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Molts and Plumages of Ducks (Anatinae): An Evaluation of Pyle (2005)

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Abstract.—Ducks are unusual because males of most Holarctic species acquire brightly-pigmented breeding plumages in autumn and winter and not spring as with most other birds. Based on an evaluation of molt phenology of ducks under the system of molt terminology invented by Humphrey and Parkes (1959), Pyle (2005) concluded that, for most North American duck species, the molt that produces bright plumages is basic in nature, the molt that typically produces a short-lived, dull "eclipse" plumage in spring or summer is alternate in nature, and the annual wing molt that largely occurs between these two molts is part of the subsequent recharacterized prebasic molt. For various reasons, it appears more likely that the timing of conventional prealternate molts in most Holarctic duck species has accelerated forward over time to autumn and winter in response to selection for early courtship and pairing, with resulting changes in the duration of alternate and basic plumages. These reasons include acceleration in the timing of the prealternate molt in sea ducks after they reach the age of first breeding. An accelerated timing of prealternate molts can explain why certain ducks exhibit an ephemeral, limited first prebasic molt, which appears to be a lost molt and not a virtually nonexistent, unique preformative molt as maintained by Pyle (2005). The accelerated timing hypothesis also can explain why the extent of prealternate molts may have become more complete and the extent of prebasic molts may have become less complete in certain ducks. The accelerated timing hypothesis appears more parsimonious from an evolutionary perspective than the system of Pyle (2005), and does not require the categorical rejection of plumage color and pattern in molt homology analyses, as advocated by Pyle (2005). *Received 13 May 2011, accepted 28 July 2011.*

Key words.—Anatinae, duck, H-P system, molt, molt terminology, plumage.

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Conventional North American molt terminology was invented by Humphrey and Parkes (1959) to facilitate identification of homologies among molts and plumages across species through use of the neutral terms "basic", "alternate", and "supplemental", rather than terms that refer to breeding status, plumage, or season of the year. Under the Humphrey-Parkes ("H-P") system, adult birds undergo a regular, typically complete or nearly-complete definitive prebasic ("adult post-breeding", using traditional European terminology) molt that includes the wings and produces a basic plumage each molt cycle, which typically is a year in duration (Humphrey and Parkes 1959). Also, many adult birds undergo a typically partial definitive prealternate ("adult pre-breeding" using the same) molt between prebasic molts that produces an alternate plumage. Typically, young birds undergo a partial molt soon after the prejuvenal molt, or first prebasic ("post-juvenal") molt, and, if applicable, a first prealternate ("first pre-breeding") molt. Other less common molts are classified as presupplemental under the H-P system.

Many migratory birds acquire a brightly-pigmented ("bright") alternate plumage in spring and form pair bonds just before the breeding season after males and females arrive on the breeding grounds (Poole and Gill 1992-2003). For reasons that are not well understood (Rodway 2007), there has been an emphasis on early courtship and pairing in most Holarctic duck species (subfamily Anatinae) and males acquire bright alternate plumages in autumn and winter and form pair bonds in late autumn, winter or during spring migration, well in advance of nesting activities (Weller 1965, 1976; Cramp 1977; Rohwer and Anderson 1988; Hohman *et al.* 1992). Following acquisition of their bright alternate plumages and establishment of pair bonds or initiation of reproduction, males and females of most Holarctic duck species undergo a prebasic body molt in spring or summer that typically produces a short-lived, dull basic or "eclipse" plumage. The basic plumage provides camouflage for females during nesting and for both sexes during a synchronous wing molt that renders the birds flightless and generally follows the prebasic body molt (Palmer 1976a, b; Hohman *et al.* 1992). In certain duck species, particularly in the *Anas*, *Aythya*, and *Somateria* genera, the timing of the prebasic molt differs by sex. Typically, females of these species commence the prebasic body molt in late winter or spring and complete it with a related wing molt after cessation of nesting activities in summer, while males undergo a prebasic body molt and related wing molt in the summer sometime after the female starts incubation (Palmer 1976a, b; Hohman *et al.* 1992). The split prebasic molt in females and difference in timing of this molt between males and females in these species have led to some confusion (Palmer 1976a; Pyle 2005), in part because females nest in a dull basic plumage while males exhibit a bright alternate plumage. Uniquely among Holarctic ducks, male Ruddy Ducks (*Oxyura jamaicensis*) acquire a bright alternate plumage primarily in spring, well after most other male ducks have acquired their bright alternate plumages (Palmer 1976b; Brua 2002; Pyle 2005). Also, Ruddy Ducks are different in that they do not engage in early courtship and pairing, likely because males form weak or no pair bonds on the breeding grounds and may be promiscuous (Siegfried 1976; Oring and Sayler 1992; Brua 2002).

The molt and plumage terminology for ducks under the H-P system is widely accepted in North America (Palmer 1976a, b; Poole and Gill 1992-2003) and the above-described sequence and extent of molts and plumages have been accepted throughout the world with different terminologies (Dement'ev and Gladkov 1967; Cramp 1977).

