Molts and Plumages of Ducks (Anatinae)

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Abstract.—Ducks are unusual in that males of many species acquire brightly pigmented plumages in autumn rather than in spring. This has led to confusion in defining molts and plumages, using both traditional European terminology and that proposed by Humphrey and Parkes (1959). To investigate molt patterns in waterfowl relative to molt and plumage nomenclature, 2,227 specimens of ducks and geese were examined. Both the "first prebasic" ("post-juvenile" using traditional European terminology) and the "definitive prebasic" ("adult post-breeding") body molts in most ducks, the latter producing the cryptic spring (female) and summer (male) plumages preceding the wing molt, are considerably more variable and less extensive than reported. By contrast, the "definitive prealternate" ("adult pre-breeding") body molt of most ducks, which follows the wing molt and produces the brightly colored plumages of males, is complete or virtually so. Based upon presumed homologies with the molts of geese, the wing molt and ensuing complete body molt of ducks are better considered the prebasic rather than the prealternate molt and, thus, the bright feathering of male ducks should be considered the basic plumage. The incomplete and ephemeral cryptic plumages, attained by some ducks in spring and summer, may have evolved more recently in species that benefit from camouflage at this time, and should be considered alternate plumages. The molts and plumages of the adult Ruddy Duck (*Oxyura jamaicensis*) appear to be homologous with those of other Anatine ducks, with a slight temporal shift in the hormonal cycles that control pigment deposition (as opposed to differences in molt patterns) explaining the differences in plumage-coloration patterns in males. Because feather pigment-deposition patterns are controlled by various factors related to seasonal and reproductive phenomena, which differ considerably both among and within taxa, plumage color should not be a critical factor in attempts to define homologous molts and plumages. *Received 25 July 2004, accepted 12 January 2005.*

Key words.—*Anas*, *Anser*, duck, molt terminology, *Melanitta*, *Oxyura jamaicensis*, plumage, Ruddy Duck, scoter.

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Among birds, many ducks (Subfamily Anatinae) are unusual in that brightly pigmented plumages of males are acquired in autumn rather than spring. In boreal species, feathers of the wing tracts (including the primaries, secondaries, and wing coverts) are replaced synchronously in the late summer or early autumn, in between two separate molts of body-feather tracts (Cramp and Simmons 1977; Hohman *et al.* 1992; Bellrose and Holm 1994). In *Anas*, *Aythya*, and *Somateria*, the body molt prior to the wing molt occurs in the early spring in females and in the summer in males, often producing a cryptic plumage that provides camouflage for females during nesting and for both sexes during the flightless period accompanying wing molt (Hohman *et al.* 1992). Jackson (1915) first suggested that this summer body molt in males be aligned with the wing molt to form the complete annual molt. Because the body feathering produced by this molt was cryptic, Jackson considered it the "winter plumage," followed by a partial molt into the brightly pigmented "summer plumage," which occurs primarily in winter. Variations of this interpretation have persisted in the literature (Schiøler 1921; Witherby *et al.* 1939; Dement'ev and Gladkov 1952; Oberholser 1974; Cramp and Simmons 1977; Marchant and Higgins 1990; but see Sutton 1932; Stresemann 1948). Consequently, the bright plumages acquired in autumn have been referred to as "nuptial" or "breeding," and the cryptic summer plumages acquired in spring and summer as "eclipsed" or "non-breeding," despite confusion resulting from the fact that females of these genera nest in "non-breeding" plumage (*cf.* Cramp and Simmons 1977).

Humphrey and Parkes (1959) cited such confusion in support of their revised molt and plumage nomenclature, which excluded terms correlated with "seasonal, reproductive, developmental, or other phenomena" within the annual cycle. The "Humphrey-Parkes" (H-P) system attempts to recognize homologous molts across taxa by defining a "molt cycle" (usually a year in boreal species) during which a single complete or near-complete molt occurs and is termed the "prebasic molt." Additional, less-complete inserted molts, defined by the shedding of feathers more than once within the molt cycle, are termed "prealternate molts," and if more than one inserted molt occurs, the second inserted molt (defined by the replacement of feathers three times within the molt cycle) is termed the "presupplemental molt." Regarding molts in adult ducks, Humphrey and Parkes concurred with previous opinion that the spring/summer body molt should be aligned with the wing molt, terming this the complete prebasic ("post-breeding" of traditional European terminology) molt resulting in "basic plumage," followed by the partial prealternate ("prebreeding") molt in autumn resulting in "alternate plumage." Humphrey and Parkes reasoned that the bright plumage stage in males has evolved more recently, and should be considered the alternate plumage to conform to nomenclature in other birds that have bright seasonal plumages.

