRST BASIC PROBLEM REVISITED: REPLY TO COMMENTARIES ON HOWELL ET AL. (2003)

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DETERMINING EVOLUTIONARY HOMOLOGIES OF MOLTS AND PLUMAGES: A COMMENTARY ON HOWELL ET AL. (2003)

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Abstract. Howell et al. (2003) argue that the Humphrey-Parkes (H-P) system of molt terminology is flawed because it requires using traditional first prebasic molt as the starting point for plumage succession that results in noncorrespondence between nomenclature and presumed homology in first basic plumages. However, the H-P system does not require this. Second, they argue that plumage color can be a misleading criterion for evaluating plumage homologies. I show, however, that the timing and extent of molts, and thus their homologies, can de documented more accurately by using plumage color than by not doing so. Howell et al. (2003) propose a revised H-P system. To follow their system, one must accept their notion that no first-cycle molts are homologous with prebasic molts in subsequent molt cycles. However, this is not so as many species have a molt in their first cycle that is homologous to definitive prebasic molt. In addition, Howell et al.'s (2003) system does not offer any new or better criteria for identifying homologies than those suggested by Humphrey and Parkes (1959) and, thus, is not an improvement on the H-P system. First-cycle molts and plumages of most birds are poorly known. Therefore, we will not have sufficient data to determine whether new molts have been evolutionarily added to the first cycle, as suggested by Howell et al. (2003), until the molts of many more species of birds are studied. Further, these studies must be done on closely related species, not phylogenetically distant ones as proposed by Howell et al. (2003).

Key words: homology, Humphrey-Parkes, Larus, *molt,* Passerina, *plumage.*

Determinación de las Homologías Evolutivas de la Muda y el Plumaje: Un Comentario sobre Howell et al. (2003)

Resumen. Howell et al. (2003) aducen que el sistema Humphrey-Parkes (H-P) de terminología para la muda es erróneo porque requiere utilizar la primera muda prebásica como el punto de partida para la sucesión del plumaje, lo que resulta en falta de correspondencia entre la nomenclatura y las presuntas homologías en los primeros plumajes básicos. Sin embargo, el sistema H-P no requiere esto. Segundo, ellos argumentan que el color de plumaje puede ser un criterio engañoso para evaluar las homologías del plumaje, pero yo demuestro que el momento y la extensión de las mudas, y por tanto sus homologías, pueden documentarse con mayor exactitud utilizando el color del plumaje que no haciéndolo. Howell et al. (2003) proponen un sistema H-P revisado que implica aceptar su noción de que ninguna de las mudas del primer ciclo es homóloga con mudas prebásicas de ciclos de muda subsiguientes. Sin embargo, esto no es así, pues muchas especies tienen una muda en su primer ciclo que es homóloga a la muda prebásica definitiva. Adicionalmente, el sistema de Howell et al. (2003) no ofrece criterios nuevos o mejores para identificar las homologías que aquellos sugeridos por Humphrey and Parkes (1959), por lo que no representa un mejoramiento del sistema H-P. Las mudas y los plumajes del primer ciclo de la mayoría de las aves son poco conocidos. Por lo tanto, hasta que no se estudie la muda en muchas más especies de aves, no tendremos suficientes datos para determinar si nuevas mudas se han adicionado evolutivamente al primer ciclo como Howell et al. (2003) sugirieron. Más aún, dichos estudios deben hacerse en especies estrechamente relacionadas, no en aquellas filogenéticamente distantes como Howell et al. (2003) propusieron.

Molting, the shedding and replacement of feathers (Humphrey and Parkes 1959), is critical to many aspects of the survival and reproduction of birds including thermoregulation, flight, and, in many species, changes in plumage color associated with age, sex, body condition, and reproductive condition (i.e., breeding versus nonbreeding; Palmer 1972, Payne 1972, Walsberg 1983, Jenni and Winkler 1994).

Birds older than approximately one year of age undergo at least one molt, often two molts, and rarely three or four molts, per molt cycle. A molt cycle ''runs from a given plumage or molt to the next occurrence of the same plumage or molt'' (Humphrey and Parkes 1959:3). Molt cycles are a year in length in most species, but are shorter or longer in birds that reproduce on a schedule less than or greater than a year in length, respectively. Within species, after completion of the first molt cycle, the number of molts, and their resulting plumages, per cycle remains fixed in all subsequent molt cycles.

After hatching and prior to onset of the complete molt of all body and flight feathers that occurs in all birds at approximately one year of age, young birds undergo from zero to three molts; this is their first molt cycle. Within species, and among closely related species, (1) the number of molts in the first molt cycle may differ from the number of molts in subsequent molt cycles, and (2) each of these molts may or may not be similar in extent, timing, and resulting plumage color to that of any molt in subsequent molt cycles.

To study the evolution and adaptive significance of molts and the plumage patterns that result from them, it is essential to be able to determine the evolutionary homology of molts and plumages within species as well as among species. To this end, Humphrey and

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Parkes (1959, 1963) developed a practical, versatile, and simple system for identifying molt and plumage homologies. A consequence of their system for identifying molt and plumage homologies was a new system for naming molts and plumages. Humphrey and Parkes (1959) argued that previous nomenclatural systems failed to accurately describe molts and plumages or to identify homologies because these systems described molts and plumages *in terms* of life-history phenomena rather than *in relation* to them, that is, molt and plumage nomenclature ''must consist of terms which are independent of other terminologies applied to birds'' (p. 14). The Humphrey-Parkes (H-P) system has proven to be so useful that it has gained wide acceptance among ornithologists in North America and elsewhere; for example, it has been explicitly adopted by the American Ornithologists' Union (AOU 1998), and is the standard used in all taxonomically broad academic treatises on North American birds (Palmer 1962, 1976a, 1976b, 1988a, 1988b, Poole et al. 1992–2003, Pyle 1997) published since Humphrey and Parkes (1959).

