Molt Homologies in Ducks and Other Birds: A Response to Hawkins (2011) and Further Thoughts on Molt Terminology in Ducks

Author: Pyle, Peter

Source: Waterbirds, 36(1) : 77-81

Published By: The Waterbird Society

URL: https://doi.org/10.1675/063.036.0111

Molt Homologies in Ducks and Other Birds: A Response to Hawkins (2011) and Further Thoughts on Molt Terminology in Ducks

Peter Pyle

The Institute for Bird Populations, Point Reyes Station, CA, 94956, USA

E-mail: ppyle@birdpop.org

Abstract.—Humphrey and Parkes (1959) developed a molt and plumage nomenclature (the "H-P" system) based on the evolution of prebasic molts in birds from ecdysis events in reptiles, followed by later evolution of inserted molts responding to lineage-specific constraints and adaptations in Aves. Pyle (2005) revised H-P molt and plumage terminology of ducks by tracing the evolution of their molts from geese, whereas Hawkins (2011) defended traditional molt and plumage terminologies that defined molts relative to present-day breeding seasonality, ensuing plumage coloration, and other proximal factors. Apart from misinterpreting H-P's evolutionary approach, Hawkins (2011) confused the first-cycle terms of H-P, Howell *et al.* (2003), and Pyle (2005), and presented no new data or ideas to support traditional molt terminology in ducks. It is unlikely that inserted molts evolved in ancestral taxa based on yet-to-occur adaptations involving plumage color, and it is inconsistent to define homologous molts based on similar ensuing feather coloration while disregarding the substantially different coloration of homologous plumages within many avian lineages. Here the terminology of Pyle (2005) is defended, an alternative interpretation for the initial evolution of two (rather than one) inserted molts in the definitive cycles of female and male ducks is elaborated upon, and the future application of metabolic signatures to trace homologous molts in ducks and other bird lineages is suggested. Prebasic molts in ducks and other birds likely evolved from whole-scale restorative events common to all vertebrates, whereas distinguishable and less-comprehensive endocrinological and metabolic processes may accompany inserted molts. *Received 10 July 2012, accepted 9 October 2012*

Key words.—ducks, metabolism, molt, plumage coloration, terminology, waterfowl.

Waterbirds 36(1): 77-81, 2013

Humphrey and Parkes (1959) developed a terminology to describe the molts and plumages of birds with the goal of tracing the evolution of molts and identifying homologous molts in extant taxa. Their ("H-P") system is best understood by assuming that the periodic (usually annual) complete or near-complete molt in birds has evolved from the complete shedding of skin (ecdysis) of reptiles through ancestral to present-day avian taxa. Under H-P terminology, this complete or near-complete molt is termed the *prebasic molt*, and the period from the beginning of one prebasic molt to the beginning of the next prebasic molt is termed a *basic molt cycle*.

Through time and adaptation, extra inserted molts have evolved within the basic molt cycles of birds. Evolutionarily, the first inserted molt to evolve within *definitive* (e.g., second or later) basic molt cycles is termed the *prealternate molt*, while subsequent molts to evolve are termed *presupplemental molts* (Humphrey and Parkes 1959; Pyle 2007, 2008). Howell *et al.* (2003) modified and substantially clarified H-P terminology of the first-basic cycle by synonymizing the complete prejuvenal molt with the *first prebasic molt*, and considering the unique extra inserted molt that occurs within the first cycle of most birds as the *preformative molt* (formerly considered the "first prebasic molt" under H-P terminology). If two unique first-cycle molts occur, the second to evolve along an ancestral lineage is termed the *auxiliary preformative molt.*

Understanding the evolutionary approach of the H-P system is essential to correct application and use of H-P terminology, yet many ornithologists still attempt to define H-P molts based on present-day factors such as extent, location, timing of molt relative to breeding, and ensuing plumage color, regardless of how the molts evolved. Understanding H-P terminology also relies on the premise that evolution has acted to shape molt strategies, and that "plumages" are simply resultant artifacts of molts (Humphrey and Parkes 1959). Thus, although color patterns of feathers may shape the timings and extents of molts once the molts have evolved, the original evolution of an inserted molt in ancestral taxa was likely to replace worn feathers rather than for reasons related to resultant color patterns or other aspects of plumage (Pyle and Kayhart 2010; Wolfe and Pyle 2011).