Pyle (2005) conducted an extensive study of specimens of North American ducks and geese to evaluate their molt phenology relative to the H-P system. Pyle (2005) examined at least 20 specimens collected during each month of the year for each of four groups, which consisted of six species of Anserine geese, eleven species of *Anas* ducks, three species of *Melanitta* scoters, and one species of *Oxyura* (the Ruddy Duck). Pyle (2005) concluded that with the exception of the Ruddy Duck, the first and definitive prebasic body molts in the Anatinae were considerably more variable and less extensive, and the definitive prealternate body molt was more extensive (complete or virtually so) than reported by other authorities. Based on these findings and presumed homologies with the molts of geese and the Ruddy Duck, both of which typically exhibit a wing-body molt sequence (Palmer 1976a, b; Pyle 2005), Pyle (2005) recharacterized the nature and sequence of the definitive molts in most North American duck species. Specifically, Pyle (2005) combined the annual wing molt with the subsequent conventional definitive prealternate body molt to form a complete prebasic molt and deemed the partial conventional prebasic body molt to be a prealternate molt (Table 1). As recharacterized, the complete prebasic molt produces bright plumages and the partial prealternate molt produces dull plumages.

Further, Pyle (2005) found that, with the exception of color and pattern produced, the conventional prebasic and prealternate molts of the Ruddy Duck closely resemble the recharacterized molts of other duck species, and that a slight shift in hormonal cycles that control pigment deposition explains the differences in the time of acquisition of bright plumage coloration in males. The result is that the conventional complete prebasic and partial prealternate molts of the Ruddy Duck continue to produce dull basic and bright alternate plumages, respectively, which is the opposite result of the recharacterized molts of other North American duck species. Finally, for reasons noted below, Pyle (2005) deemed both the first prebasic and first prealternate molts of ducks to be unique preformative molts that are not homologous with conventional definitive prebasic and prealternate molts, respectively (Table 1).

Pyle (2005)'s analysis of the molts and plumages of ducks under the H-P system has been adopted by mainstream ornithological literature (e.g., Howell 2010; Kaufman 2011) and authors who have not adopted this analysis have been criticized for not doing so (Barry 2007; Benesh 2007). However, the system of Pyle (2005) conflicts with various primary and secondary sources on the Anatinae. As a result, ornithologists and other persons do not know whether to use conventional H-P terminology or the molt terminology of Pyle (2005) in describing

Table 1. Differences between the H-P system and Pyle (2005)'s application of the modified H-P terminology of Howell *et al.* (2003b) to the Anatinae.

	Plumage Name		Molt Replacing the Plumage		
Molt Cycle	H-P system	Pyle (2005)	H-P system	Pyle (2005)	Typical Extent of Molt[a]
First	Natal down	Natal down	Prejuvenal molt	Prejuvenal or 1st prebasic molt	Complete
	Juvenal plumage	Juvenal or 1st basic plumage	1st prebasic molt	Auxiliary preformative molt	Partial
	1st basic plumage	Auxiliary formative plumage	1st prealternate molt	Preformative molt	Partial
Second (H-P system)	1st alternate plumage	Formative plumage	2nd prebasic molt	1st prealternate molt	Complete and partial, respectively
Second (Pyle 2005)	2nd basic plumage	1st alternate plumage	2nd prealternate molt	2nd prebasic molt	Partial and complete, respectively
Third (H-P system)	2nd alternate plumage	2nd basic plumage	3rd prebasic molt	2nd prealternate molt	Complete and partial, respectively
Third (Pyle 2005)	3rd basic plumage	2nd alternate plumage	3rd prealternate molt	3rd prebasic molt	Partial and complete, respectively
	3rd alternate plumage	3rd basic plumage		3rd prealternate molt	Partial
		3rd alternate plumage			

[a]**Complete molts include the remiges, while partial molts do not.**

the molts and plumages of ducks. The purpose of this article is to suggest a different interpretation of the molts and plumages of ducks than Pyle (2005) and that it is premature to adopt the system of Pyle (2005).

MOLTS AND PLUMAGES OF DUCKS

Based on existing literature, the timing of conventional prealternate molts appears to have accelerated forward over time in most Holarctic duck species as a result of selection for early courtship and pairing (Humphrey and Clark 1964). The accelerated timing of prealternate molts likely explains why the first prebasic molt is more or less reduced and, in some cases, virtually absent in certain Holarctic ducks and the conventional first and definitive prealternate molts often commence prior to completion of the preceding prebasic molts (Palmer 1976a, b; Cramp 1977). Much of the confusion regarding the molts and plumages of Holarctic duck species may be explainable on this basis and without having to recharacterize the nature of both first-cycle molts and the nature and sequence of definitive molts in most ducks as proposed by Pyle (2005).

First Cycle Molts

Pyle (2005: 216) concluded that the first prebasic molt "does not appear to exist in most genera of Anatinae," and, thus, deemed this molt a unique auxiliary preformative molt under the modifications to the H-P system proposed by Howell *et al.* (2003b). Studies of ducks indicate that the extent of the first prebasic (or equivalent) molt in the Anatinae varies widely, however, ranging from a brief, limited renewal of feathers on the Mallard (*Anas platyrhynchos*) (Schiöler 1921; Witherby *et al.* 1939; Palmer 1976a) to an extensive replacement of plumage on the Common Merganser (*Mergus merganser*) (Erskine 1971), Bufflehead (*Bucephala albeola*) (Erskine 1972), and Northern Shoveler (*Anas clypeata*) (Schiöler 1921; Howell 2010) (Appendix). In certain Holarctic duck species, most clearly in the *Anas* and *Aythya* genera, the first prebasic molt is transitory and limited to an extent that it is virtually absent or easily overlooked and overlaps with a more extensive first prealternate molt (Schiöler 1921; Witherby *et al.* 1939; Humphrey and Clark 1964; Palmer 1976a). The similarity between first and definitive basic feathers, the variably limited extent of the first prebasic molt, and the short duration of the first basic plumage suggest that the first basic plumage in these birds is not a virtually nonexistent, unique formative plumage, but rather a phylogenetic remnant that may now lack any biological function (Schiöler 1921; Witherby *et al.* 1939; Salomonsen 1949; Snyder and Lumsden 1951; Oring 1968).