Shortly after its publication, the H-P system was criticized by Stresemann (1963) and Amadon (1966). Despite wide and increasing acceptance, it continues to be criticized, inaccurately, in my view (e.g., Willoughby 1986, 1992a, 1992b, Howell and Corben 2000b). Most recently, and based largely on the work of Howell et al. (1999) and Howell and Corben (2000a, 2000b), Howell et al. (2003:636) claim to have identified ''an inconsistency in the H-P system: the noncorrespondence between nomenclature and presumed homology in so-called first basic plumages.'' Howell et al.'s (2003) stated objectives were to (1) review current misuse of, and supposed inconsistency in, the conventional H-P system, (2) describe four molt strategies that they argue are homologous across North American and Australian birds, (3) define and name first-cycle molts and plumages which they argue are not homologous with any molts or plumages in the definitive molt cycle, (4) discuss how to identify presumed homologies, if any, between plumages in first and subsequent cycles within and among taxa, and (5) provide case studies to illustrate how their modified nomenclatural system can be applied to diverse taxa and accurately reflect presumed homology in molts and plumages. They claim that their ''revised [H-P] framework of first-cycle molts and plumages defines a more useful starting point for addressing questions about the evolution of molt strategies, and about potential molt and plumage homologies'' (p. 637).

I argue that Howell et al. (2003) fail to identify a noncorrespondence between H-P nomenclature and presumed homology in first basic plumages, and misrepresent aspects of the H-P system. Further, they present an arbitrary and illogical system for identifying molt and plumage homologies that (1) ignores many fundamental principles regarding the expression of morphological characters, including variation at the individual, population, and species levels, and (2) is based on incorrect conclusions derived from incomplete or incorrect data.

MISUSE AND PURPORTED INCONSISTENCY OF THE HUMPHREY-PARKES SYSTEM

Howell et al. (2003) are correct that the H-P system has been applied incorrectly to many species of birds, and that this has resulted in names of molts and plumages that reflect incorrect homologies. However, such widespread misunderstanding and misuse of the H-P system does not reflect shortcomings of the system, but rather reflects the inherent complexity of molt and plumage cycles in birds, and a poor understanding of molt by many biologists who study birds: The latter results largely from a view that molt is unimportant in the life-history of birds and boring to study (reviewed by Leu and Thompson 2002).

Howell et al. (2003) acknowledge that molt and plumage homologies among closely related species may be determined by comparing the timing of, extent of, and change in plumage color resulting from each molt in the entire molt and plumage sequence of one species with that of other closely related species. However, they argue that if homologies determined in this fashion are ''founded on an arbitrary point of reference. . . , then broader patterns of homology could be obscured'' (p. 637). Thus, they maintain that ''to recognize potential molt homologies it seems more helpful to identify and compare patterns of plumage succession across a broad range of taxa'' (p. 637).

The ''arbitrary point of reference'' to which Howell et al. (2003) refer is the first prebasic molt (and first basic plumage) which they believe (1) is not homologous across birds, and, (2) is the necessary starting point for determining molt and plumage homologies according to the H-P system. To the contrary, the H-P system does not use first prebasic molt as the necessary starting point for determining molt and plumage homologies. In addition, as noted by Howell et al. (2003), non-prebasic molts probably have evolved independently multiple times. Therefore, correct homologies are more likely to result from comparison of molts and plumages among closely related species than among distantly related species, which are more likely to have molts and plumages that are similar due to evolutionary convergence rather than homology. In turn, accurate broad patterns of molt and plumage homologies can be achieved best by comparing molts and plumages among many different groups of closely related taxa (e.g., Cardinalidae, Thraupidae, and Emberizidae), as Thompson and Leu (1994) demonstrated. Howell et al. (2003) acknowledge this when they state (p. 636) that ''determining [homology] can be problematic, if not impossible,'' and ''one should therefore be aware of a potential distinction between homologies of nonbasic plumages *within* a species compared to homologies *between* species'' (p. 648; italics in original).

Similarly, many other molt scholars, some of whom Howell et al. (2003) noted, have expressed disbelief that molt and plumage homologies can be determined across all birds given their huge diversity of molt strategies (Amadon 1966, Palmer 1972, Jenni and Winkler 1994). Thus, the gauntlet has been thrown down. It is our challenge to see if broad molt and plumage homologies can be discerned, and it is my belief that the strategy for doing so is by working from the bottom up (studying closely related taxa) rather than the top down (studying distantly related taxa) as advocated by Howell et al. (2003).

PURPORTED CAUSES OF MISUSE OF THE HUMPHREY-PARKES SYSTEM

Howell et al. (2003) contend that misuse of the H-P system results from (1) using traditional first prebasic molt as the starting point for plumage succession; (2) using plumage color as a criterion for evaluating molt and plumage homologies, and (3) a widespread misconception that the H-P plumage terms basic and alternate are simply synonyms for traditional nonbreeding (or winter) and breeding (or summer) plumages. I agree wholeheartedly with the last point, but disagree with the first two points.

Regarding the first point, Howell et al. (2003) state that ''the inherent inconsistency stems from the H-P system taking its starting point of cyclic plumage succession as the highly variable molt that replaces juvenal plumage with so-called first basic plumage'' (p. 637). While it is true, as Howell et al. (2003) note, that Humphrey and Parkes (1959) did not discuss the possibility of the first postjuvenal molt being any molt other than first prebasic molt, Humphrey and Parkes did not preclude this possibility, and did not take first prebasic molt as the ''starting point.'' Indeed, Howell et al. (2003) acknowledge that Humphrey and Parkes (1959) advocated interpreting molt and plumage homologies of ''immature'' (predefinitive) molts and plumages by using definitive prebasic molt and definitive basic plumage as ''landmarks,'' and working backward toward natal plumage. However, Howell et al. (2003) mistakenly argue that by doing so ''the first cycle has to be fixed from the start of the 'first prebasic molt' and [if] a conventional first basic plumage is absent, then in its stead some other plumage will be named first basic'' (p. 638).

This argument has two major flaws. First, it overlooks the likelihood that molts, including traditional first prebasic molt, have been evolutionarily lost in different species or populations, or developmentally suppressed at the individual and population level in response to environmental conditions (e.g., hatching date, food supply, day length) or experimental (hormonal) manipulation (Beebe 1914a, Jenni and Winkler 1994, Ros 1999). If, for example, a species (or population) does not exhibit a first prebasic molt at the same approximate age at which closely related species do, and if all other molts and plumages appear homologous, then it is reasonable to conclude that first prebasic molt has been evolutionarily lost or is being developmentally suppressed in this species.

Second, Howell et al. (2003) interpret the H-P system as requiring that the first molt cycle must begin with the first prebasic molt. I believe this interpretation is unreasonably strict and incorrect. For example, it precludes the possibility of a presupplemental molt preceding the traditional first prebasic molt as has been documented in many passerines (Thompson and Leu 1994). In 1959, presupplemental molts were only known to occur in definitive cycles, not in the first cycle; thus, Humphrey and Parkes (1959) confined their discussion of presupplemental molts to definitive cycles stating that they may precede or follow prealternate molts depending on the functions that such additional molts serve. By extension, I see no reason why presupplemental molts could not evolve to precede the traditional first prebasic molt. In fact, it is likely that such presupplemental molts are widespread among passerine, and possibly nonpasserine, birds but have gone unnoticed (reviewed by Thompson and Leu 1994).