Palmer (1972) further elaborated upon H-P molt and plumage terminology in ducks and subsequently (Palmer 1976) applied it to the molts and plumages of all North American species. Palmer defined duck molts in the first cycle as consisting of a partial "first prebasic" ("post-juvenile") molt of all or most body feathers in late summer, followed rapidly by another partial "first prealternate" ("first pre-breeding") molt of all body feathers in autumn and winter, resulting in bright first-winter plumages in males. The Ruddy Duck (*Oxyura jamaicensis*) differs from other North American species in that adult males acquire bright plumage during a prealternate molt in spring rather than in autumn, and the complete prebasic molt consists of the wings followed by the body molt in early autumn (Palmer 1976). The H-P molt and plumage terminology for ducks described by Palmer (1972, 1976) has been widely accepted in North America (Hohman *et al.* 1992; Poole and Gill 1992-2003), and this sequence and extent of molts and plumages (albeit with different terminologies) has been accepted throughout the world (Dement'ev and Gladkov 1952; Cramp and Simmons 1977; Marchant and Higgins 1990).

Despite an extensive literature, gaps remain in our understanding of the precise timing and extent of molts in ducks (Hohman *et al.* 1992). Palmer (1976) described the first prebasic (post-juvenile) molt as involving most or all body feathers; however, the few studies that have critically examined this molt either have involved captive ducks subjected to non-natural feeding and lighting regimes that likely affected molts (Weller 1957, 1970), or have found it at most to include only a few feathers of the head or underparts (Mendall 1958; Oring 1968; Bellrose and Holm 1994). Furthermore, studies such as that of Hochbaum (1944) have suggested that the summer body molt in certain adult ducks, defined as part of the prebasic or post-breeding molt, might be limited to a small proportion of feathers or be lacking altogether, such that males molted directly from one bright plumage to the next, without a more cryptic summer plumage. Humphrey and Parkes (1959) and Palmer (1976) acknowledged Hochbaum's (and other similar) findings, but did not discuss the discrepancy in H-P terminology that results from the replacement of alternate with alternate feathering without an intervening basic plumage.

To investigate molt phenology in ducks relative to molt and plumage terminology, 2,227 specimens of North American ducks and geese (Anserinae), the latter widely considered ancestral to ducks (Delacour and Mayr 1945; Palmer 1976), were examined. The objectives were: (1) to confirm the timing and determine the extent of each molt in ducks; and (2) to attempt tracing the evolution of homologous molts from Anserinae (which lack additional inserted molts) to Anatinae in order to properly apply molt terminology to ducks.

METHODS

Specimens of geese and ducks were examined at the California Academy of Sciences (CAS), San Francisco; the Museum of Vertebrate Zoology (MVZ), University of California at Berkeley; the Museum of Wildlife and Fisheries Biology (MWFB), University of California at Davis; the Provincial Museum of Alberta (PMA), Edmonton; and the National Museum of Natural History (USNM), Washington, D.C. Specimens examined were collected throughout the year (sample range 119-230 per month) and throughout North and Central America.

Age when collected and sex were determined for each specimen, as based primarily on plumage of the wing (*cf.* Palmer 1976; Carney 1992) combined with information noted on the specimen label. Juveniles could be recognized by their more rounded feathers, contrasting with the larger and squarer feathers of adults (Palmer 1972, 1976; Cramp and Simmons 1977; Marchant and Higgins 1990). Based on specimen availability (especially in summer) and divergent molt and plumage patterns, six species of Anserine geese (*Anser albifrons*, *Chen canagica*, *C. caerulescens*, *C. rossi*, *Branta canadensis*, and *B. bernicula*), 11 species of *Anas* ducks (*strepera*, *penelope*, *americana*, *rubripes*, *platyrhyncos*, *fulvigula*, *discors*, *cyanoptera*, *clypeata*, *acuta*, and *crecca*), three species of *Melanitta* scoters (*perspicillata*, *fusca*, and *nigra*), and one species of *Oxyura* (Ruddy Duck) were selected for detailed examinations of molt and plumage phenology. For each of these four groups, at least 20 specimens collected during each month of the year were examined.

For each taxon, temporal periods of molt resulting in each plumage stage were determined, and extent of the molt resulting in the plumage was estimated. Specimens (N = 575) were considered to be undergoing "active molt" if >10% of contour feathers within any of six body regions (defined by Billard and Humphrey 1972) were found to be missing or growing. Contour feathers throughout these regions were lifted and examined (*cf.* Pyle and Howell 2004), and the proportion of pins or developing feathers was estimated. Within this group, specimens on which the primaries and secondaries were missing or growing (N = 79) were considered in "wing molt". Temporal ranges for body-feather molts and wing molts were calculated based on mean Julian date of specimens in active molt ±2 S.D., to encompass an estimated 96% of the molting periods.