Although selective forces have resulted in limited, fleeting first prebasic molts in certain individuals, populations and species of the Anatinae, this is not a reason to deem these molts unique preformative molts. Indeed, when a molt is limited or absent in certain individuals, populations or species but not closely-related individuals, populations or species, then it is reasonable to conclude that this molt has been evolutionarily reduced or lost in such individuals, populations or species and that existing molts and plumages are homologous (Thompson 2004).

Pyle (2005) concluded that the first prealternate molt in ducks is a unique preformative molt under Howell *et al.* (2003b) because it is variable in timing and extent. The differences in timing and extent of the first prealternate molt across and within Holarctic duck species are likely attributable to a variety of factors, including differences in the extent and duration of the first basic plumage and selection for early courtship and pairing, as discussed below. Regardless, homologous molts may vary in timing and extent (Humphrey and Parkes 1959). Moreover, there are no scientific studies that indicate that the presumably homologous first prealternate molts in ducks are formative in nature due to their variability or otherwise.

Pyle (2005) stated that his findings with respect to the extent of the first prebasic molt in the Anatinae were consistent with three studies of individual duck species (i.e., Mendall 1958; Oring 1968; Bellrose and Holm 1994), and did not discuss other studies (e.g., Schiöler 1921; Erskine 1971, 1972) that described extensive first prebasic molts in the Anatinae. Oring (1968) has been viewed as consistent with the H-P system, while Mendall (1958) and Bellrose and Holm (1994) appear inconclusive and are not inconsistent with the accelerated timing hypothesis (Appendix).

Acceleration of Timing of Prealternate Molts

The hypothesis that the timing of conventional prealternate molts has accelerated forward over time to autumn and winter in most Holarctic duck species is supported by studies of Common Mergansers by Erskine (1971) and Buffleheads by Erskine (1972) and the general timing of the acquisition of alternate plumages in Holarctic ducks. Each of the Common Merganser and Bufflehead has a variable partial first prealternate molt in its first spring, the typical time of acquisition of alternate plumages in many Holarctic birds, but following the next prebasic molt in the second summer, the prealternate molt is accelerated to autumn (Erskine 1971, 1972). A similar pattern is exhibited by eiders as they typically undergo a first prealternate molt in spring but undergo subsequent prealternate molts in autumn after the summer prebasic molt (Humphrey and Clark 1964). Other sea ducks, such as the Common Goldeneye (*Bucephala clangula*), may have a first prealternate molt in winter and thus may not exhibit as pronounced a forward shift in the second prealternate molt as sea ducks that have first prealternate molts in spring (Eadie *et al.* 1995). However, the overall pattern is similar.

The prealternate molt in sea ducks likely shifted over time from spring to autumn because they typically do not begin breeding until their third calendar year (Weller 1976; Poole and Gill 1992-2003), and, thus, selection has not favored the acquisition of a bright plumage in their first autumn. The accelerated timing of prealternate molts in sea ducks suggests that selection has favored the early acquisition of bright plumages to facilitate early courtship and pairing.

In the case of species in the *Aix*, *Anas*, and *Aythya* genera, selection appears to have resulted in an even earlier acquisition of bright alternate plumages than in sea ducks as males of many species exhibit the first prealternate molt in their first autumn (Palmer 1976a, b; Cramp 1977; Pyle 2005). Selection has resulted in an even earlier acquisition of bright plumages in these birds because they typically breed in their second calendar year (Poole and Gill 1992-2003). However, as in sea ducks, in some *Anas* species (Mallard, American Wigeon (*Anas americana*), Northern Shoveler) some males may exhibit the ancestral pattern and not begin the first prealternate molt until late winter or early spring (Humphrey and Clark 1964; Wishart 1985), which further suggests that the timing of prealternate molts has accelerated over time in these species.

Acceleration in the timing of conventional prealternate molts in most Holarctic duck species also is suggested by interspecific variability in the time of pairing and initiation and length of courtship (i.e., courtship activity and mate sampling, including trial liasons, before pairing). Studies of the variability in the time of pairing and onset of courtship in ducks show that this variability is largely accounted for by phylogenetic relationships (Weller 1965; Rohwer and Anderson 1988; Rodway 2007). For example, in general, Anatini (dabbling ducks) and Mergini (sea ducks) begin courtship earlier than Aythyini (bay ducks), and Anatini pair earlier than Aythyini and Mergini, resulting in longer courtship for Mergini than either Anatini or Aythyini (Rodway 2007). When compared with the presumably ancestral pattern of pair formation exhibited by geese and swans, the variability in the timing of reproductive behavior in Holarctic ducks suggests that selection has acted primarily to accelerate life history events related to pair formation (Rodway 2007). These life history events include the acquisition of bright plumage, which is closely related to the initiation of reproductive behavior (Weller 1965; Hepp and Hair 1983; Hohman *et al.* 1992) and a prerequisite for pairing by males in most ducks (Hohman *et al.* 1992).