Applying molt terminologies to most Northern Hemisphere ducks has been particularly challenging because 1) dull plumages result from spring and summer molts, whereas bright plumages for breeding result from fall molts, the opposite of many other birds with inserted molts; 2) breeding males and females appear to show separate timings and/or extents of inserted definitive molts; and 3) body molts may overlap one another and, at times, may seem continuous. Humphrey and Parkes (1959) concluded that partial body molts in spring (female) or summer (male) ducks should be coupled with the late-summer wing molt to form the complete prebasic molt, whereas Pyle (2005) argued that the complete body molt during and following the wing molt, producing colorful plumages in males of some species, should be considered part of the prebasic molt. Humphrey and Parkes' (1959) interpretation was based primarily on color patterns in males and thus, in part, contradicted stated H-P goals to assign terminology independent of life-history factors, whereas Pyle (2005) used an evolutionary approach to trace molts from geese to ducks as intended by the H-P approach. Similar differences in approach were used for first-cycle molts: Humphrey and Parkes (1959) considered the colorful plumages in first-winter males to be first-alternate plumages, whereas Pyle (2005) considered them formative plumages. A second inserted first-cycle molt, reported to occur between the prejuvenal and the preformative molt (summarized by Palmer 1976 as the "first prebasic molt"), was considered by Pyle (2005) to be either a continuation of a protracted prejuvenal molt or, if a separate molt did indeed exist, an auxiliary preformative molt.

Hawkins (2011) defended H-P and previous terminologies that defined molts and plumages in ducks primarily in relation to present-day seasonality, mating strategies, feather coloration, and other factors. Hawkins (2011) endorsed the traditional view that the complete body molt following the wing molt in ducks represents a prealternate molt. In addition to approaching molt and plumage terminology from a non-evolutionary perspective, Hawkins' (2011) evaluation suffers from a lack of original or new information and from selectively citing published information that supports traditional terminology while questioning that which does not support it. For example, Hawkins (2011) questioned the results of Hochbaum (1944) that prealternate molts (using terminology of Pyle 2005) can be less than complete because they were based on captive birds, while citing the results of numerous other studies based on captive birds (e.g., Weller 1957; Oring 1968) that he interpreted as supporting his and traditional theories.

It is unclear how Hawkins (2011) evaluated first-cycle molts because he interchanged and confused the molt terminology of Humphrey and Parkes (1959), Howell *et al.* (2003), and Pyle (2005). Nonetheless, Hawkins (2011) incorrectly assumed that Pyle (2005) identified the preformative molts in ducks based solely on their current "variable timing and extent" rather than an evaluation of evolutionary homologies. Similar problems apply to Hawkins' (2012) criticisms of first-basic terminologies proposed by Howell *et al.* (2003), whereby Hawkins (2012): 1) implied that Howell *et al.* (2003) invented a new definition of molt; 2) proposed a terminology that removes the basic plumage from the first cycle; and 3) repeated previous claims that the Howell *et al.* (2003) approach is contrived and complicated, when it in fact simplifies and clarifies molt terminology substantially (Howell 2010). The authors of Howell *et al.* (2003) and Pyle (2005) invite others to carefully compare their reasoning and evaluations with those of Hawkins (2011, 2012) and decide for themselves.

Preformative molts have evolved to accommodate variable feather-maintenance needs within a species' first cycle (reviewed by Howell *et al.* 2003; Howell 2010). The variable nature of this molt in geese and ducks (using the terminology of Pyle 2005) is typical of Aves in being more protracted in species that do not breed at 1 year of age (including geese, *Melanitta*, and *Sometaria*), whereas it is earlier and more compressed in those that can breed during their first summer (including *Aix*, *Anas*, and *Aythya*) (Pyle 2008). Variation in location, timing, and extent of inserted molts across present-day bird species results from adaptation after an inserted molt has evolved but, of course, cannot relate to the original evolution of the incipient inserted molt in ancestral taxa. Likewise, it is unlikely for an incipient inserted molt to evolve based on yet-to-occur adaptations related to plumage coloration, and it is inconsistent to define homologous molts based on similar ensuing feather colors while disregarding the substantially different coloration of homologous plumages within a species or genus. Examples among waterfowl include different colorations of homologous basic plumages (*sensu* Pyle 2005) between morphs of Snow Geese (*Chen caerulescens*), between congeneric species such as Brant (*Branta bernicula*) and Red-breasted Goose (*B. ruficollis*), and between males of subspecies such as Mallard (*Anas platyrhynchos platyrhynchos*) and Mexican Duck (*A. p. diazi*).