In specimens not showing active feather replacement (N = 1,652), extent of the previous molt was estimated by critically examining body feathers for contrasts in size, shape, quality, wear, and coloration, as compared to those of corresponding feather tracts in specimens collected in the plumage or molt antecedent to the plumage in question. For males of most North American Anatinae, the proportion of feathers replaced within each tract (to the nearest 10%) was estimated by changes in color between succeeding feather generations in most tracts. The assumption was not made, however, that change in feather color equated to change in feather generation. Therefore, qualitative assessments of feather color were performed on each feather generation in male ducks (excluding three taxa, Mottled Duck *Anas fulvigula*, Black Duck *A. rubripes*, and "Mexican Duck" *A. platyrhynchos diazi*, that lack bright plumages in males), in consideration of relative feather wear. In juveniles of both sexes, replacement of feathers could be assessed by contrasts in shape and wear between the smaller and rounder juvenal feathers and the replaced, larger and squarer feathers. The term "cryptic" is used to indicate duller or browner feathers typical of juvenal plumage, females, and many males in summer, and the term "brightly colored" is used to indicate pigmented display feathers acquired by males for courting. For female ducks, assessment of molt extent in adults was more difficult due to greater similarities in plumage pigmentation patterns between successive generations; thus, data from females were interpreted with more caution. In Anserinae, feathers in both sexes were large and more readily assessed for comparative feather-replacement patterns.

For each specimen, the timing of rectrix and tertial replacement as well as the number of feathers replaced (symmetrically on both sides of the tail or both wings) during the preceding molt was recorded. Over 1,400 specimens of 18 other species of North American ducks were also examined for general evaluation of molt and plumage patterns in comparison with taxa examined more critically.

Throughout the results section I follow the "traditional" molt and plumage terminology of Humphrey and Parkes (1959), as detailed by Palmer (1972, 1976). Traditional European terms for each molt in ducks are also indicated. A "revised" H-P terminology, presented in Figure 1 and the discussion, includes modifications based on the results of this study and those proposed by Howell *et al.* (2003) for first-cycle molts.

RESULTS

Within each taxonomic grouping, few significant differences were found in the timing or extent of molt between species. Within *Anas*, the traditional "prealternate" ("prebreeding") molts of *A. discors*, *A. cyanoptera*, and *A. clypeata* (Blue-winged Teal, Cinnamon Teal, and Northern Shoveler), pooled, occurred significantly later than in other species (see below). Thus, except in these cases, species within each taxon were pooled to derive summary statistics on molt timing and extents. Likewise, little geographic variation (based on collection locality) appeared to be evident.

Molt in Anserinae

The temporal period for the traditional first prebasic (post-juvenile) molt in geese, based on 124 specimens in active molt, was 22 September to 6 March (Fig. 1A), commencing on the summering grounds and concluding on the wintering grounds. This molt included approximately half of the body feathers, on average (Table 1): most or all of the head and neck, and much of the upper back (including the scapulo-humerals), breast, and sides, but little of the belly, lower back or rump (Table 2). At least one tertial was replaced on 29% of individuals and rectrices had been replaced on 81% of the specimens (mean 7.1 ± 7.8 [S.D.] of 16 rectrices). The sequence of body molt in both geese and ducks, as based on proportions of feathers in active molt, generally proceeded anterior-ventrally, commencing