Acceleration of the timing of prealternate molts in most Holarctic duck species likely has contributed to a shift forward in the timing of the prebasic molts in these species (Weller 1968) and had other effects on their molts and plumages, as discussed below.

Changes in Duration of Alternate and Basic Plumages

The duration of conventional alternate plumages in most Holarctic ducks has increased as the timing of conventional prealternate molts has accelerated, with a resulting decrease in the duration of conventional basic plumages. For example, Ruddy Ducks exhibit a long-lasting, dull basic plumage that is worn through much of autumn and winter, while Holarctic ducks that engage in early courtship and pairing exhibit dull basic or "eclipse" plumages in spring and summer that typically are much shorter in duration in comparison to that of the Ruddy Duck (Palmer 1976a, b; Cramp 1977). (In the scoters, the basic or "eclipse" plumages may differ from the alternate plumages only by the lack of bright gloss (Palmer 1976b; Cramp 1977).

According to Pyle (2005:218), the "ephemeral and highly variable cryptic plumages found in ducks in spring and summer presumably have evolved more recently, primarily in those species benefiting from an ensuing camouflaged plumage." Not all of these plumages are ephemeral, however, as the blue-winged ducks (i.e. Blue-winged Teal (*Anas discors*), Cinnamon Teal (*Anas cyanoptera*), and Northern Shoveler) and the Garganey (*Anas querquedula*) acquire conventional definitive alternate plumages substantially later than their Holarctic cogeners, in late autumn and winter, including into March in the case of the Garganey (Weller 1976; Cramp 1977; Dubowy 1985; Pyle 2005). As a result, males may wear conventional basic plumages for up to almost half the year in the case of the blue-winged ducks (Weller 1976) and about nine months of the year in the case of the Garganey (Cramp 1977; Spear *et al.* 1988). Although detailed information is not known in all cases, these species generally form pairs later than other Holarctic *Anas* species (Weller 1965; Paulus 1983; Rohwer and Anderson 1988), which likely accounts for why they have longer-lasting conventional definitive basic plumages and may have longer-lasting and more archaic (complete) first basic plumages than these other species (Appendix).

In contrast to Holarctic ducks, and with the exception of populations of Ruddy Duck and Cinnamon Teal that may have originated in North America, most sexually dichromatic ducks in the Southern Hemisphere lack a dull "eclipse" plumage in summer (Weller 1967, 1968). Thus, these species exhibit "permanent" sexual dimorphism, which likely is a derived condition (Weller 1968). Weller (1968) suggested that the "permanent" sexual dimorphism exhibited by these ducks, and the non-dimorphic plumages exhibited by many other Southern Hemisphere ducks, enable them to engage in courtship and breeding activities throughout the year and thus breed in tropical and subtropical habitats when rainfall and other conditions permit.

The variability in the duration of "eclipse" plumages in ducks appears to reflect the amount of the year in which these birds are or may be engaged in courtship and breeding and suggests that the short-lived, dull "eclipse" plumages of many Holarctic ducks have been reduced in duration as a result of selection for early courtship and pairing and are relics of primitive plumage patterns (Humphrey and Parkes 1959; Weller 1968). In accord are Snyder and Lumsden (1951: 9), who concluded that the "eclipse" plumage in the Cinnamon Teal "is [a] relic, and not an innovation."

Effects of Changes in Duration of Alternate and Basic Plumages on Underlying Molts

Holarctic ducks have extensive conventional prealternate molts, which likely reflect an increase in the duration of conventional alternate plumages over time and the protection needed by ducks in their highly aquatic habitats. Palmer (1976a, b) described extensive and typically complete definitive prealternate head-body molts in Nearctic Anatinae, and Cramp (1977) generally described extensive definitive prealternate head-body molts for Palearctic Anatinae using different terminology. Pyle (2005) found that conventional definitive prealternate head-body molts were essentially complete in both sexes of all species of *Anas* and *Melanitta*, and all other genera of Anatinae, which he examined less critically, also appeared to have complete or nearly-complete conventional definitive prealternate head-body molts. Pyle (2005) found that conventional first prealternate head-body molts ranged in extent from 38-72% in *Anas* and *Melanitta*, while Palmer (1976a, b) described extensive and typically complete first prealternate head-body molts in Nearctic Anatinae.

As the duration of conventional alternate plumages increased and the duration of conventional basic plumages decreased, it is possible that the extent of conventional prebasic molts in the Anatinae decreased. Such a decrease appears likely in the case of the first prebasic molt in most Holarctic ducks. In regard to definitive molts, Palmer (1976a, b) described complete conventional definitive prebasic molts in Nearctic Anatinae, and with one exception, the Velvet Scoter (*Melanitta fusca*), Cramp (1977) did the same for Palearctic Anatinae using different terminology. In contrast, Pyle (2005) concluded that the conventional definitive prebasic head-body molt was not complete in any individual of *Anas* and *Melanitta*, and he found little evidence of this molt in *Melanitta*. Pyle (2005) also found that the extent of conventional definitive prebasic head-body molts in *Aix* and *Somateria* generally resembled those of *Anas*.