Howell et al.'s (2003) second point is that plumage coloration should not be used to help identify homologies because ''the physiological processes that govern pigmentation and molt timing are independent. . . (Voitkevich 1966)'' (p. 638). This claim is an incorrect generalization. To date, remarkably little is actually understood about the physiological processes that govern various aspects of molt, feather growth, and pigmentation. Although some physiological processes (e.g., appropriate levels of sex steroid hormones) that influence timing of molt also influence feather pigmentation in some species, other physiological processes that influence timing of molt (e.g., appropriate levels of prolactin, A. Dawson, unpubl. data) and feather growth have no influence on feather pigmentation (Thompson 1998).

As ostensible support for their claim, Howell et al. (2003) cite a number of ecologically and phylogenetically disparate species in which individuals of the same sex undergoing the same molt grow feathers that differ subtly to markedly in color. This view shows a lack of appreciation for the physiological processes responsible for individual variation in phenotypic expression. Although many species exhibit significant variation within and among individuals in the color of feathers grown over the course of a single molt, the magnitude of this variation typically is considerably less than that between successive plumages and, therefore, does not pose a serious obstacle either to identifying molts and plumages or correctly determining their homologies. Thus, plumage color is a useful character in two ways. First, in species that change color between successive plumages, old and new feathers can be distinguished from one another based on differences in plumage color. When molts overlap at the individual or population level, as occurs in many species including gulls (Laridae, Dwight 1925, Cramp 1983, Higgins and Davies 1996, Olsen and Larsson 2003), differences in plumage color between different feather generations (plumages) allows one to identify which growing feathers belong to which plumage. Thus, by using plumage color to identify the plumages to which feathers likely belong, the timing and extent of molts can de documented more accurately than if plumage color was not used. Second, these data may then be used to help determine molt and plumage homologies among closely related species. Therefore, to ignore plumage color when determining molt and plumage homologies among closely related species is to throw the baby out with the bathwater.

Howell et al. (2003) correctly note that traditional first prebasic molt in many species differs from definitive prebasic molt in that it often (1) is more limited in extent and, they claim, absent in some species, and (2) occurs at a somewhat different time of year. Thus, they assert that these differences lend support to the idea that traditional first prebasic molts are not homologous with definitive prebasic molts. I disagree. Although definitive prebasic molts usually are complete, completeness of molt *per se* is not a defining criterion of definitive prebasic molts. Indeed, definitive prebasic molt is partial in some species (e.g., some Old World *Phylloscopus* warblers; Humphrey and Parkes 1959, Williamson 1976, Jenni and Winkler 1994, Pyle 1997). Similarly, a difference in the timing of traditional first prebasic molt relative to that of definitive prebasic molt does not, by itself, indicate lack of homology between these molts; Humphrey and Parkes (1959:7) stated that ''the temporal position of a homologous molt in the cycles of plumage succession may vary among different groups of birds or among individuals of a species.''

The conceptual point here is that, for determining molt homologies, timing, extent, and resulting plumage color of molt are useful criteria to be evaluated within the context of the life histories of closely related species; these criteria are not rigid rules to be followed in a biological vacuum (Rohwer et al. 1992).

DEFINING THE FIRST PLUMAGE CYCLE

Believing that traditional first prebasic molt (or any other molt in the first cycle) is never homologous with definitive prebasic molt, Howell et al. (2003:638) propose that this supposed problem can be resolved by ''two logical steps: (1) assuming the ancestral molt strategy is the simplest possible,'' as Humphrey and Parkes also assumed, ''and (2) defining juvenal plumage as the first basic plumage,'' (p. 638) thus proposing that all juvenal plumages are homologous, a proposal that was made by Humphrey and Parkes as well. They term this ancestral molt strategy the Simple Basic Strategy (SBS). Further, they propose that ''molts corresponding to those present in the Simple Basic Strategy occur in all birds and. . . *are the only molts that should be considered homologous across all species*'' (p. 638; italics in original). Other molt strategies are viewed as building upon the SBS by the evolutionary addition of extra molts into molt cycles. They also define the first plumage cycle ''as the period between the attainment of juvenal plumage and the acquisition of the next basic plumage via a complete, or nearly complete, molt *that corresponds to a molt in the Simple Basic Strategy*'' (p. 639, italics mine).

Juvenal plumage results from a complete prejuvenal molt of all down feathers (in species that have down), and thus satisfies the criterion that basic plumage usually results from a molt that is complete or nearly so; however, Howell et al. (2003) present no additional data which suggest that juvenal and definitive basic plumages are homologous and, therefore, might justify renaming juvenal plumage to first basic plumage. Otherwise, I agree, in principle, with the arguments above regarding the SBS, and homology of juvenal and basic plumages throughout all species of birds.

CONSISTENCY OF THE HUMPHREY-PARKES SYSTEM

Howell et al. (2003) state, and I concur, that it is preferable that the names of all prebasic molts and basic plumages be consistent across all species and numbered according to the cycle in which they occur. They present examples of many species in which all individuals undergo their first complete molt at approximately one year of age, but some individuals or populations precede this with an additional partial molt, traditionally called first prebasic molt, which Howell et al. (2003) view as a novel molt that is not homologous with definitive prebasic molt. They refer to this molt strategy as the Complex Basic Strategy (CBS); of the four molt strategies proposed by Howell et al. (2003, table 1) this is the most common one exhibited by North American and Australian birds.

Howell et al. (2003) correctly note that partial molts in the first molt cycle pose potential difficulties to determining molt and plumage homologies. However, their examples do not prove that these molts are evolutionarily new molts added to the SBS rather than prebasic molts whose extent has been reduced and temporally (developmentally) advanced in some individuals or populations relative to others. Indeed, such variability within and among populations in the timing and extent of molts, including traditional first prebasic molt, is well known (Jenni and Winkler 1994). For example, in Northern Cardinals (*Cardinalis cardinalis*) and Phainopeplas (*Phainopepla nitens*), first prebasic molt is confined solely to replacement of body plumage in many birds, whereas other birds undergo a complete first prebasic molt that is indistinguishable in its timing, extent, and resulting plumage color from that of definitive prebasic molt (Miller 1933, Sutton 1935, Thompson and Walsberg 1993, Thompson and Leu 1994, Halkin and Linville 1999, Chu and Walsberg 1999). Consistent with their definition, above, of the first plumage cycle, Howell et al. (2003:646) state that ''complete postjuvenal molts are not prebasic if they do not correspond to prebasic molts in the SBS.'' However, this is not the case with the first prebasic molt in Northern Cardinals or Phainopeplas (Thompson and Leu 1994). Therefore, in these species, I can think of no reason, even following Howell et al.'s system, not to conclude that the complete first prebasic molt of some individuals or populations is homologous both to partial first prebasic molt as well as to definitive prebasic molt of other individuals and populations.