Perhaps the most unusual aspect of molt in Northern Hemisphere ducks is that females and males show different timings of their inserted definitive prealternate molts (*sensu* Pyle 2005), to a degree shown within few if any other bird taxa (Howell 2010). This difference suggests an alternative interpretation of molt and plumage terminology in ducks, discussed by Pyle (2007) in relation to molts in ptarmigan, in which two inserted molts may have evolved in ancestral ducks of both sexes, one of which regressed over time in females and the other of which regressed in males. Howell (2010) supported this approach, citing evidence that some male ducks may have a limited extra inserted spring molt additional to the partial summer molt, and L. Jonsson (pers. commun.) documented what appears to be an extra inserted summer molt, following the inserted spring molt, in at least some female *Anas*. Other researchers have documented near-continuous molt of body feathers in both sexes of ducks during this time period (Heitmeyer 1987; Hohman *et al.* 1992), which could represent the overlap of two molts. Thus, as in ptarmigan, both sexes of ancestral *Anas* ducks may have had both prealternate and presupplemental molts that have evolutionarily regressed in certain cases based on sex-specific pressures (Pyle 2007).

In such case, it would be difficult to determine which of the two (spring or summer) molts evolved first in ancestral duck and/or ptarmigan taxa and thus should be considered the prealternate molt (Humphrey and Parkes 1959; Pyle 2007). Howell (2010) speculated that primitive and monochromatic Southern Hemisphere Anatini may have had only a single spring molt and that this would then be considered the present-day prealternate molt; however, this idea was based on incomplete molt data described with traditional terminology and concepts (Weller 1968) and on proposed phylogenies of Anatini (Livezey 1991) that may need revision. Both Anatini and Mergini can show similar sex-specific inserted molt patterns, suggesting that the insertion of these molts may have preceded a Mergini-Anatini split, and it is also possible that the two inserted molts in ducks resulted from a splitting of an original inserted molt that can no longer be identified as pertaining to either of the present-day inserted molts. Both molt patterns and relationships within Galloanseres require more study before conclusions about the placement of the inserted molts in ducks can be drawn.

The classification of plumages as basic or alternate in ducks is complicated by overlap in feather generations and similarities in the appearance of succeeding feathers. Use of museum specimens to describe molting patterns (e.g., Palmer 1976; Pyle 2005) can be challenging, whereas fresh skins which can be examined both externally and internally for the presence of developing follicles may provide more accurate snapshots of molt; but in both cases the assumption that follicles produce discrete feather generations (alternate or basic) may be overly simplistic. Techniques such as isotopic analyses that accurately characterize feather generations may be needed to fully understand patterns of feather replacement in birds. Regardless, the attempts of Humphrey and Parkes (1959), Howell *et al.* (2003), and Pyle (2005) to define molts of birds and ducks in an evolutionary context rather than as based on proximal factors (Hawkins 2011, 2012) greatly clarifies our approach to the study of molts and plumages in these and other taxa.

I suggest that endocrinological and metabolic factors could also be considered in tracing homologous molts. There is increasing evidence that the complete prebasic molt in birds involves more than just feather replacement but is accompanied by a whole restoration of body tissues affiliated with increases in metabolic rate, increases in whole body protein synthesis, osteoporosis, loss of body fat, and suppression of the immune system as regulated in part by thyroidal activity (Voitkevich 1966; Murphy 1996; Kuenzel 2003). Similar metabolic processes also appear to occur during ecdysis and/or molt in fish, reptiles, and mammals (King 1972) as well as during the complete prebasic molt (*sensu* Pyle 2005) of ducks (e.g., Fox and King 2012), suggesting that the prebasic molt may be part of a restoration process ancestral to most or all vertebrates. Such substantive physiological processes may not occur contemporaneously with partial inserted molts, which may have originally evolved in birds simply to replace worn feathers (Pyle and Kayhart 2010; Wolfe and Pyle 2011). Chu (1940) and Höhn (1949) found different patterns of thyroidal activity responding to the separate body molts in Mallards. Further examination and comparison of endocrinological and metabolic processes during the spring, summer, and fall body molts of male and female ducks, along with those of other birds, may help confirm the correct application of H-P terminology in ducks.