Pyle (2005) conflicts with studies that found complete conventional definitive prebasic (or post-nuptial) molts in various species, including Redhead (*Aythya americana*) (Weller 1957), Gadwall (*Anas strepera*) (Oring 1968), Common Merganser (Erskine 1971), Mallard (Young and Boag 1981; Heitmeyer 1987), American Wigeon (Wishart 1985), Mottled Duck (*Anas fulvigula*) (Gray 1993), Wood Duck (*Aix sponsa*) (Bellrose and Holm 1994), and Canvasback (*Aythya valisineria*) (Thompson and Drobney 1995). With respect to the extent of the conventional definitive prebasic molt in *Melanitta*, Pyle (2005) conflicts with Dwight (1914). While Pyle (2005:211, Fig. 1) portrayed an adult molt that is limited or absent in some to most individuals in the period May through July and no spring molt prior to this time, Dwight (1914:298, 301) stated that "[c]ontrary to general opinion" an extensive molt of "the body plumage and the tail" takes place in the spring in both sexes of the scoters, and that "[n]o birds of many examined in March or April fail[ed] to show abundant growth of new feathers."

Although Pyle (2005) conflicts with individual studies of various duck species, Hochbaum (1944) supports his position with regard to the extent of the conventional definitive prebasic body molt in North American ducks. Hochbaum (1944) noted that some authorities believe that the Canvasback has an incomplete "eclipse" plumage, and stated that in captive Canvasbacks, Redheads, and Lesser Scaup (*Aythya affinis*) the extent of the definitive prebasic body molt is quite variable and not always complete. Hochbaum (1944) also found that the definitive prebasic body molt in males of these species became increasingly reduced in extent with age, to the point where some seven or eight year old males molted directly from one alternate body plumage to another and had no prebasic body molt. Hochbaum (1944) should be evaluated with caution because captive birds can exhibit atypical molts if conditions in captivity are not representative of those encountered in the wild (Palmer 1972; Heitmeyer 1988). Moreover, another study did not find similar results in recently-shot Canvasbacks, including males that were several or more years old (Thompson and Drobney 1995).

Pyle (2005) and Hochbaum (1944) suggest that the extent of conventional definitive prebasic body molts may have decreased over time in certain individuals, populations and species in the Anatinae as the duration of basic plumages decreased. Whether, and if so to what extent, this has occurred in specific species needs to be addressed by detailed studies of the molts of such species. However, even if the extent of the conventional definitive prebasic molt has become less complete and the extent of the conventional definitive prealternate molt has become more complete in certain species, this does not mean that these molts are not basic and alternate in nature, respectively. Indeed, Humphrey and Parkes (1959) recognized the possibility that in certain species the typical extent of the definitive prebasic molt (complete) and definitive prealternate molt (partial) may be reversed. Moreover, completeness is not a prerequisite to deeming a definitive molt basic in nature (Rohwer *et al.* 1992; Thompson 2004), and numerous species may have incomplete definitive prebasic molts (Humphrey and Parkes 1959; Pyle 1997).

Identity of the Wing Molt

Because wing feathers typically are either the last or among the last feathers to be dropped and replaced in connection with a conventional definitive prebasic molt in most Holarctic ducks (Palmer 1976a, b; Cramp 1977; Bellrose and Holm 1994), it is possible for Pyle to maintain that the wing molt actually is part of the conventional definitive prealternate body molt and to recharacterize this combined molt as the definitive prebasic molt. The bright areas on the wings of many duck species (e.g., wigeons, eiders) also suggest that the wing molt is part of the definitive prealternate molt (Sutton 1932; Stresemann 1948, contra Salomonsen 1949).

Most authorities have concluded that the wing molt is part of the conventional definitive prebasic body molt (Salomonsen 1949; Weller 1976), but the rationale for this conclusion is not made clear. A likely important factor in reaching this conclusion is the frequent substantial overlap between the wing and prebasic body molts in many duck species (Jackson 1915; Erskine 1971; Dubowy 1985; Hohman *et al.* 1992; Hohman 1993; Hohman and Crawford 1995; Thompson and Drobney 1995; Cooke *et al.* 1997; Howell *et al.* 2003a). However, in some individuals, populations or species of duck the wing molt also may overlap with the following definitive prealternate body molt (Palmer 1976a, b; Cramp 1977).

Another important factor in determining the identity of the wing molt in ducks is the timing of the initial wing molt in relation to the prejuvenal, first prebasic and first prealternate molts. Because wing molts typically do not occur with partial first prebasic and first prealternate molts, they are deemed to be part of the conventional definitive prebasic body molt based on the principle that the best way to identify a bird's molts and plumages is "by starting at the beginning and describing events in chronological order" (Palmer 1972:97).