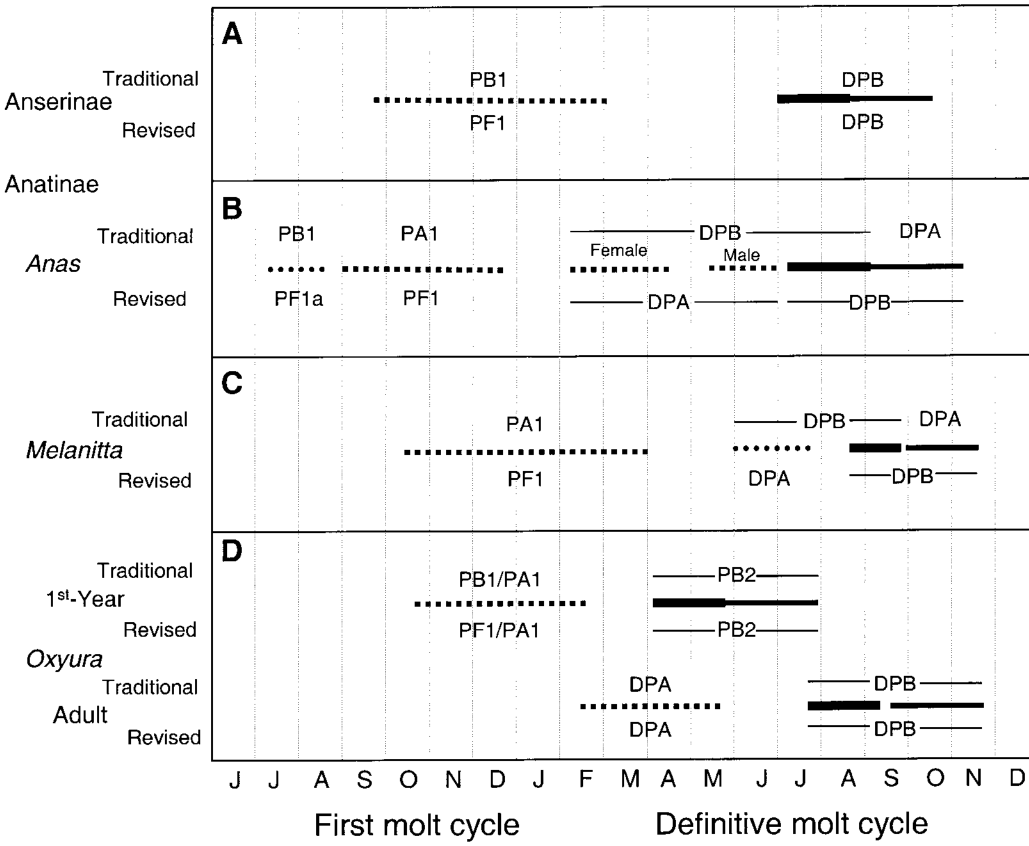

Figure 1. Graphic representation of the timing of molts in North American waterfowl and a comparison of molt terminologies; see text for methods used to determine commencement and termination dates. Extents of molts are represented by line style and thickness: dotted lines represent molts of body tracts that are very limited, or absent in some to most individuals; dashed lines represent body molts that are partial and occur in most or all individuals; thinner solid lines represent body molts that are complete or nearly complete in all individuals; and thicker solid lines represent wing molts. Abbreviations for traditional molts are as follows: PB1—first prebasic (post-juvenile) molt; DPB—definitive prebasic (adult post-breeding) molt; PA1—first prealternate (first pre-breeding) molt; and DPA—definitive prealternate (adult pre-breeding) molt. The temporal periods for males and females were separated only when the sex-specific difference in timing was significant (ANOVA, P < 0.05).

with the head, neck, upper back, breast, and flanks, and concluding with lower scapulars and vent. Typically, the tertials and rectrices were the last feathers to be replaced during this molt, often in winter or early spring, following replacement of body feathers.

During the definitive prebasic (adult post-breeding) molt in adult geese, wing molt occurred from 30 June to 22 August (N = 22; Fig. 1A). In individuals, replacement of wing feathers preceded molt of body feathers, tertials, and rectrices, which occurred from 11 August to 15 October (N = 16; Fig. 1A). This sequence of molt was exemplified by series of adult Emperor Geese (*Chen canigula*; CAS 31159-31166, MVZ 60844-60845) and Brant (*Branta bernicula*; CAS 31168 and 31170-31176) from Nunivak Island, Alaska, collected in August and September 1927: specimens that were completing growth of the primaries (e.g., CAS 31159-60, MVZ 60844-45, and CAS 31170-31172) had just begun molt of the body feather tracts. The longest scapulars and rectrices were the last feathers replaced during this molt. The definitive prebasic molt of geese was complete or nearly so (Table 1), a small proportion of upper wing coverts, rectrices, and/or feathers of other tracts (Table 2) occasionally being retained.

Table 1. Variation in overall extent of body molts in North American geese (Anserinae) and ducks (Anatinae) according to traditional H-P terminology (traditional European terminology in parentheses). See Figure 1 for the seasonal timing of these molts. Extent of molt is quantified as mean percentage of feathers replaced from six body tracts (see Table 2), as determined for each molt from specimen examination (see text). Samples of Anatinae are separated into males (M) and females (F) due to sex-specific differences in molt and plumage strategies. Asterisks following male N-values represent sex-specific differences in extent (ANOVA; *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$).

		Molts											
		First prebasic (post-juvenile)			First prealternate (first pre-breeding)			Definitive prebasic (adult post-breeding)			Definitive prealternate (adult pre-breeding)		
Taxon	Sex	%	S.D.	N	%	S.D.	N	%	S.D.	N	%	S.D.	N
Anserinae		49	18	56				98	5	340			
Anatinae													
Anas	M	7	10	17	72	14	162***	33	20	99***	99	3	148
	F	12	4	9	59	25	128	54	28	54	100	1	90
Melanitta	M	0	0	19	47	14	29*	3	7	12	100	2	84
	F	0	0	13	38	11	29	1	3	11	100	0	65
Oxyura	M	30	20	20	0	0	10	100	0	35	50	10	42**
	F	32	16	22	0	0	7	100	0	25	40	14	32

First-cycle Molts in *Anas* and *Melanitta*

Among all Anatinae genera examined, apparent active molt during June through mid-August, involving the replacement of cryptic with cryptic feathering in males, was found solely in *Aix*, *Anas*, and *Aythya*. Determination of the timing and extent of this traditional "first prebasic" ("post-juvenile") molt, especially in females, was difficult due to apparent overlap with the traditional "first prealternate" ("first pre-breeding") body molt. Assuming that the acquisition of cryptic feathers in males was part of the first prebasic molt and that the brightly colored feathers were acquired during the first prealternate molt, as conventionally defined, the range of 19 specimens of *Anas* in active molt (with incoming feathers cryptic in males) was 7 July-22 August (Fig. 1B). Twenty-two other specimens of juvenile *Anas* collected during this time period did not show evidence of active molt, fully retaining small and rounded juvenile feathers. Likewise, no juvenile *Melanitta* collected in July to mid October (N = 32) were in active molt (Table 1, Fig. 1C). Juveniles (N = 77) of other genera (*Somateria*, *Clangula*, *Bucephala*, and *Mergus*) collected in July to mid-October, also showed no evidence of molt. In male *Anas*, the first prebasic molt was limited to 8-19% of the head, neck, upper back, breast, and sides (Table 2) and did not include any tertials or rectrices (see below).