ACKNOWLEDGMENTS

I thank Lars Jonsson, Andrew Engilis Jr., Steve N.G. Howell, Danny Rogers, and Chris Corben for discussions on molt concepts in waterfowl and suggestions on this response. Two anonymous reviewers helped improve the content and presentation. This is contribution # 448 of The Institute for Bird Populations.

LITERATURE CITED

Chu, J. P. 1940. The endocrine system and plumage types. III. Further experiments on the relation between the thyroid gland and plumage patterns in domestic fowls and ducks. Genetics 39: 493-502.

Fox, A. D. and R. King. 2012. Body mass loss amongst moulting Pochard *Aythya ferina* and Tufted Duck *A. fuligula* at Abberton Reservoir, South-east England. Journal of Ornithology 152: 727-732.

Hawkins, G. L. 2011. Molts and plumages of ducks (Anatinae): an evaluation of Pyle (2005). Waterbirds 34: 481-494.

Hawkins, G. L. 2012. The 'first basic problem' revisited: a re-evaluation of Howell *et al.* (2003). Wilson Journal of Ornithology 124: 409-419.

Heitmeyer, M. E. 1987. The prebasic moult and basic plumage of female Mallards (*Anas platyrhynchos*). Canadian Journal of Zoology 65: 2248-2261.

Hochbaum, H. A. 1944. The Canvasback on a prairie marsh. American Wildlife Institute, Washington, D.C.

Hohman, W. L., C. D. Ankney and D. H. Gordon. 1992. Ecology and management of postbreeding waterfowl. Pages 128-189 *in* Ecology and Management of Breeding Waterfowl (B. D. J. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadler and G. L. Krapu, Eds.). University of Minnesota Press, Minneapolis.

Höhn, E. O. 1949. Seasonal changes in the thyroid gland and effects of thyroidectomy in the Mallard, in relation to moult. American Journal of Physiology 158: 337-344.

Howell, S. N. G. 2010. Peterson reference guide to molt in North American birds. Houghton Mifflin Harcourt Company, Boston, Massachusetts.

Howell, S. N. G., C. Corben, P. Pyle and D. I. Rogers. 2003. The first basic problem: a review of molt and plumage homologies. Condor 105: 635-653.

Humphrey, P. S. and K. C. Parkes. 1959. An approach to the study of molts and plumages. Auk 76: 1-31.

King, J. L. 1972. Adaptive functions of vertebrate molting cycles. American Zoologist 12: 77-93.

Kuenzel, W. J. 2003. Neurobiology of molt in avian species. Poultry Science 82: 981-991

Livezey, B. C. 1991. A phylogenetic analysis and classification of recent dabbling ducks (Tribe Anatini) based on comparative morphology. Auk 108: 471-508.

Murphy, M. E. 1996. Energetics and nutrition of molt. Pages 158-198 *in* Avian Energetics and Nutritional Ecology (C. Carey, Ed.). Chapman & Hall, New York, New York.

Oring, L. W. 1968. Growth, molts, and plumages of the Gadwall. Auk 85: 335-380.

Palmer, R. S. 1976. Handbook of North American birds, vols. 2 and 3. Waterfowl (parts 1 and 2). Yale University Press, New Haven, Connecticut.

Pyle, P. 2005. Molts and plumages of ducks. Waterbirds 28: 208-219.

Pyle, P. 2007. Revision of molt and plumage terminology in Ptarmigan (Phasianidae: *Lagopus* spp.) based on evolutionary considerations. Auk 124: 508-514.

Pyle, P. 2008. Identification guide to North American birds, part II. Slate Creek Press, Point Reyes Station, California.

Pyle, P. and R. Kayhart. 2010. Replacement of primaries during the prealternate molt of a Yellow Warbler. North American Bird Bander 35: 178-181.

Voitkevich, A. A. 1966. The feathers and plumage of birds. English translation. October House Inc., New York, New York.

Weller, M. W. 1957. Growth, weights, and plumages of the Redhead, *Aythya americana*. Wilson Bulletin 69: 5-38.

Weller, M. W. 1968. Notes on some Argentine Anatids. Wilson Bulletin 80: 189-212.

Wolfe, J. D. and P. Pyle. 2011. First evidence for eccentric prealternate molt in the Indigo Bunting (*Passerina cyanea*): possible implications for adaptive molt strategies. Western Birds 42: 257-262.