Sequence of Wing and Body Molts and Molt Homologies between Ducks and Geese

Pyle (2005) combined the wing molt with the ensuing conventional definitive prealternate body molt in most Holarctic duck species based in part on presumed molt homologies with geese and the Ruddy Duck, which he found exhibit a wing-body molt sequence. Uniformity in molt sequence is not a criterion for determining homologies among molts, however, and the timing of the wing molt in relation to the body molt may vary within a single genus and even within a single species (Humphrey and Parkes 1959; Barr *et al.* 2000; Howell and Pyle 2005; Mcintyre and Barr 2010). Thus, the conventional prebasic molts of most Holarctic ducks may be homologous with those of geese and the Ruddy Duck even if most Holarctic ducks have a delayed wing molt and geese and the Ruddy Duck do not.

The difference between most ducks and geese in the sequence of the wing and body molts reflects differing selective forces. For example, geese are considerably larger than ducks, and thus less vulnerable to predators (Sargeant and Raveling 1992). As a result, geese, and the even larger swans, have not needed to evolve a delayed wing molt that presumably reduces predator risk to ducks by making them flightless only after they have substantially replaced bright alternate feathers with dull basic feathers.

The considerations relating to geese do not apply to much smaller Ruddy Ducks. Pyle (2005) found no overlap between the wing and body molts in thirteen dried specimens of Ruddy Duck, but Hohman (1993) found a considerable overlap between the wing and body molts based on an examination of 44 recently-shot Ruddy Ducks, and Palmer (1976b) indicated that the timing of this wing molt may overlap the body molt. Regardless, it appears inadvisable to assume that all duck species exhibit a wing-body molt sequence based on similarities in molt sequence between the Ruddy Duck and geese. The Ruddy Duck has different breeding and molt strategies as compared with other Holarctic duck species, exhibits a rare double wing molt (Hobson *et al.* 2000; Jehl and Johnson 2004), and is a member of a distinctive tribe (*Oxyurini*) that traditionally has been viewed as the most distantly related to geese among Anatinae tribes (Livezey 1986) but actually appears to be closely related to geese and not within the Anatinae (Gonzalez *et al.* 2009).

Based on similarities in timing and extent, Pyle (2005) concluded that the conventional first and definitive prealternate body molts of most North American duck species were homologous with the conventional first and definitive prebasic body molts of geese and the Ruddy Duck. The similarities in the timing and extent of these molts likely are due to acceleration of the timing and the substantial extent of conventional prealternate molts in most Holarctic ducks, and thus are not indicative of underlying molt homologies.

Plumage Color and Pattern

Pyle (2005)'s analysis of the molts and plumages of ducks under the H-P system is based on the position that plumage color and pattern are irrelevant in a molt homology analysis. Pyle's position is inconsistent with traditional molt homology analyses (e.g., Oring 1968; Heitmeyer 1987) and the H-P system (Rohwer *et al.* 1992; Thompson 2004).

Pyle (2005) maintained that in most North American duck species (other than the Ruddy Duck) the color produced by the definitive prebasic (conventional prealternate) molt has changed independent of the timing and extent of this molt and that dull conventional definitive basic plumages are a more recent innovation and alternate in nature. The color and pattern produced by a molt may change over time as a result of selection and likely has done so in ducks (Humphrey and Parkes 1959; Palmer 1972). However, it seems unlikely that the color and pattern produced by prebasic and prealternate molts effectively have been reversed in most Holarctic ducks, with the result that the bright courtship plumage is the basic plumage and the dull plumage is the alternate plumage. The apparent uniqueness of this result across avian taxa supports this view.

Pyle (2005: 217) also suggested that because the bright male plumage of ducks is "masked by more cryptic feathering in females and summer males by elevated levels of estrogen irrespective of testosterone levels," the bright male plumage "might appropriately be considered the basic plumage." The bright, male-like plumage that has been found to result from inhibition of the gonadal hormone estrogen in dichromatic species in the Anseriformes and two other ancestral avian orders (Kimball and Ligon 1999) is not the basic plumage for purposes of the H-P system. Rather, the basic plumage is the result of complex interactions among genes, hormones, and pigments during a prebasic molt. These complex interactions do not always produce bright, male-like plumages, as indicated by female, juvenile, and nonbreeding male Mallards and sexually monomorphic species such as the American Black Duck (*Anas rubripes*).

Evolutionary Considerations

According to Pyle (2005), definitive prebasic (conventional prealternate) molts in North American ducks have remained relatively static in timing and extent while plumage color-deposition cycles have changed according to the constraints of breeding and courting regimes. It appears more likely, however, that the timing and extent of molts in most Holarctic ducks have changed over time and that ducks exhibit molt patterns that are similar to most other birds that have a basic-alternate-basic molt pattern.

According to Pyle (2005), it is unlikely that the conventional definitive prebasic molt has evolved to become sexually divergent. However, sexual differences in molting patterns are common in all waterfowl (Hohman *et al.* 1992). Moreover, the split conventional definitive prebasic molt exhibited by females in *Anas*, *Aythya*, and *Somateria* is not exhibited by females in *Bucephala* and *Mergus* (Erskine 1971, 1972; Edie *et al.* 1995) as both sexes molt in summer, or apparently in *Melanitta* as both sexes exhibit a split molt with a later molt of the wings under conventional molt terminology (Dwight 1914; Palmer 1976b; Cramp 1977). Sexually divergent split definitive prebasic molts also are not exhibited in Western Palearctic Gadwall and possibly other Palearctic ducks that exhibit them in North America (Cramp 1977). Finally, both sexes of the Long-tailed Duck (*Clangula hyemalis*) exhibit a split definitive prebasic molt involving the head and body feathers (Palmer 1976b; Howell *et al.* 2003a), which further indicates the variability in the Anatinae in this regard.

