



REVISION OF MOLT AND PLUMAGE TERMINOLOGY IN PTARMIGAN (PHASIANIDAE: *LAGOPUS* SPP.) BASED ON EVOLUTIONARY CONSIDERATIONS

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ABSTRACT.—By examining specimens of ptarmigan (Phasianidae: *Lagopus* spp.), I quantified three discrete periods of molt and three plumages for each sex, confirming the presence of a definitive presupplemental molt. A spring contour molt was significantly later and more extensive in females than in males, a summer contour molt was significantly earlier and more extensive in males than in females, and complete summer–fall wing and contour molts were statistically similar in timing between the sexes. Completeness of feather replacement, similarities between the sexes, and comparison of molts with those of related taxa indicate that the white winter plumage of ptarmigan should be considered the basic plumage, with shifts in hormonal and endocrinological cycles explaining differences in plumage coloration compared with those of other phasianids. Assignment of prealternate and pre-supplemental molts in ptarmigan necessitates the examination of molt evolution in Galloanseres. Using comparisons with Anserinae and Anatinae, I considered a novel interpretation: that molts in ptarmigan have evolved separately within each sex, and that the presupplemental and prealternate molts show sex-specific sequences within the definitive molt cycle. *Received 13 June 2005, accepted 7 April 2006.*

Key words: evolution, *Lagopus*, molt, nomenclature, plumage, ptarmigan.

Revisión de la Terminología de la Muda y el Plumaje en *Lagopus* spp. (Phasianidae) con Base en Consideraciones Evolutivas

RESUMEN.—Examinando especímenes de *Lagopus* spp. (Phasianidae), cuantifiqué tres períodos discretos de muda y tres plumajes para cada sexo, confirmando la presencia de una muda presuplementaria definitiva. Una muda de contorno de primavera ocurrió significativamente más tarde y de forma más extensa en las hembras que en los machos, una muda de verano de contorno ocurrió significativamente más temprano y más extensamente en los machos que en las hembras, y las mudas de alas y contorno completas de verano-otoño fueron estadísticamente similares entre sexos. El reemplazo completo de las plumas, las similitudes entre sexos y la comparación de los patrones de muda con aquellos de taxones relacionados, indican que el plumaje blanco de invierno de *Lagopus* spp. debe ser considerado el plumaje básico. Los cambios en los ciclos hormonales y endocrinológicos explicarían las diferencias en la coloración del plumaje con relación a otros fasianidos. La asignación de mudas prealternas y presuplementarias en *Lagopus* spp. requiere de un mayor conocimiento sobre la evolución de la muda en Galloanseres. Mediante comparaciones con Anserinae y Anatinae, desarrollé una nueva interpretación: las mudas en *Lagopus* spp. han evolucionado separadamente en cada sexo, y las mudas presuplementarias y prealternas presentan secuencias específicas para cada sexo en el ciclo de muda definitiva.

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DEFINITIVE SUPPLEMENTAL PLUMAGES, defined by Humphrey and Parkes (1959) as plumages produced by a third feather replacement within a single definitive molt cycle, have been reported in few species of birds. It is often difficult to distinguish true presupplemental molts from suspended or protracted prealternate or prebasic molts, during which each feather follicle is activated twice, at most, within a cycle (Stresemann 1948). When a protracted or suspended molt overlaps with shifts in color-deposition cycles, feathers can alter their coloration or pattern during the course of a single molt (Voitkevich 1966, Pyle 2005), leading to a false interpretation that an extra (presupplemental) molt has occurred. Such interactions between protracted prealternate or prebasic molts and color-deposition cycles, along with individual and age-specific variation in the timing of these events, appear to explain the putative definitive presupplemental molt of the Long-tailed Duck (*Clangula hyemalis*; Salomonsen 1941, Stresemann 1948, Pyle 2005) and provide an untested explanation for definitive presupplemental molts proposed for shorebirds (e.g., Jukema and Piersma 1987, Piersma and Jukema 1993).