The first prealternate molt of body feathers was variable in both timing and extent. In *Anas*, this molt occurred from 2 September to 16 November in most (eight) species (N = 38; Fig. 1B) but significantly later (ANOVA, $F_{1,63} = 83.8$, $P < 0.001$), 16 October to 18 January, in *A. discors*, *A. cyanoptera*, and *A. clypeata* (N = 26; see above). In *Melanitta*, the first prealternate molt occurred from 15 October to 31 March (N = 43; Fig. 1C). Replacement of juvenile tertials and rectrices occurred in late autumn, winter, or early spring, concurrent with the termination of the first prealternate molt, rather than with the first prebasic molt. Replacement of these feathers is thus considered part of the first prealternate molt.

The extent of the first prealternate molt in these two genera ranged from 38% of

Table 2. Variation in extent of body molts in geese (Anserinae) and male ducks (Anatinae) according to traditional H-P terminology (see Table 1). Extent of molt is quantified as the mean percentage of feathers replaced from each of six body tracts as defined by Billard and Humphrey (1972). No replacement (0%) was recorded during the traditional first prebasic (post-juvenile) molt of *Melanitta* or the traditional first prealternate (first pre-breeding) molt of *Oxyura* for any of the six tracts (Table 1).

		Head and neck		Upper back/breast		Scapulo-humerals		Mid-back and rump		Sides and flanks		Lower breast/belly	
Taxon/Molt	N	%	S.D.	%	S.D.	%	S.D.	%	S.D.	%	S.D.	%	S.D.
Anserinae													
First prebasic	156	81	26	67	32	66	28	11	9	63	27	10	9
Definitive prebasic	340	99	4	99	6	99	4	97	10	99	4	98	8
Anatinae													
Anas													
First prebasic	26	12	19	19	19	0	0	0	0	9	22	0	0
First prealternate	290	97	6	92	9	92	10	37	29	84	17	33	32
Definitive prebasic	153	46	29	52	31	43	33	11	13	40	23	5	8
Definitive prealternate	238	100	2	99	4	100	3	100	6	100	2	99	5
Melanitta													
First prealternate	58	73	22	66	25	66	18	6	6	68	21	0	0
Definitive prebasic	23	5	12	5	12	0	0	0	0	7	16	0	0
Definitive prealternate	149	100	1	99	4	100	0	99	5	100	2	99	4
Oxyura													
First prebasic	44	46	30	45	31	54	36	1	3	35	25	0	0
Definitive prebasic	60	100	0	100	0	100	0	100	0	100	0	100	0
Definitive prealternate	74	81	16	75	14	85	15	5	5	54	18	0	0

feathers in female *Melanitta* to 72% of feathers in male *Anas* (Table 1). In both genera, this molt was more extensive in males than in females (Table 1), and in males it included a greater proportion of head, neck, upper back, breast, and side feathers than belly, lower back, or rump feathers (Table 2). Replacement of at least one tertial occurred in 36% of *Anas* and 21% of *Melanitta*, and replacement of rectrices occurred in 89% of *Anas* (mean 9.1 ± 9.2 feathers of 16 total) and 66% of *Melanitta* (mean 6.5 ± 7.3 of 14 total). Because patterns of feather pigmentation were used to define this molt (see above) the proportions indicated in Tables 1 and 2 reflect the proportion of bright plumage encountered in first-alternate (first-winter) males of these genera. The timing and extent of the first prealternate molts of *Aix* and *Aythya* generally resembled those of *Anas*, being confined to autumn and early winter, whereas in other duck genera (*Somateria*, *Clangula*, *Bucephala*, and *Mergus*) they resembled those of *Melanitta*, being protracted through winter and early spring.

Definitive Molts in *Anas* and *Melanitta*

Replacement of body feathers during the traditional "definitive prebasic" ("adult postbreeding") molt was not complete in any individual of *Anas* and *Melanitta* (Tables 1 and 2). In *Anas* this partial body molt was highly sex-specific, occurring from 5 February to 19 April in females, and from 13 May to 1 July in males (Fig. 1B), and included a higher proportion of feathers in females than in males (Table 1). Among males, bright upperpart and breast feathers were replaced by cryptic feathers (Table 2), and females also replaced feathers predominantly among these tracts. Among both sexes of *Anas*, one or more tertials was replaced in 64% of birds, and one or more rectrices was replaced in 70% of birds (mean 6.8 ± 11.4 of 16 feathers).

This molt also showed a high degree of individual variation, especially among females (Table 1). For example, an adult female Gadwall (*Anas strepera*) collected at Los Banos, California, on 8 May 1908 (CAS 11997) had replaced 90% of its body feathers, five inner secondaries (including tertials) on each wing, all 16 rectrices, and all but the distal 20% of the greater, median, and lesser secondary coverts; whereas another adult female Gadwall collected at the same location on 10 August 1908 (CAS 12464) had replaced only 27% of its body feathers and no tertials, rectrices, or wing coverts. Other adult females in this series (CAS 11998, 12277, 12585, and 12464) had intermediate spring molt extents. The definitive prebasic body molts of *Aix* and *Somateria* generally resembled those of *Anas* in the timing and extent of each sex.