Unlike the system of Pyle (2005), the accelerated timing hypothesis does not assume that each of the conventional first-cycle molts in the Anatinae is a unique preformative molt and that Holarctic ducks other than the Ruddy Duck have evolved an apparently unique prebasic and prealternate molt pattern in terms of color produced. As a result, this hypothesis appears more parsimonious from an evolutionary perspective than the system of Pyle (2005).

The molt patterns of most Holarctic ducks differ from those of several ducks in the Southern Hemisphere, which typically have a complete annual conventional prebasic molt in the late austral summer and a partial conventional prealternate molt in austral spring (Weller 1967, 1968). Because most groups of waterfowl probably originated in the Southern Hemisphere (Livezey 1986), the Southern Hemisphere molt pattern may be ancestral (Howell 2010). The accelerated timing of prealternate and prebasic molts exhibited by most Holarctic ducks as compared with ducks in the Southern Hemisphere likely is significantly attributable to the selection pressures associated with breeding in strongly migratory species and the imbalance in the sex ratios in most duck populations (Bellrose *et al.* 1961; Sargeant and Raveling 1992). However, detailed knowledge of the differences between the molt patterns of ducks in the two hemispheres and the reasons therefor are lacking.

Finally, while Holarctic ducks may represent an extreme in terms of a shift in the timing of prealternate molts, other species or populations of species with a basic-alternate-basic molt pattern appear to be undergoing selection for the early acquisition of alternate plumages in time frames that are similar to those of some ducks. These include the Common Murre (*Uria aalge*) and some other alcids (Birkhead and Taylor 1977; Harris and Wanless 1990; Ainley *et al.* 2002).

FUTURE RESEARCH

The accelerated timing hypothesis takes into account all relevant studies in English, but must be viewed as provisional for three reasons. First, while there is an extensive literature on waterfowl, there are few complete, detailed studies of the molts and plumages of individual duck species (Heitmeyer 1987). Secondly, the molt descriptions in sources such as Palmer (1976a, b) are not quantitative and often do not specify data sources. Thirdly, the existing literature contains numerous conflicting statements regarding molts and plumages in the Anatinae (Erskine 1971; GLH, pers. observ.), which likely reflect the difficulties in identifying these molts, particularly the first prebasic molt. These difficulties are primarily due to plumage similarities among age classes, particularly in females (Erskine 1972; Palmer 1976a, b), the overlap that frequently occurs in molts (Palmer 1976a, b), the rapid and fleeting nature of the first prebasic molt in many species (Palmer 1976a, b), the rapidity in which feathers may be replaced in certain areas, particularly the head and body (Bellrose and Holm 1994), differences in the timing and extent of molts between the sexes (Schiöler 1921; Palmer 1976a, b; Heitmeyer 1987; Hohman *et al.* 1992), and the constant molting that may be exhibited by some ducks (Dwight 1914; Hohman *et al.* 1992). The difficulties in analysis are exacerbated by a lack of birds in museum collections in molt or in pre-definitive plumages (Erskine 1971, 1972; Palmer 1976a, b) and the difficulties involved in identifying complicated molts based on the dried specimens that do exist, as compared with live or freshly-killed birds that can provide more accurate information (Dwight 1914; Combs and Fredrickson 1995). The result of these considerations is that the molts of ducks generally are poorly understood (Heitmeyer 1987).

Thus, there is a need for further research on the molts and plumages of ducks. Most importantly, there is a need for comprehensive studies of the molts and plumages of both sexes of individual duck species, which should particularly focus on the extent of the conventional first and definitive prebasic body molts and the identity of the wing molt. Also, studies should focus on whether the duration of conventional definitive basic plumages or the extent of conventional definitive prebasic molts in ducks decrease with age, which would indicate selection for the acquisition of conventional alternate plumages as birds mature and become more experienced. More generally, research that increases understanding of the variation in the timing of courtship and pairing, age of first breeding, and timing of reproduction in ducks likely will enhance understanding of the timing, extent, and color produced by molts in ducks.

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Appendix

Studies of the Conventional First Prebasic Molt in the Anatinae

Aix. A detailed study of the molts of captive juvenile Wood Ducks (*Aix sponsa*) by Bellrose and Holm (1994) found a limited first prebasic molt that involved only certain parts of the head, while a prior study of this bird by Grice and Rogers (1965) found no evidence of this molt. It is unknown whether these results are partly attributable to the difficulties in distinguishing similar succeeding plumages, as suggested by Palmer (1972, 1976b), or the possible effects of captivity on molts in the case of the study by Bellrose and Holm (1994).

Anas. There is a wide variability in the extent of the first prebasic molt in this genus. At one extreme, in a multi-species study of Palearctic dabbling ducks that evaluated 2,500 specimens, Schiöler (1921) found a complete second juvenal (first prebasic) head-body-tail molt in both sexes of the Northern Shoveler (*Anas clypeata*). The Blue-winged Teal (*Anas discors*) (Palmer 1976a; Weller 1976; Howell 2010) and Garganey (*Anas querquedula*) (Palmer 1976a) also reportedly have a similarly extensive first prebasic (or preformative) molt, but detailed studies are lacking. Schiöler (1921) also found an extensive or distinct second juvenal (first basic) plumage in female Teal (A*nas c. crecca*), Pintail (*Anas acuta*), and Eurasian Wigeon (*Anas penelope*), but only traces of this plumage in males of these species and in both sexes of the Mallard (*Anas platyrhynchos*), which he considered evidence of a lost plumage.