Ptarmigan (*Lagopus* spp.) have long been assumed to have three body molts per year: a "spring molt" into a display plumage in February–June, a "summer molt" into a cryptic fall plumage in July–September, and a "fall molt" into a white winter plumage in September–November (Dwight 1900, Salomonsen 1939). Replacement of the wing and tail feathers spans the period between the summer and fall molts. Although molts in ptarmigan have attracted substantial attention in relation to protective-coloration theory and mechanisms of plumage deposition (Höst 1942, Watson 1973, Stokkan 1979, Höhn and Braun 1980), the extents of each molt have not been quantified, and the existence of a third molt (as opposed to a protracted or suspended second molt) has not been fully documented. Furthermore, the application of Humphrey and Parkes's (1959; hereafter "H-P") terminology to these molts and ensuing plumages has not been consistent. In recent summaries of the three species in North America, for example, the fall body molt into the white winter plumage has been variously termed the "presupplemental molt" (Braun et al. 1993), the "prealternate molt" (Holder and Montgomerie 1993), and the "prebasic molt" (Hannon et al. 1998).

Humphrey and Parkes (1959) devised their molt and plumage terminology to reflect evolutionary homologies; however, few studies considering H-P nomenclature have attempted to trace the evolution of the molts in question. Most studies have focused on the end products rather than the derivation of molts. Through specimen examination, I quantified the timing and extents of definitive body molts in North American ptarmigan. Here, I propose revisions to H-P terminology for molts and plumages that consider the evolution of molt strategies in taxa ancestral to *Lagopus*.

METHODS

I examined 423 specimens of Willow (*L. lagopus*), Rock (*L. muta*), and White-tailed (*L. leucura*) ptarmigan, 288 specimens of Dusky (*Dendragapus obscurus*) and Sooty (*D. fuliginosus*) grouse, and 98 specimens of Greater Sage-Grouse (*Centrocercus urophasianus*) collected in North America (see Acknowledgments for collections). The species of grouse were selected on the basis of sufficient specimen samples and varying molt strategies: Dusky and Sooty grouse have only a single basic plumage per cycle, and Greater Sage-Grouse have both basic and alternate plumages, at least in males (Dwight 1900, Patterson 1952, Bendell 1955, present study). For each specimen, I assigned (1) sex and age of the bird when collected, based on information on the specimen label, characteristics of the two outer primaries, and coloration of nonwhite plumages (Dwight 1900, Salomonsen 1939, Petrides 1945); (2) whether or not active molt of body feathers and primaries had been occurring when collected; and (3) the proportion of each body-feather generation present, reflecting the extents of previous molts. I excluded specimens with incomplete data, as well as hatching-year individuals collected during the first summer or fall, before completion of the first-fall molt into the white first-winter plumage.

On each specimen, the contour feathers were lifted and examined for the presence of pin or developing feathers, which indicate active molt (Pyle 2005). Temporal ranges (95% confidence intervals [CI]) for body-feather and primary molts were calculated on the basis of Julian dates from specimens collected in active body and primary molts, respectively. For specimens not showing active feather replacement at the

time of collection, as well as those that had just begun active molt (having replaced <10% of feathers), the proportion of the overall body plumage acquired during the previous molt was estimated through the critical examination of body feathers for contrasts in wear and coloration. The assumption was not made, however, that feather color equated to feather generation (cf. Jacobsen et al. 1983); rather, generations were assessed on the basis of a careful evaluation of wear (Pyle 2005).

RESULTS

No species-specific differences were found in the timing of contour-feather or primary molt when sexes were analyzed separately (analysis of variance [ANOVA], $P > 0.33$), and only one significant species-specific difference was found in extent: the spring body molt in males was more extensive in 21 Willow Ptarmigan (mean \pm SE = $31.2 \pm 13.0\%$ of all body feathers) than in 22 Rock Ptarmigan ($9.6 \pm 8.9\%$; ANOVA; $F = 40.6$, $df = 1$, $P = 0.002$). However, because these molts were similar in timing and overlapped in extent, they are assumed to be homologous, and all data from the three species have been pooled for the present study.

