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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 plumaje. 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 ho-

mologous, 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 of-

ten 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 postjuvinal molt as first prebasic. In species with complete postjuvinal 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 postjuvinal 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 postjuvenile 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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