Similarly, in some to all species of many nonpasserine and passerine families, such as doves (Columbidae), cuckoos (Cuculidae), many New World flycatchers (Tyrannidae), starlings (Sturnidae) and weaver finches (Ploceidae), young birds undergo a complete postjuvenal molt at the same approximate time that birds in older age cohorts undergo their complete definitive prebasic molt (Stresemann and Stresemann 1966, Poole et al. 1992–2003, Jenni and Winkler 1994, Pyle 1997). Therefore, in these species as well, the traditional first prebasic molt must be homologous with definitive prebasic molt. The competing hypothesis proposed by Howell et al. (2003) that this molt is evolutionarily new is less parsimonious.

HOWELL ET AL.'S FOUR MOLT STRATEGIES

Howell et al. (2003) describe four molt strategies beginning with, and building upon, the Simple Basic Strategy (SBS) that they allege ''encompass all known patterns of plumage succession'' (p. 643). Howell et al.'s table 1, which categorizes the molt strategies exhibited by species belonging to all families of North American and Australian birds into one or more of four molt strategies, is a valuable summary and a potentially useful guide for directing researchers to groups of birds to study that may be especially helpful for clarifying issues regarding molt and plumage homologies in birds. However, Howell et al. (2003) present no credible case for the existence in any species of either of two molt strategies, the Complex Basic Strategy (discussed above) and the Simple Alternate Strategy; indeed, considerable empirical data refute the existence of these strategies.

The Simple Alternate Strategy applies to species that purportedly have only a single molt in their first molt cycle, which Howell et al. (2003) argue is homologous to definitive prealternate molt. This molt strategy was first described for Western Gulls (*Larus occidentalis*), in which Howell and Corben (2000a, 2000b) claim that (1) young birds have a single protracted molt that occurs at the same time (late August to mid-April) as definitive prealternate molt in adults and, therefore, is homologous to it, and (2) definitive prealternate molt overlaps the last 3 months of definitive prebasic molt.

However, Howell et al. (2003) do not explain how they identified birds growing basic versus alternate plumage during the months that these two molts supposedly overlap. This illustrates a more general and serious problem throughout Howell et al. (2003): the only criteria that they offer for identifying molt and plumage homologies are calendar timing of molt and completeness of molt being indicative of a prebasic molt.

Howell et al.'s (2003) results regarding Western Gulls conflict with our knowledge of the sequence and timing of molts in Western Gulls and all other species of gulls (Dwight 1925, Cramp 1983, Poole et al. 1992–2003, Higgins and Davies 1996, Olsen and Larsson 2003). The only significant study to date of molt in Western Gulls other than Howell and Corben (2000a, 2000b), was Dwight's (1925) in which he stated that (1) the first postjuvenal molt in Western Gulls occurs in September, October and November, and that a subsequent ''prenuptial'' (definitive prealternate) body molt occurs in March and April; and (2) all older cohorts undergo a complete postbreeding (definitive prebasic) molt in August and September and partial prenuptial (definitive prealternate) molt in March and April. Thus, the protracted molt, if it exists, begins many months earlier than definitive prealternate molt and, therefore, is not homologous to it.

In addition, Howell and Corben's (2000a) study on Western Gulls was based mainly on visual observations of birds. Relative to examination of specimens in the hand, observations through binoculars or spotting scopes preclude the ability to collect data on molt intensity or distinguish between old and new or growing feathers that are similar in feather color, and reduces the ability to estimate the extent of new (or growing) versus old feathers, especially in species that undergo little, if any, change in plumage color between successive plumages, as is the case in the ''white-headed'' gulls, including Western Gulls. Thus, I believe that these factors contributed to Howell and Corben (2000a) failing to discern the protracted molting period in young Western Gulls as two separate molts rather than a single molt.

Howell and his colleagues (Howell and Corben 2000a, Howell 2001, Howell et al. 2003) claim that the Simple Alternate Strategy also occurs in species in at least eight families of nonpasserines. Data regarding many of these species either indicate that they do not follow a Simple Alternate Strategy, or are inadequate to document which molt strategy they exhibit. For example, based on Beebe (1914b), Howell et al. (2003) claim that White Ibises lack a ''postjuvenal'' molt, and have only a single protracted first prealternate molt. Beebe (1914b:244) states only that White Ibis do not change plumage color ''during the first summer and autumn, but late in winter, usually about February, a moult begins. . . .This moult is not a short, well defined one but proceeds slowly throughout the year.'' Such a brief and anecdotal account is not adequate basis for definitively stating that this species pursues a Simple Alternate Strategy.

Similarly, based on Snyder and Russell (2002), Howell et al. (2003) claim that Carolina Parakeets (*Conuropsis carolinensis*), an extinct species, exhibited a Simple Alternate Strategy. Carolina Parakeets laid eggs in March and April and fledged young at least as early as 4 June. Yet, Snyder and Russell (2002) state only that they found 9 young (hatch-year or second-year) birds without molt between 7 October and 17 January, and 43 birds with molt between 17 December and 12 June; they present no data regarding the existence of any postjuvenal molts in Carolina Parakeets between early June and early October because no such data exist. Again, such an incomplete understanding of molt is not adequate basis for concluding that this species exhibited a Simple Alternate Strategy. Thus, Howell et al. (2003) have not made a convincing case that a Simple Alternate Strategy occurs in any species.

FIRST-CYCLE MOLTS AND PLUMAGES

Howell et al. (2003:647) suggest that ''it is most parsimonious to consider molts and plumages present in definitive cycles to have homologous counterparts in the first cycle, unless good evidence exists to the contrary,'' a notion that I agree with. They further state that in species following Simple Alternate and Complex Alternate Strategies, ''first-cycle plumages can be identified that appear homologous with definitive alternate plumages'' (p. 647). Yet, again, they do not present criteria other than timing and completeness of molt for homologizing molts or plumages. Thus, it is a mystery to me how Howell et al. (2003) concluded that some first-cycle molts can be ‘‘identified’’ as homologous with definitive prealternate molt while they simultaneously conclude that other supposedly ‘‘inserted’’ molts that are identical to definitive prebasic molt are not homologous with definitive prebasic molt.