Analysis of collection dates for actively molting ptarmigan indicated three discrete periods of molt and three discrete plumages for each sex, corresponding to the spring, summer, and fall molts and summer, fall, and winter plumages described in the literature (Table 1 and Fig. 1). Furthermore, comparison of feather generations confirmed that a proportion of feathers had been replaced three times during the definitive molt cycle. The proportion of spring feathers remaining in fall plumage ($74.5 \pm 9.0\%$

in 11 females and $6.7 \pm 4.6\%$ in 47 males), for example, was significantly less than the proportion of these feathers in summer plumage ($90.1 \pm 9.5\%$ in 27 females and $18.6 \pm 13.1\%$ in 28 males; ANOVA: $F = 4.67$, $df = 1$, $P = 0.001$ in females and $F = 5.89$, $P < 0.001$ in males). This indicates replacement of at least some feathers during both the spring and summer molts, with the fall molts (including 100% of body feathers in each sex; Table 1) representing a third replacement within the molt cycle.

The spring contour molt of females was significantly later and more extensive than that of males, and the summer contour molt was significantly earlier and more extensive in males than in females (Table 1). Although the fall contour molt also averaged slightly later in females than in males, both the timing and the extent of this molt were statistically similar in both sexes (Table 1). The sex-specific date ranges for primary molt were also statistically similar among 80 females (13 June–29 September) and 130 males (3 June–1 October; ANOVA, $F = 2.60$, $df = 1$, $P = 0.265$).

Timing and extent of molts in Dusky and Sooty grouse and Greater Sage-Grouse are shown in Figure 1. Analysis based on 164 specimens of adult Dusky and Sooty grouse revealed that molt of primaries occurred from 31 May to 3 October ($n = 56$) and that only one complete body-feather molt occurred, from 7 August to 22 October ($n = 50$). The timing of primary molt was similar to that recorded for ptarmigan (ANOVA, $F = 0.40$, $df = 1$, $P = 0.526$) and, among the three molts in ptarmigan, the body molt was most similar in timing to that of the fall molt ($F = 0.03$, $df = 1$, $P = 0.864$).

Specimen examination revealed that Greater Sage-Grouse males had a limited molt (mean

TABLE 1. Timing and extent of molts in female and male ptarmigan.

	Spring molt		Summer molt		Fall molt	
	Date range ^a	Extent (%) ^b	Date range ^a	Extent (%) ^b	Date range ^a	Extent (%) ^b
Females	22 Apr–9 Jun <i>n</i> = 15	90 \pm 10.1 <i>n</i> = 46	3 Jul–1 Aug <i>n</i> = 10	13 \pm 5.9 <i>n</i> = 20	11 Aug–3 Nov <i>n</i> = 31	100 \pm 0.0 <i>n</i> = 75
Males	6 Apr–19 May <i>n</i> = 17	20 \pm 15.4 <i>n</i> = 44	24 May–15 Jul <i>n</i> = 47	77 \pm 10.7 <i>n</i> = 66	5 Aug–31 Oct <i>n</i> = 52	100 \pm 0.0 <i>n</i> = 81
Difference (<i>P</i>) ^c	0.002	0.000	0.000	0.000	0.624	1.000

^a Date ranges represent 95% confidence intervals based on Julian dates of birds actively molting when collected.

^b Extent represents proportion of body feathers replaced (\pm SD) on birds that had completed the molt in question.

^c Statistical difference (*P* value) between the sexes (ANOVA).