There was little evidence for a definitive prebasic body molt in *Melanitta* (Table 1). Of 29 specimens examined during or just prior to wing molt, only two adult Surf Scoters (*M. perspicillata*), a female (CAS 73173) collected 8 July and a male (MVZ 115902), collected 25 August, showed evidence of this molt, in each case having replaced feathers of the nape and a small proportion of feathers within tracts of the upper back, upper breast, sides, and flanks (Table 2). Other adult Surf Scoters collected in late July and August (e.g., MVZ 31654 and 135919) showed no evidence of this molt (all feathers of males being worn and bright), and neither did a series of first-summer White-winged Scoters (*M. fusca*) collected at Monterey Bay, California, on 29 August during wing molt (MVZ 18827-18831). In this series, the body tracts consisted of a mixture of very worn juvenal and moderately worn first-alternate (mean 44%) feathers (brightly colored in males), but no feathers that could be attributed to the traditional "second prebasic" ("first post-breeding") molt.

The wing molt of *Anas* occurred from 6 July to 4 September and that of *Melanitta* from 16 August to 23 September (Fig. 1B-C). The traditional "definitive prealternate" ("adult pre-breeding") body molts succeeded the wing molts, occurring from 26 August to 6 November in most *Anas* (N = 198; Fig. 1B); 7 October-4 February in *A. discors*, *A. cyanoptera*, and *A. clypeata* (N = 60; later than in other *Anas*, ANOVA $F_{1,237} = 95.7$, $P < 0.001$); and 29 September to 16 November in *Melanitta* (Fig. 1C). This body molt was essentially complete in both sexes and all species of both genera (Tables 1 and 2), and included the acquisition of bright plumage in males. Rectrices, and ornamental tertials and scapulars in *A. discors*, *A. cyanoptera*, and *A. clypeata*, were the last feathers to develop during this molt, as late as January or later on the winter grounds. All other genera of Anatinae, examined less critically, also appeared to have complete or near-complete definitive prealternate body molts.

Molts in *Oxyura*

The first prebasic (post-juvenile) molt of the Ruddy Duck (*Oxyura*) differed from those of *Anas* and *Melanitta* in occurring during the late autumn and winter, from 19 October to 18 February (N = 19; Fig. 1D), and in being more extensive, including 30-33% of the body feathering (Table 1). Critical examination of 71 first-year Ruddy Ducks collected between 13 July and 12 April indicated that most or all of the juvenile plumage was retained through the first winter and early spring in many birds. Some birds had begun a body-feather molt with feathers of the face being replaced as early as 27 October (CAS 73241), whereas others collected as late as 22 February (CAS 22028) remained in complete or near-complete juvenile feathering. In males, this molt was primarily confined to the head, neck, upper back, breast, and sides (Table 2). Feathers replaced during the earlier portions of this molt (October-December) were cryptic in coloration whereas those replaced during later portions of this molt (January-March) were intermediate in color between cryptic and bright feathering. No tertials or rectrices were replaced during this molt.

The body molt described above spanned the periods of the traditional "first prebasic" ("post-juvenile") and "first prealternate" ("first pre-breeding") molts, but appeared to involve only a single replacement of feathers. Thus, 17 first-year birds collected between 25 February and 12 April showed no evidence of a separate first prealternate molt (Table 1). Subsequently, a first-year male collected on 7 May (CAS 13877) and a first-year female collected on 21 May (CAS 12058) were undergoing wing molt concurrent with complete rectrix molt, and eight other specimens of both sexes collected between 11 May (CAS 66554) and 29 September (USNM 197847) had new wing feathers and were undergoing a complete body molt, or had plumage and wear patterns consistent with a recent complete wing and body molt in first-year birds. Five of six males in this group showed a variable proportion of rufous coloration to the tips of the upper-back and upper-breast feathers. Thus, a complete second prebasic (first post-breeding) molt appears to occur between April and August in the *Oxyura* (Fig. 1D).

The definitive prealternate (adult pre-breeding) molt in the *Oxyura*, as traditionally defined, occurred from 12 February to 18 May (N = 35; Fig. 1D), and was partial (Table 1), replacing cryptic with bright feathers in appropriate body areas of males (Table 2). Most (85%) birds had replaced most to all rectrices (mean 11.0 of 14 feathers) during the prealternate molt. The extent of the prealternate molt was significantly greater in males than in females (Table 1).

Thirteen adult Ruddy Ducks collected during the definitive prebasic (adult post-breeding) molt indicated that the wing molt occurred from 24 July to 9 September and that body molt occurred following the wing molt, from 17 September to 23 November (Fig. 1D). Eight males undergoing this molt were replacing worn bright feathering with fresh cryptic feathering. The prebasic body molt following the wing molt was complete in all 48 specimens examined (Table 1). Ten of 29 adult males in basic plumage showed bright rufous bases to some of the larger scapulars and/or feathers of the hind flanks.