Having ostensibly identified molts and plumages in the first cycle that are not homologous to any definitive molt or plumage, Howell et al. (2003) correctly recognize the need to find appropriate names for these molts and plumages if, in fact, they exist. They argue, correctly in my opinion, that using the terms *presupplemental* and *supplemental* wrongly implies homology of these nonrepeated first-cycle molts and plumages with presupplemental molts and plumages in the definitive cycles of other species. Their proposal to call all such first-cycle plumages *formative* plumages attained by *preformative* molts, where formative plumage is defined as ‘‘any nonbasic plumage present in the first cycle but not in subsequent cycles,’’ (p. 648) seems reasonable in that the terms are clearly defined and do not contradict or interfere with other aspects of the H-P system.

CASE STUDIES

Howell et al. (2003:637) state that one of the objectives of their paper is to ‘‘provide case studies to illustrate how [their] modified H-P system reflects presumed homology in all basic plumages.’’ Unfortunately, their case studies fail to do so; they are little more than a list of various taxa (Ardeidae, Anatidae, Galliformes, Charadriiformes, ‘‘near-passerines,’’ and passerines), and the molt strategies (SBS, CBS, SAS, or CAS) that they believe each taxon exhibits. They provide little or no explanation regarding how they reached these conclusions. Thus, readers hoping to learn criteria and guidelines for identifying molt homologies that could, in turn, be used to interpret molt data (e.g., previously published descriptions) in terms of Howell et al.’s (2003) proposed revision find little guidance in this section.

In their subsection regarding passerines, Howell et al. (2003:650) correctly state that ‘‘Thompson and Leu (1994) considered the first postjuvenal plumage of *Passerina* buntings as a first supplemental plumage, followed by conventional first basic.’’ They claim that this ‘‘involves a novel concept in molt terminology since, by H-P convention, Thompson and Leu’s (1994) supplemental plumage occurs *before* the start of the first plumage cycle.’’ To the contrary, Howell et al. (2003:639) defined the first plumage cycle ‘‘as the period between the attainment of juvenal plumage and the acquisition of the next basic plumage.’’ Thus, the first postjuvenal molt that Thompson and Leu (1994) called a presupplemental molt occurs during the first molt cycle, not before it.

In addition, Howell et al. (2003) reject the premise, adopted in previous work by Rohwer et al. (1992) and Thompson and Leu (1994), that one of the two body molts undergone by young *Passerina* buntings in their first summer and fall had to be a prebasic molt. Instead, Howell et al. (2003) propose that these two body molts are preformative molts. However, once again Howell et al. (2003) do not provide any criteria by which to distinguish between first-cycle molts that are preformative versus those that are homologous with molts in the definitive cycle. The second body molt of *Passerina* buntings is similar in timing, extent, and to various degrees in the resulting change in plumage color, to that of older birds undergoing definitive prebasic molt (Thompson and Leu’s 1994) and, therefore, is homologous with definitive prebasic molt.

HOWELL ET AL.’S PROPOSED REVISION TO THE HUMPHREY-PARKES SYSTEM

Howell et al. (2003) were motivated to propose a revised nomenclature for molt and plumage homologies because of two perceived failings of the H-P system. First, they argued that that using traditional first prebasic molt as the starting point for plumage succession leads to noncorrespondence between nomenclature and presumed homology in first basic plumages (e.g., in supposed SAS species which ostensibly lack a first prebasic molt). However, I have shown that the H-P system does not require using traditional first prebasic molt as the starting point for plumage succession; nor do first prebasic molts that have been evolutionarily lost or developmentally suppressed pose a problem for identifying molt and plumage homologies. Second, they argue that plumage color should not be used for evaluating molt and plumage homologies. However, I have shown that by using plumage color to identify the plumages to which feathers likely belong, the timing and extent of molts, and thus their homologies, can be documented more accurately than if plumage color is not used. Thus, because Howell et al.’s (2003) criticisms of the H-P system are incorrect, there is no need to revise the H-P system: it still works.

Despite the lack of need or justification for a revised H-P system, does Howell et al.’s (2003) system offer advantages over the H-P system? Unfortunately not. To follow their revised H-P system, one must accept their notion that no first-cycle molts are homologous with prebasic molts in subsequent cycles. However, this is not so as many species have a molt in their first cycle that is homologous to definitive prebasic molt (Thompson and Leu 1994). In addition, Howell et al. (2003) offer only two guidelines for identifying molt homologies: (1) molts that have similar timing are homologous, and (2) molts that are complete or nearly so are prebasic. However, Humphrey and Parkes (1959) and subsequent authors (Rohwer et al. 1992, Thompson and Leu 1994) also advocated use of these same guidelines as well as additional criteria (plumage color, extent of molt). Thus, Howell et al.’s system does not offer any new or better criteria for identifying homologies than those suggested by Humphrey and Parkes (1959) and others.

Last, Howell et al. (2003) maintain that our knowledge of molts and plumages of North American and Australian birds is relatively good. To the contrary, our knowledge of the sequence of molts and plumages, especially during early postjuvenal development, is remarkably incomplete and inaccurate (Leu and Thompson 2002). For example, previously unrecognized early postjuvenal molts and plumages have been ‘‘discovered’’ and documented in recent years in many species, including such geographically widespread and well-studied species as Indigo Buntings (*Passerina cyanea*; Rohwer 1986) and Northern Cardinals (Thompson and Leu 1994) clearly demonstrating that early postjuvenal molts and plumages of birds in North America are poorly known. Therefore, although it is possible that some first-cycle molts may be evolutionarily new molts as suggested by Howell et al. (2003), or evolutionarily lost or developmentally suppressed molts as I suggested previously, we will not have sufficient data to determine this until molts and plumages in the first cycle are studied quantitatively, in detail, in many more species of many more groups of birds. Further, to do so, it is essential that these studies be done on groups of closely related species of birds (i.e., from the bottom up), rather than across phylogenetically diverse taxa as proposed by Howell et al. (2003). Such additional knowledge may justify revising the H-P system in the future; until then, there is no reason to revise the H-P system.