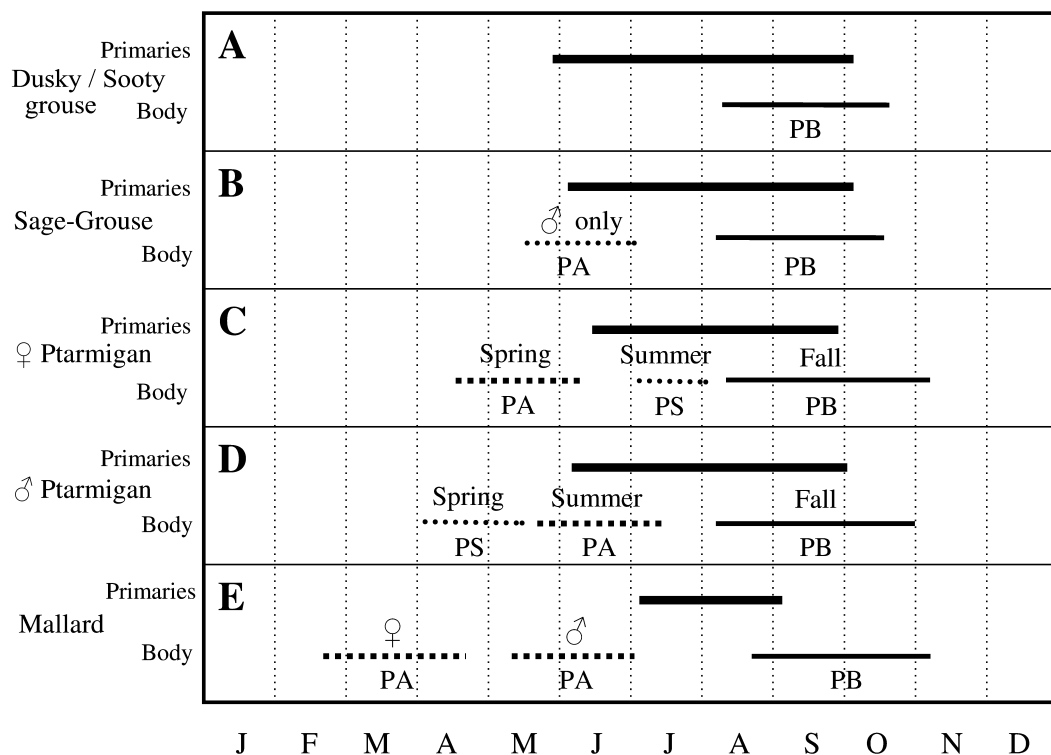


FIG. 1. Timing and extent of molts in ptarmigan and related taxa. Wing molt (as defined by primary replacement) is indicated by thick solid lines, complete body-feather molts are indicated by thin solid lines, partial (>50%) body molts are indicated by dashed lines, and limited (<50%) body molts are indicated by dotted lines. For ptarmigan, traditional contour-molt terminology is indicated above the lines, and one proposed terminology (based on comparison with related taxa) is indicated below the lines. See text for alternative nomenclatures regarding the prealternate and presupplemental molts.

14%; $n = 9$) of head and throat feathers that occurred from 16 May to 1 July ($n = 12$), separate from the more complete fall body molt. The limited molt was most similar in timing to the summer molt of male ptarmigan ($F = 2.02$, $P = 0.160$), but it was significantly less extensive ($F = 164.1$, $P < 0.001$). The black throat and white breast feathers of males were replaced by brown feathers, resulting in protective coloration during the period of flight-feather molt. No additional body molts were detected in females, but the small sample size of females collected in February–June ($n = 3$), when additional molts might be expected, may have precluded detection. Molt of primaries in Greater Sage-Grouse (sexes combined) occurred from 3 June to 3 October ($n = 33$), and a complete molt of body feathers occurred from 6 July to 16 October ($n =$

22). Again, the timing of primary molt was similar to that recorded for ptarmigan (ANOVA, $F = 0.19$, $df = 1$, $P = 0.661$), and the complete body molt was most similar in timing to that of the fall molt of ptarmigan ($F = 0.95$, $df = 1$, $P = 0.330$).

DISCUSSION

Quantification of specimen data reported here supports the detailed treatises on the sequences of molts presented by Dwight (1900) and Salomonsen (1939) and confirms that a definitive presupplemental molt occurs in ptarmigan. Abundance of nutritional resources during summer and fall in Arctic and alpine regions has presumably enabled the evolution of two inserted molts in ptarmigan, not afforded other species with energetic constraints related

to migration or reduced resource allocation in temperate or tropical areas (Murphy and King 1991). The extra molts are presumably adaptations to mate-selection strategies and predation pressure (Salomonsen 1939, Braun et al. 1993), with the spring molt of females and the summer molt of males providing protective coloration for nesting (female) and wing molt (both sexes). I found no evidence for a fourth molt per cycle in male ptarmigan, as reported by Johnsen (1929), and suspect that it can be explained by the protracted summer molt of males combined with shifts in pigment-deposition cycles (Salomonsen 1939).