DISCUSSION

Molt Timing, Extent, and Sequence

The timing of molts in all four waterfowl taxa and the extent of molts in geese and the Ruddy Duck (*Oxyura*) documented here, correspond closely to those reported in the literature (Humphrey and Clarke 1964; Palmer 1976; Cramp and Simmons 1977; Hohman *et al.* 1992). The apparent temporal shift in the second prebasic (first post-breeding) molt of Ruddy Ducks, from the second autumn to the first spring, may help explain the supposed "double-wing molt" in this species (see Jehl and Johnson 2004). The extent of both the traditional first prebasic (post-juvenile) and the traditional definitive prebasic (adult post-breeding) body molts in Anatine ducks, however, are considerably less extensive than previously reported.

The traditional "first prebasic molt" of Palmer (1976) does not appear to exist in most genera of Anatinae, and likewise may not exist in most or all species of *Anas*, *Aix*, or *Aythya*. Dwight (1914) concluded as much for scoters, but Palmer describes an extensive molt during this period. During protracted molts of several months or more, pigment deposition can vary as a function of hormonal change, irrespective of the timing of feather replacement (Schiøler 1921; Voitkevich 1966; Oring 1968; Cramp and Simmons 1977; see below). In young male ducks, feathers renewed earlier during the juvenile period (July-August) appear to be cryptic, whereas those renewed later (September-December) are brightly colored; yet all might be part of the same molt. Thus, clinal variation in pigment deposition within a single molt may have resulted in the conclusion that two molts occur when, in fact, each follicle may have been activated only once during a single protracted molt. Cryptic feathers have been noted among the brightly colored feathers of first-year male ducks throughout the winter and spring (Oring 1968; Palmer 1976; this study), and these could represent feathers replaced earlier during the traditional first prealternate molt, before hormonal changes controlling pigment saturation had occurred (see below). Alternatively, young ducks continue to develop in size throughout their first autumn (Weller 1957; Oring 1968) and feathers developed during the juvenile period may represent follicles that have matured and been activated for the first time as part of a protracted pre-juvenile molt, rather than consisting of a separate molt. In either case, the traditional first prebasic or post-juvenile molt appears to be absent in many individuals and species of Anatinae, and is rudimentary at best in others. Similar results were reported by others who critically examined this molt (Mendall 1958; Oring 1968; Bellrose and Holm 1994).

In *Anas*, *Melanitta*, and other Anatine genera the traditional "first prealternate" ("first pre-breeding") and "definitive prealternate" ("adult pre-breeding") molts closely resemble, respectively, the first prebasic (post-juvenile) and definitive prebasic (adult post-breeding) molts in Anserinae and the Ruddy Duck (Fig. 1, Tables 1 and 2). These two sets of molts show parallels in timing, extent by body region, and sequence, with replacement of body-feathers succeeding that of the wings, and the tertials, longer scapulars, and rectrices being among the last feathers replaced. The traditional definitive prealternate body molts in most ducks are essentially complete, as is typical of prebasic molts in geese, Ruddy Ducks, and other birds. By contrast, the traditional definitive prebasic body molts in ducks are highly variable both intra- and inter-specifically, apparently being absent in some individuals within most genera, and thus are more typical of prealternate molts in most birds. The molts of the Ruddy Duck differ from those of other ducks primarily (if not solely) in the sequence in which bright pigment-deposition occurs in males. Thus, apart from feather color, the traditional "definitive prealternate" ("adult pre-breeding") body molts of most Anatinae appear homologous with the definitive prebasic (adult post-breeding) body molts of the Ruddy Duck, and vice versa (Fig. 1).

Molt Cycles versus Color-deposition Cycles

Humphrey and Parkes (1959) regarded plumage brightness as a determinant factor in assigning plumage nomenclature in ducks; however, the mechanisms that control season-specific pigment deposition in feathers are complex and differ among various taxa of birds (Endler *et al.* 1988; Owens and Short 1995; Kimball and Ligon 1999). Seasonal variation in plumage brightness has been correlated with inter-related fluctuations in sex hormones, thyroid secretions, and pituitary gland activity, each of which is variably influenced by genetic control (Voitkevich 1966; Payne 1972). In Anatinae, the bright male plumage has been considered the "neutral" plumage state (Stresemann 1948), being masked by more cryptic feathering in females and summer males by elevated levels of estrogen irrespective of testosterone levels (Voitkevich 1966; Oring 1968; Greij 1973; Endler *et al.* 1988), a pattern that appears to be unique to Anseriformes and Galliformes among North American orders (Kimball and Ligon 1999). Thus, if feather pigmentation is to be considered in defining homologous plumages, the "neutral" (brightly pigmented) plumage of ducks might appropriately be considered the basic plumage. Alternatively, because feather-pigment deposition seems to be under the control of various factors including the sex hormones, it could be considered part of "seasonal, reproductive, developmental, or other phenomena" (Humphrey and Parkes 1959), and therefore should not be a critical factor in determining homologous molts and plumages (see also Howell *et al.* 2004). The repeated acquisition and loss of brightly pigmented male coloration among taxa of the "Mallard (*Anas platyrhynchos*) group" in North America and the Hawaiian Islands, perhaps as determined by no more than two gene pairs (Johnsgard 1961), might support this conclusion.