This paper is dedicated to the life and memory of Peter F. Cannell who, more than anyone else, inspired my interest in molt in birds while working with him on Bowdoin College’s field station on Kent Island, Maine, in the summer of 1980. I thank Francis Wiese for translating portions of O. and M. Heinroth’s (1926) Die Vögel Mitteleuropas, and Dan Gibson, Steve Howell, Philip Humphrey, Ron LeValley, David Melville, Keith Russell, and Philip Unitt for comments on an earlier version of this paper. David Dobkin and Hugh Powell provided invaluable—if painful—editorial advice.

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THE FIRST BASIC PROBLEM REVISITED: REPLY TO COMMENTARIES ON HOWELL ET AL. (2003)

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Abstract. In this issue, Jenni and Winkler, Piersma, Thompson, and Willoughby offer commentaries on our modifications (Howell et al. 2003) to the Humphrey-Parkes system for naming molts and plumages (Humphrey and Parkes 1959; the H-P system). Piersma generally accepts our revision and outlines how its use could improve our ability to understand other cyclic life-history phenomena. Both Jenni and Winkler and Willoughby disagree with the philosophy of the H-P system, particularly its ability to reveal homologies. Thompson accepts the H-P system but argues that our elaboration on the system is faulty. However, we believe that despite a diversity of opinion concerning our proposal there is much common ground, including agreement regarding the homology of juvenal and basic plumages across species and the utility of the new term ''formative.'' The main points we review here are the potential dichotomy between homologies of molt and homologies of plumage coloration; the caution that should be applied when using plumage coloration to identify presumed homologous molts; and a clarification of definitions of plumage, molt, and the first plumage cycle. We remain convinced that our modified version of the H-P system represents a significant improvement in terminology, and will better reflect the homologies of molts.

Key words: *homology, molt terminology, plumage.*

El Problema del Primer Plumaje Básico: Respuesta a los Comentarios sobre Howell et al. (2003)

Resumen. En este número, Jenni y Winkler, Piersma, Thompson y Willoughby ofrecen comentarios sobre nuestras modificaciones (Howell et al. 2003) al sistema Humphrey-Parkes para nombrar las mudas y los plumajes (el sistema H-P; Humphrey and Parkes 1959). Piersma en general acepta nuestra revisión y esboza cómo su uso podría mejorar nuestra habilidad

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para entender otros fenómenos cíclicos de las historias de vida. Tanto Jenni y Winkler como Willoughby están en desacuerdo con la filosofía del sistema H-P, particularmente en cuanto a su habilidad para revelar homologías. Thompson acepta el sistema H-P, pero aduce que nuestra elaboración sobre éste es errónea. Sin embargo, creemos que a pesar de la diversidad de opiniones en torno a nuestra propuesta existen muchos puntos en los que convenimos, incluyendo la homología de los plumajes juveniles y básicos a través de las especies y la utilidad del nuevo término *formativo.* Los puntos principales que aquí revisamos son la dicotomía potencial entre las homologías de la muda y las homologías de la coloración del plumaje, la cautela que debe tenerse al usar la coloración del plumaje para identificar mudas presuntamente homólogas y una clarificación de nuestras definiciones de plumaje, muda y el primer ciclo del plumage. Seguimos convencidos de que nuestra versión modificada del sistema H-P representa un mejoramiento significativo en la terminología, que reflejará mejor las homologías de las mudas.

Recently, we (Howell et al. 2003) proposed modifications to the system for naming molts and plumages introduced by Humphrey and Parkes (1959, 1963; the H-P system). Subsequent commentaries (Jenni and Winkler 2004, Piersma 2004, Thompson 2004, Willoughby 2004) reviewed our proposals, and we thank these authors for their thoughtful opinions, and editor David Dobkin for encouraging this discussion.

We have little to add to our original paper (Howell et al. 2003), which we believe offers logical arguments to support our review of the H-P system, but discussing our revision in light of the above-noted commentaries may help readers come to grips with the much-neglected subject of molt in birds. Of the four commentaries, Piersma (2004) accepts our revision as a useful advance in comparing molts among species. We thus address this commentary to points raised by Jenni and Winkler, Thompson, and Willoughby.

THE HOMOLOGY QUESTION

We recognize that the most difficult aspect of our proposed revision may be acceptance of the idea that preformative molts (which include most conventional first prebasic molts) are not homologous with definitive prebasic molts, despite the frequent phenotypic similarities of the resulting plumages. However, even in species where preformative molts are complete, leading Thompson (2004:202) to state that such molts ‘‘must be homologous with [the] definitive prebasic molt,’’ we see no evidence to support their homology with prebasic molts. We maintain that such molts are simply one end of a continuum in which the preformative molt replaces from one to all of a bird’s feathers (Howell et al. 2003). Our view appears more parsimonious to us because of great variation in the timing and extent of preformative molts, even in closely related species, and because it reveals an underlying pattern in which the prebasic molts of all birds can be aligned and named consistently with respect to the cycles in which they occur (Howell et al. 2003).

We do not disagree, however, that the coloration of formative and definitive basic plumages may be homologous, simply that the molts producing them are not homologous. This potential dichotomy in homologies of color and homologies of molt seems to be an underappreciated point; its recognition has been particularly hindered by different meanings attributed to the word ‘‘plumage’’ (discussed later).

Willoughby (2004) and Jenni and Winkler (2004) are advocates of the traditional, life-history-dependent approach to naming plumages. This system relies primarily on perceived functions or timings of plumages as they relate to a bird’s life cycle (particularly the breeding season). Thus, their approach to plumage nomenclature differs philosophically from that of Humphrey and Parkes, who advocated divorcing nomenclature from other aspects of a bird’s life cycle in order to better understand patterns of molt. Despite their overall rejection of the H-P system, both Willoughby (2004) and Jenni and Winkler (2004) agree in principle with our revision of the first cycle. Their main argument is that the H-P system, including our modification of it, does not effectively reflect phylogenetic molt homologies.

Humphrey and Parkes (1959:2) prefaced their approach with the caveat ‘‘It is, of course, impossible to be certain that plumage sequences which appear to be exactly equivalent in various groups of birds are truly homologous in the phylogenetic sense; however, we believe it is not only useful but even necessary to treat such equivalence *provisionally* as homology. . . ’’ (emphasis ours). Howell et al. (2003) generally used the term ‘‘presumed homology’’ to underscore the provisional nature of this assumption. Such acknowledgments of uncertainty appear to have been overlooked by Willoughby (2004), Jenni and Winkler (2004), and others. We have no objection to calling presumed homologous molts ‘‘comparable,’’ as advocated by Jenni and Winkler (2004:190), but we argue that there is value in pursuing the quest for homology rather than viewing it as an unattainable goal. We also suggest that if homologies of color and of molt are treated separately, the revised H-P system does provide a terminology that can reflect molt homologies.

