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MOLT CHRONOLOGY OF AMERICAN COOTS IN WINTER[1]

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Abstract. We examined molt chronology of American Coots (*Fulica americana*) wintering in Alabama. Molt intensity was quantified by converting percentages of developing feathers sampled in 10 feather regions to molt scores (Total Molt Score) and by estimating percentage of total feather mass undergoing molt (%MOLT). Percent occurrence of molting birds was greatest in December (95%) and lowest in January (28%). Molt intensity was higher during October–December than in January and February, with lowest molt intensity occurring in January. This pattern was consistent between Total Molt Score and %MOLT, however, the magnitude of values for Total Molt Score was twice that for %MOLT. We assert that %MOLT provides a more biologically meaningful assessment of molt. Low molt intensity coupled with adequate protein and energy content of the diet resulted in minimal additional nutrient demands due to molt for wintering coots at Guntersville Reservoir.

Key words: American Coot, Fulica americana, *molt, nutrition, winter.*

Periodic replacement of feathers is essential to the protection, thermoregulation, locomotion, and communication functions of avian plumage. Because molt is nutritionally costly (Murphy 1996), its timing in the annual cycle has important ecological implications. For many species, the timing of molt represents a tradeoff between the need to replace worn or inappropriate plumage and allocation of nutrients to other important events in the annual cycle (Moore et al. 1982). For example, Darwin's finches typically molt on a regular cycle, but suspend molt to nest when food availability increases (Grant 1986). For Northern Pintails (*Anas acuta*) and Mallards (*A. platyrhynchos*), molt is delayed in winters of poor habitat conditions and/or low food availability (Miller 1986, Heitmeyer 1987). Clearly, knowledge of the timing and intensity of molt is critical for a complete understanding of nutritional requirements throughout the annual cycle.

American Coots (*Fulica americana*) breed throughout much of the northern U.S. and southern Canada, and winter in large numbers across the southern U.S., Mexico, and Central America (Alisauskas and Arnold 1994). Despite their abundance and ubiquitous distribution, chronology of molt for this species is poorly documented. In a study of captive coots, Gullion (1953) reported one complete wing molt per year occurring in late summer, but did not present data for molt of body plumage. Although wing molt is complete in free-living coots before fall migration, molt in some body regions still is occurring when these birds

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leave northern breeding areas (C. D. Ankney and T. W. Arnold, unpubl. data). However, data concerning the intensity and chronology of molt in coots during fall and winter are unavailable. In this study, we examined coots during late fall and winter at a reservoir in northern Alabama to determine intensity and chronology of molt during the nonbreeding season.

METHODS

We collected coots by shooting from October 1992 through February 1993 at Guntersville Reservoir, a 275-km^2 impoundment of the Tennessee River in Jackson and Marshall Counties, Alabama, and Marion County, Tennessee. Sex was determined internally in the field. In the laboratory, we assessed molt using a grab sample method described by Titman et al. (1990), whereby three grabs (1–2 cm^2) were taken from each of 10 feather groups following Miller (1986): (1) head, (2) neck, (3) back, (4) scapular, (5) rump, (6) breast, (7) side, (8) belly, (9) tertials, and (10) tail. Wing, undertail coverts, and leg feathers were not sampled. We defined pinfeathers as contour feathers with a vascularized calamus or visible feather sheath at or above the skin surface. We recorded total number of contour feathers and number of pinfeathers in each sample, and calculated the percentage of pinfeathers within each feather group.

We quantified overall intensity of molt in two ways. First, we assigned each feather group a score of 0–10: 0–1% pinfeathers = 0, 1.1–10% = 1, 10.1–20% = 2, . . . , 90.1–100% = 10. We then calculated a Total Molt Score (range = 0–100) for each bird by summing molt scores from all 10 regions (Miller 1986). To obtain a more nutritionally meaningful measure of molt intensity, we estimated the percentage of total plumage mass undergoing molt (%MOLT). We determined dry mass of plumage in non-molting coots (n = 2; 1 male, 1 female) by plucking and drying to constant mass (60°C) all contour feathers. We then calculated mean percentage dry mass of feathers in each feather group (PTOT), and calculated %MOLT using the formula:

$$\%\mathrm{MOLT} = \sum_{r=1}^{n} (\mathrm{PTOT}_r \cdot \mathrm{PIN}_r)$$

where PTOT_r = proportion of total feather mass in feather group r, and PIN_r = proportion of pinfeathers in feather group r.

We used Chi-square analysis (SAS 1988) to test for differences in percent occurrence of molting birds among months. Because PIN, Total Molt Score, and %MOLT were not normally distributed after arcsine transformation (Shapiro-Wilk W; $P < 0.001$), we performed analyses for these variables on ranked data. We tested for the effects of sex, month, and their interaction on PIN within each region, and on Total Molt Score and %MOLT, using analysis of variance (ANOVA) and Tukey-Kramer mean separation.