In the Ruddy Duck, 10 of 25 definitive-basic males showed rufous on the bases of some of the longer scapulars and feathers of the hind flanks. These are among the last feathers replaced during the prebasic molt in ducks (Billard and Humphrey 1972); thus, it appears that the hormonal changes resulting in bright rufous plumage in males were occurring as the prebasic molt was completing in November, accounting for the deposition of rufous pigment to the bases of these feathers. By contrast, five of six birds collected in second-basic plumage showed rufous-tipped feathers to the upper back and upper breast, areas of the body where molt commences, indicating that these birds had begun the second prebasic body-feather molt before hormonal changes producing rufous pigment deposition had subsided. The time period for attainment of bright rufous feathering in male Ruddy Ducks thus may begin as early as November, representing a deferred shift of only 1-2 months from these seasonal-specific pigment-deposition cycles in other Anatine ducks. Likewise, it appears that the second prebasic molt of body feathers can begin before this hormonal period subsides, perhaps as early as April or May, assuming that the wing molt can complete by this time. Variation in these patterns, as related to individual variation in both hormonal activity and molt timing, underscores: (1) that molt and pigment-deposition cycles are independent of each other (Voitkevich 1966); (2) the need to divorce pigment deposition patterns from factors used to determine molt homologies (Howell *et al.* 2004); and (3) that the prebasic molt of the Ruddy Duck correspond to the prealternate molts of Anatinae, with plumage differences explained primarily by a slight shift in the hormonal cycles that control pigment deposition.

Molt and Plumage Terminology in Anatinae

Under traditional European terminology, the "post-breeding" spring and summer body molts in adult ducks have been assumed to be complete and are linked with the ensuing wing molt (Cramp and Simmons 1977). In addition, this molt occurs before breeding in females of some ducks (Fig. 1), resulting in females breeding in "non-breeding" plumage. The nomenclature proposed by Humphrey and Parkes (1959) avoids this latter problem by divorcing molt and plumage terminology from that of the breeding cycle. However, based upon apparent homologies with the molts of Anserinae and the Ruddy Duck, it appears that the prebasic and prealternate molts of most Anatinae have been transposed under the conventional H-P system. By re-defining the molts and plumages of male Anatine ducks such that the body molt producing the bright male (and female) plumages in autumn is considered part of the prebasic molt rather than the prealternate molt, an apparent homology presents itself that was previously absent (Fig. 1).

Under such a re-interpretation, the putative "first prebasic" molt (Palmer 1976) of *Aix*, *Anas*, and *Aythya*, if it occurs, could be considered a presupplemental molt according to traditional H-P terminology (Thompson and Leu 1994), or an "auxiliary preformative" molt according to the modifications of Howell *et al.* (2003). If present, this first autumn molt could be a novel molt to replace the smaller and poorer-quality juvenal feathers of the face and throat (which may become abraded during feeding), and of the breast and flanks (perhaps to improve water repellency and flotation), rather than being a more extensive and protracted molt homologous to the traditional first prebasic molt of geese and the Ruddy Duck. Following Howell *et al.* (2003), the traditional "first prealternate" molt of Palmer (1976) should be considered the "preformative molt" in most Anatine ducks, homologous to the preformative (traditional first prebasic) molts of geese and Ruddy Ducks (Fig. 1). If only a single first-cycle molt occurs in Ruddy Duck, as suggested by this study, it could be considered the first prealternate molt according to the modifications of Howell *et al.* (2003).

It is possible, as experimental studies have suggested (Voitkevich 1966), that molting is a continuous process interrupted by inhibitors accompanying other energy-demanding processes such as breeding and migration and, thus, it cannot be categorized into evolutionarily meaningful units. It is also possible that, in response to environmental constraints, molts could shift, change in extent, and become "offset" (Palmer 1972). For example, relative to ancestral geese, the prebasic body molts of most Anatine ducks could have evolved to precede the wing molt, become much less complete, and become sexually divergent, while a novel, complete body-feather replacement following the wing molt has evolved and remained fairly static in both sexes and all genera of Anatinae. It seems considerably more likely, however, that prebasic molts have remained relatively static while the hormonal and other mechanisms for brightly pigmented plumage have evolved according to the constraints of breeding and courting regimes (Rohwer and Anderson 1983). Thus, the bright plumages of adult male ducks (other than Ruddy Duck) in late autumn and winter should be considered basic plumages, which are completely renewed annually as in other birds. The ephemeral and highly variable cryptic plumages found in spring and summer presumably have evolved more recently, primarily in those species benefiting from an ensuing camouflaged plumage, and thus should be considered the alternate plumages according to H-P terminology.

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