We would like to think that a genetic basis will eventually be discovered that can reveal homologies of molts within and between species, and that this unexplored avenue will provide an independent means of evaluating hypotheses. For example, an alternative interpretation to the six-month cycles described by Miller (1961) for equatorial populations of the Rufous-collared Sparrow (*Zonotrichia capensis*), is that the prealternate molt has become complete (or nearly so), and that the basic cycle is still an annual one, as in temperate populations of *Zonotrichia*. Studying the breeding and molt cycles of Rufous-collared Sparrow populations progressively farther north and south could test this hypothesis, but identifying a genetic coding for prebasic and prealternate molts in *Zonotrichia* sparrows could resolve the issue more convincingly.

PROBLEMS WITH ‘‘PLUMAGE’’ AND COLOR

Beyond the philosophical divergences discussed above, we find ourselves in close agreement with much of what Willoughby (2004) and Jenni and Winkler (2004) argue. But the similarities in our views are often masked by different meanings attributed to the same words. Foremost among these is the word ''plumage.'' Humphrey and Parkes (1959) defined a plumage strictly as a single generation of feathers, having a one-to-one correspondence with molts, rather than emphasizing the color and pattern of the feathers. However, Jenni and Winkler, and Willoughby, associate the word plumage with its traditional meaning of a bird's feathering, including its color and pattern (for which the H-P system provides the terms ''feather coat'' and ''aspect''). For example, the glossy, unspotted breeding aspect of a European Starling (*Sturnus vulgaris*) is simply its worn basic plumage in H-P terms, but this is its breeding plumage in the life-history system.

Hence the argument by Jenni and Winkler (2004: 188) for a system that ''dissociates molt and plumage cycles where necessary,'' to reflect the fact that some birds enter the ''adult molt cycle'' at a different time to when they enter the ''adult plumage cycle.'' The implication seems to be that the H-P system is incapable of such a dissociation because, by definition, only molts produce plumages. If we consider that Jenni and Winkler are using the term ''plumage'' in the sense of the H-P term ''aspect,'' then we wholeheartedly agree with the dissociation of aspect from molt, since one of our contentions is that the process of molt is controlled separately, at least in part, from processes determining plumage coloration. Indeed, apparently in accordance with Jenni and Winkler, we (2003) termed cycles subsequent to the first cycle as definitive molt cycles, even though plumage may not have attained a definitive aspect.

As another difference of definition, Jenni and Winkler place an emphasis on the *shedding* of feathers in a molt, quoting Humphrey and Parkes (1959) in support of this. However, Humphrey and Parkes (1963:498), noted that ''one of the major points of our 1959 paper is that molt is a *growth phenomenon* resulting in a new generation of feathers; loss of the previous generation of feathers is a relatively unimportant by-product of this process. . . '' (emphasis ours).

Willoughby (2004) suggests that by eliminating plumage color and pattern from an evaluation of homology, we remove all means for testing hypotheses of homology. Rather, we caution that color and pattern are not infallible criteria (nowhere do we ''explicitly forbid'' using plumage color, *contra* Willoughby 2004: 195), and that reliance on these characters has clouded an appreciation of potential molt homologies. There is ample evidence in the literature that in certain situations the color of incoming feathers can be influenced by factors (e.g., breeding state, hormonal cycles) that do not have such a strong effect on timing or extent of molt (Voitkevich 1966, Herremans 1999).

Willoughby (2004) correctly applies our modification of the H-P system to interpret the molt sequences of four cardueline finches, and we find his figure 1 helpful in representing presumed homologous molts in these species. His statement (2004:195) that ''the American Goldfinch's alternate plumage appears homologous in coloration with the definitive basic plumages of the Lesser and Lawrence's Goldfinches,'' exemplifies a fundamental difference in our approaches to the determination of homologies. We agree that these colors may be homologous, but we argue that the molts producing these colored plumages are not homologous. If we ignore colors, an underlying pattern immediately appears in which the molts are extremely similar, differing only slightly in timing and in the presence of an inserted prealternate molt in some birds but not others. This supports our view that at least the prebasic molts of these birds, which closely resemble those of numerous other species across a broad spectrum of taxa, are much more conservative characters than are color patterns, which appear to be controlled, and to have evolved, separately.

A further area in which we advocate caution interpreting color and pattern relates to Thompson's (2004: 201) suggestion that ''in species that change color between successive plumages, old and new feathers can be distinguished from one another based on differences in plumage color.'' In our view, this method is circular. The acid test of whether a particular feather is basic or alternate is how many times the feather follicle has been activated in a plumage cycle. This is not automatically revealed by color; for example, the alternate plumages of nonbreeding shorebirds that resemble basic plumages in aspect (Chandler and Marchant 2001), or the basic plumages of Black-chested Prinia (*Prinia flavescens*) that resemble alternate plumage in aspect (Herremans 1999).

THE FIRST PLUMAGE CYCLE

A critical part of any nomenclature is defining the first (basic) plumage cycle, something first attempted by Howell and Corben (2000b). Humphrey and Parkes (1959:3) explicitly defined a plumage cycle in terms of adult birds, but they did not define the first cycle. Thompson (2004:200) claims that ''the H-P system does not use first prebasic molt as the necessary starting point for determining molt and plumage homologies,'' but this was surely implicit in Humphrey and Parkes' system. They (1959:1) proposed ''to discuss plumage succession beginning at the time of loss of the juvenal plumage,'' and they always defined the first postjuvenal molt as first prebasic. In species with complete postjuvenal molts, such as the House Sparrow (*Passer domesticus*), so-called definitive basic plumage is attained by the conventional first prebasic molt and so, by H-P convention, this ''adult'' plumage explicitly marks the start of a basic plumage cycle. If other first cycles (in species with partial postjuvenal molts) did not begin with a basic plumage, then they would not be comparable to first cycles like those of the House Sparrow. This would be contrary to one of four desirable attributes of H-P terminology: ''The nomenclature must be consistent'' (Humphrey and Parkes 1959:14). Furthermore, Rohwer, Thompson, and Young (1992:299) stated explicitly that ''the first cycle begins with a prebasic molt,'' although they did not specifically define the first cycle.