On the basis of plumage coloration, both Dwight (1900) and Salomonsen (1939) considered the fall molt of ptarmigan into white winter plumage to be an inserted molt compared to those of other species of Phasianidae; thus, those authors considered the summer body molt combined with the wing molt to constitute the "complete annual molt." Results of the present study, however, indicate that the summer molt is variable and incomplete (especially in females) and, therefore, should not be considered part of the complete prebasic molt as defined by Humphrey and Parkes (1959). Rather, completeness of feather replacement, similarities between the sexes in timing and extent, and comparison with molts of grouse (Fig. 1) indicate that the fall molt should be aligned with the wing molt to constitute the prebasic molt, as described for Willow Ptarmigan by Hannon et al. (1998). Thus, the white winter plumage should be considered the basic plumage in ptarmigan, with shifts in hormonal and endocrinological cycles explaining the difference in plumage color pattern compared with other species of Phasianidae (cf. Voitkevich 1966, Pyle 2005).

Humphrey and Parkes (1959) did not provide specific methods for defining presupplemental versus prealternate molts in ptarmigan and other taxa supposed to undergo three molts per definitive cycle, but they stated that the designation of the supplemental plumage would "depend on the functional basis for the evolution of such an additional plumage." Thus, the first inserted molt to evolve along the ancestral lineage of ptarmigan should be considered the prealternate molt, and the second inserted molt should be considered the presupplemental molt. Extent should not necessarily be a factor

in defining these molts, and a presupplemental molt could either precede or follow a prealternate molt within a definitive molt cycle.

It is extremely difficult to trace the evolution of molts in birds (Jenni and Winkler 2004); however, broad patterns of molting can be recognized across taxa, and the presumption of homology is a useful starting point for investigating the evolution of molts (Howell et al. 2003, 2004). Galliformes and Anseriformes have recently been considered sister taxa, grouped into a single clade (Galloanseres), which may represent a basal group to all remaining birds (Cracraft 2001); thus, the molts of phasianids and ptarmigan have evolved from those of the ancestral taxa of this clade. In comparison with ancestral species of Anseriformes (Anserinae), Pyle (2005) proposed that the molt terminology of ducks (Anatinae) be revised such that the complete body molt in fall is considered part of the prebasic molt and the partial body molts in spring (females) and summer (males) be considered prealternate molts. Under this interpretation, the prealternate molts in ducks have been added to the basic molt cycle of Anserinae to provide protective coloration for females during nesting and for both sexes during synchronous wing molt.

In ptarmigan, the spring molt of females and the summer molt of males are comparable, in terms of timing, extent, and function, to the prealternate molts of Greater Sage-Grouse and Mallard (*Anas platyrhynchos*) (Fig. 1). It is possible that the inserted spring and summer molts have been derived in both sexes simultaneously in ancestral Galloanseres or ptarmigan and that they have been subject to regression or accretion based on sex-specific pressures. In this case, it is not possible, given current information, to determine which molt evolved first and, thus, which of the spring or summer molts of ptarmigan would be considered prealternate. Such an interpretation might also result in either male or female Anatinae currently having a presupplemental but not a prealternate molt, a possibility if molts have been suppressed entirely within each sex of ducks.

Alternatively, if molts in ptarmigan have evolved directly from those of Anatinae (or a common ancestor), and no other inserted molts have been suppressed in Galloanseres, the spring molt of females and the summer molt of males would be considered prealternate molts and the more limited spring molt of males and summer

molt of females would be considered presupplemental molts (Fig. 1), despite a sex-specific difference in sequence. Under this interpretation, the presupplemental and prealternate molts would not be considered homologous across sexes, given their independent derivation.

It is conceivable that the limited spring (presupplemental) molt of males, which varies both among and within species (Salomonsen 1939, Montgomerie et al. 2001, present study), has evolved more recently to advertise male fitness in taxa that otherwise (compared with Anatidae) cannot afford to molt out of the protective basic plumage until spring. A similar inserted molt appears to have evolved in male (but not female) Ruffs (*Philomachus pugnax*; Jukema and Piersma 2000). Furthermore, castrated male ptarmigan omit this molt and plumage, which suggests that it is a secondary sexual character (Stokkan 1979) and provides potential evidence for its evolution in males but not females. The evolution of the limited and ephemeral summer molt of females would be harder to explain under this scenario but may also relate to the enhancement of protective coloration as summer progresses (Salomonsen 1939). Further research on molts in ancestral and extant Galloanseres, especially on interactions between sex-specific processes and molt derivation, may allow us to trace evolutionary homologies in ptarmigan, in a manner intended by Humphrey and Parkes (1959) when they proposed their molt and plumage nomenclature.

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