A study of Gadwall (*Anas strepera)* by Oring (1968) is noteworthy because of its detail and Oring focused on the plumages during the first few months of life of this species in order to evaluate the hypothesis of molt and plumage homologies of Humphrey and Parkes (1959) in the Anatinae. Based on an analysis of 283 skins and repeated examination of approximately 250 captive live birds, Oring (1968:366) found a "previously overlooked" partial first prebasic molt on the breast, sides, and lateral upper back of both male and female Gadwalls that first appears before the prejuvenal molt is completed and overlaps with the first prealternate molt. Based on a study of recently-shot and live-trapped birds and museum specimens, Wishart (1985) noted a heavy first prebasic body molt in the American Wigeon (*Anas americana*). Based on extensive field study, review of museum specimens, and relevant sources, Cox and Barry (2005) stated that an "ordinarily undetected" formative (first basic) plumage is present in both American Wigeon and Eurasian Wigeon, but they did not discuss its extent.

Snyder and Lumsden (1951) found that males in South American populations of the Cinnamon Teal (*Anas cyanoptera*) exhibit a spotted post-juvenal (first basic) plumage that is similar to the "eclipse" plumage and that male Cinnamon Teal in North America do not, and suggested that this plumage was in the process of being lost in South American populations. According to Palmer (1976a), male North American Cinnamon Teal have an extensive first basic plumage that is unspotted, which may explain why it was not identified by Snyder and Lumsden.

Gray (1993) found no evidence of a first prebasic molt in Mottled Ducks (*Anas fulvigula*), but acknowledged the difficulty in identifying this molt and the need for additional research in this regard. Gray (1993) also found that both sexes of the Mottled Duck exhibit three, rather than two, definitive head-body-tail molts per annual cycle, and suggested that other Anatini species also exhibit three such molts.

Aythya. Based on a study of eight captive Redheads (*Aythya americana*), Weller (1970:323) found a head-neck molt and concluded that "there is little question that the first non-nuptial (first basic) plumage is present in both sexes" of this species. A study of Ring-necked Ducks (*Aythya collaris*) by Mendall (1958) did not find any evidence of a first non-nuptial (first prebasic) molt in young birds or a definitive pre-nuptial (prealternate) molt in females. Mendall (1958) appears inconclusive with respect to both of these findings because the author acknowledged difficulty distinguishing between the juvenal and alternate plumages and noted the considerable variation in the initial acquisition of adult plumage in this species.

Melanitta. Pyle (2005) stated that Dwight (1914) was consistent with his view that there is no first prebasic molt in the three North American scoters, but based on the "many pin feathers" in freshly-killed ducks that "easily escape notice in skins," Dwight (1914:297) stated that he was "convinced" that two molts accounted for plumage changes in the scoters in the first winter, a partial postjuvenal (first prebasic) molt and a partial prenuptial (first prealternate) molt. Dwight had difficulty telling when one of these molts stopped and the other began, however, as have others (Palmer 1976b; Hoffman and Bancroft 1984) due to the similarities in the basic and alternate plumages in each sex of these species. Conflicts in the sources (e.g., Dwight 1914; Palmer 1976b; Cramp 1977; Pyle 2005, 2008) as to the timing, extent, and number of first-cycle molts in the scoters indicate that further study is needed.

Bucephala. In a study of Buffleheads (*Bucephala albeola*) based primarily on museum specimens, Erskine (1972) described an extensive first prebasic molt in male Buffleheads that typically starts with the scapulars and flanks and is followed by the tail and then the remainder of the body and the head. This study found that the first basic plumage in males is acquired from late August through early October and typically is worn until the first prealternate molt in the spring. Due to a lack of specimens and studies, Erskine (1972) was unable to determine the extent of the first prebasic or first prealternate molts in female Buffleheads.

Mergus. Based on an examination of 325 banded individuals and 465 individuals killed in a shooting program, Erskine (1971) found an extensive first prebasic molt in both male and female Common Mergansers (*Mergus merganser*). According to the study, this molt starts in mid-September and completes during November and replaces feathering on the tail, tail coverts, flanks, sides, upper breast, most or all of the back and the outer scapulars with juvenal-appearing feathers that are worn until a variable partial first prealternate molt in the spring or later.

Oxyura. Pyle (2005) found a first-cycle molt in Ruddy Ducks (*Oxyura jamaicensis*) that covered 30-33% of the body and appeared to be a single molt that was most extensive following mid-winter. Feathers replaced during the earlier portion of the molt (October-December) were cryptic in coloration and those replaced during the later portion of the molt (January-March) were intermediate in color between cryptic and bright alternate feathering. Thus, this molt produced some basic feathers and no purely alternate feathers and spanned the traditional period for both the first prebasic and first prealternate molts in other birds. Nonetheless, Pyle (2005) concluded that if only a first-cycle molt occurs in the Ruddy Duck, it could be considered a prealternate molt per Howell *et al.* (2003b).