The only rationale we can see for Thompson's (2004) arguments about the first plumage cycle is to justify his novel use of the term ''presupplemental'' for a molt that preceded the conventional first prebasic molt (Thompson and Leu 1994). To this end, Thompson (2004:202) quotes, and thus apparently accepts, our 2003 definition of the first cycle. But he also offers another, new definition of the first molt cycle as the period ‘‘after hatching and prior to the onset of the complete molt of all body and flight feathers that occurs in all birds at approximately one year of age’’ (Thompson 2004:199). As worded, one cannot determine exactly when Thompson’s new first cycle begins (hatching is a physical process removed from feather growth) or ends, and, *contra* his claim, it is well established that some (perhaps many) species of nonpasserines do not replace all flight feathers in the prebasic molt at about one year of age (Langston and Rohwer 1995, Pyle 1997). More importantly, because Thompson (2004) has argued at length that most formative plumages should still be viewed as first basic plumages, his first cycle presumably ends with either the conventional first or second prebasic molt, depending on species, population, or even individual. This is contrary to his own preference that ‘‘the names of all prebasic molts and basic plumages be consistent across all species and numbered according to the cycle in which they occur’’ (Thompson 2004:202). It also reiterates the inconsistency that we highlighted in the conventional H-P system, and that we remedied by the recognition of formative plumages (Howell et al. 2003: 640–642). We find Thompson’s views here to be self-contradictory and difficult to reconcile.

THE FOUR UNDERLYING MOLT STRATEGIES

Thompson (2004:203) argues that we ‘‘present no credible case for the existence in any species of. . . the Complex Basic Strategy. . . and the Simple Alternate Strategy; indeed, considerable empirical data refute the existence of these strategies.’’ We disagree. The existence of the Complex Basic Strategy is based on our reinterpretation of many conventional first prebasic molts as preformative molts; regardless of how one interprets these molts, a wealth of empirical data document their existence.

Regarding the Simple Alternate Strategy (SAS), Thompson appears to have disregarded the molt pattern described for Western Gull (*Larus occidentalis*) by Howell and Corben (2000a). Instead he quotes Dwight (1925), which, although thorough for its time, was constrained by conventional philosophies regarding molt strategies that we (and Thompson) associate with life-history terminology (see above). By contrast, Howell and Corben (2000a) found no evidence of two added first-cycle molts, as reported by Dwight (1925), and they noted that the single added molt appeared equivalent to the prealternate molt of adults. Furthermore, Olsen and Larsson (2003; a source listed by Thompson in support of his arguments) adopted Howell’s (2001) reinterpretation of first-cycle molts in large gulls. Thus, Thompson’s argument against the existence of the SAS seems to result from misinterpretation of sources (Beebe 1914, Dwight 1925, Howell and Corben 2000a). Recognition of the SAS (for which we encourage open-minded testing) was undoubtedly hindered because H-P convention always considered the first postjuvenal molt as a prebasic molt.

We agree with Thompson that the bottom-up approach exemplified by Rohwer and his students is a vital part of molt studies. Unlike Thompson, however, we believe that enough bottom-up studies have been conducted to allow a provisional analysis of potentially homologous patterns of molting across diverse taxa. There will always be exceptions to rules, and it is human nature to focus on such anomalies, like *Sylvia* warblers, or species with multiple waves of primary molt (*Staffelmauser*). However, we suggest it is more helpful to review molt patterns common to the majority of species, and in this way we may be in a better position to identify, and perhaps explain, genuine exceptions.

In our review of molt in over 2000 species we found a remarkable consistency in underlying patterns, as shown by our table 1 (Howell et al. 2003). While these commonalities in molt patterns may be derived, we suggest it is more parsimonious to view as potentially homologous the repeated appearance, in all species, of molts corresponding to those in the Simple Basic Strategy. And, contrary to Thompson’s implications, our interpretation does not preclude molts being lost or suppressed. For example, the limited or absent preformative molts in some species or populations of raptors (Herremans and Louette 2000, PP, unpubl. data) suggest that in this group the Complex Basic Strategy and Simple Basic Strategy are not distinct entities, but linked by a continuum. Or, as we noted (Howell et al. 2003), the two first-cycle molts of a Complex Alternate Strategy could be reduced to a single molt, resulting in the Simple Alternate Strategy. Thus the four strategies are not necessarily clear cut, which is as one might expect. Nonetheless, they do help to categorize all known patterns of molting.

CONCLUDING REMARKS

Differences in opinion between our paper and the commentaries of Willoughby and of Jenni and Winkler are largely philosophical. We are encouraged, though, that they acknowledge in principle the utility of our reinterpretation of first-cycle plumages. Despite the diversity of opinions expressed in our paper and Thompson’s commentary, there is some common ground. Important points are agreement that (1) the juvenal and basic plumages in all species are presumably homologous; (2) plumages should be numbered according to the cycle in which they occur; and (3) it is reasonable to introduce the term ‘‘formative’’ for plumages that occur in the first cycle but not in definitive cycles.

We suggest that many points of disagreement could be resolved by broader acceptance of the simple idea that the color and pattern of feathers reflect different homologies than the molts that produce the feathers. Indeed, Amadon (1966) has already argued that that there is no necessary equivalence of homology between a molt and the resulting plumage—but note that he was using ‘‘plumage’’ in the sense of the H-P system’s ‘‘aspect.’’ We also note that much of the confusion that has arisen since the H-P system’s inception might have been avoided if Humphrey and Parkes had chosen a word other than ‘‘plumage’’ for a generation of feathers, and if other workers had acknowledged this word’s ambiguous meaning. For example, the homologies of plumage that Willoughby (2004) claims are, in H-P terms, homologies of aspect.

In conclusion, the system of nomenclature one chooses in molt and plumage studies will depend on one's purpose. Jenni and Winkler, and Willoughby, argue that the H-P system tells us nothing about how a bird's molts relate to its annual cycle and appearance. But this is not the point of the H-P system: it was proposed to facilitate comparisons of molt patterns among all species. It does tell us how many molts there are in a cycle, and what their presumed relationship is to molts of related species. For comparative studies of molt we agree with others (Rohwer et al. 1992, Thompson and Leu 1994) that the H-P system remains the only practical system available, and, as Piersma (2004) points out, recognition of presumed homologies in molt could serve as a helpful template against which to compare other cyclical aspects of avian life histories. Our review of the H-P system, and the recognition of formative plumages (Howell et al. 2003), constitute small steps toward a better understanding of the evolution of molt, and we look forward to further advances in this fascinating field.

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