RESULTS

Mean dry plumage mass of non-molting coots was 30.74 g (Table 1). Frequency of occurrence of molting birds varied by month (female: $\chi^2_4 = 35.7$, $P < 0.001$; male: $\chi^2_4 = 22.3$, $P < 0.001$; sexes combined: $\chi^2_4 = 57.6$, $P < 0.001$). For both sexes, the highest frequency of molt occurred in December (> 95%), and the lowest occurred in January (< 34%; Table 2). Total Molt Score and %MOLT varied by month (Total Molt Score: $F_{4,193} = 33.4$, $P < 0.001$; %MOLT: $F_{4,193} = 27.4$, $P < 0.001$), but not by sex (Total Molt Score: $F_{1,193} = 0.0$, $P = 0.97$; %MOLT: $F_{1,193} = 0.01$, $P = 0.90$) or month x sex (Total Molt Score: $F_{4,193} = 0.5$, $P = 0.76$; %MOLT: $F_{4,193} = 0.8$, $P = 0.53$). Monthly variation in molt intensity was similar for Total Molt Score and %MOLT. Molt intensity peaked in December and declined to its lowest level in January (Table 2). Percentage of pinfeathers (PIN) varied among months ($P < 0.05$) for all feather groups except tail and tertial (Fig. 1), but did not vary ($P > 0.05$) by sex or month x sex in any feather group. Highest values of PIN generally occurred from October–December for most feather groups (Fig. 1).

TABLE 1. Mean (± SE) dry mass (g) and percentage of feather mass of various feather groups of non-molting American Coots (1 male, 1 female) at Guntersville Reservoir, Alabama.

Feather Group	Dry mass	(%)
Head	0.42 ± 0.01	(1.4)
Neck	2.47 ± 0.21	(8.3)
Back	3.02 ± 0.04	(10.0)
Rump	1.32 ± 0.18	(4.3)
Side	1.97 ± 0.17	(6.4)
Scapular	1.58 ± 0.48	(5.0)
Breast	6.40 ± 0.57	(20.9)
Belly	4.03 ± 0.85	(12.9)
Tail	0.23 ± 0.07	(0.7)
Tertial	0.42 ± 0.08	(1.4)
Leg	1.45 ± 0.45	(4.6)
Wing[a]	7.46 ± 1.17	(24.2)
Total	30.74 ± 3.82	(100.0)

[a] Primaries, secondaries, primary and secondary coverts, tertial coverts, wing lining, and axillaries.

DISCUSSION

Coots wintering at Guntersville Reservoir, Alabama, molted a portion of their contour feathers throughout fall and winter. Because many coots do not complete molt before leaving northern breeding areas (T. Arnold, pers. comm.), molting feathers in fall and winter in the present study likely represent extension of the prebasic molt. It is not known whether increased molt in February reflects onset of prealternate molt, as in some dabbling duck species (Paulus 1984, Heitmeyer 1987), extended prebasic molt, or individual replacement of worn feathers, because plumages in coots are poorly understood. According to Oberholser (1974), coots undergo complete prebasic molt after breeding, and a partial prealternate molt prior to breeding. This conflicts with Gullion's (1953) assertion that coots undergo one complete molt per year. Results of the present study clearly demonstrate that molt in coots is not confined to the period surrounding the breeding season. However, additional study is needed for better understanding of the specific nature of molts in coots throughout the annual cycle.

TABLE 2. Percent occurrence of molting birds, mean percentage (%) of feather mass undergoing molt (% Molt), and Total Molt Score of American Coots wintering at Guntersville Reservoir, Alabama, October 1992–February 1993.

	Female[a]				Male[a]				Sexes Combined[b]			
Month	% Occurrence	% Molt	Total Molt Score	n	% Occurrence	% Molt	Total Molt Score	n	% Occurrence	% Molt	Total Molt Score	n
October	73.3	1.8 ± 0.5	4.4 ± 1.0	15	63.6	1.0 ± 0.5	2.9 ± 1.2	11	69.2	1.5 ± 0.4bc	3.8 ± 0.8bc	26
November	88.9	2.9 ± 0.8	6.3 ± 1.1	27	94.1	3.1 ± 0.9	6.4 ± 1.3	17	90.9	3.0 ± 0.6ab	6.3 ± 0.8ab	44
December	95.0	3.3 ± 0.5	7.5 ± 1.1	20	95.2	3.4 ± 0.7	7.9 ± 1.3	21	95.1	3.3 ± 0.5a	7.7 ± 0.8a	41
January	25.0	0.2 ± 0.1	0.3 ± 0.1	28	33.3	0.4 ± 0.4	0.9 ± 0.7	15	27.9	0.2 ± 0.1d	0.5 ± 0.2d	43
February	65.4	0.7 ± 0.2	2.0 ± 0.7	26	60.9	0.8 ± 0.3	2.3 ± 0.7	23	63.3	0.7 ± 0.2c	2.1 ± 0.5c	49

[a] Statistical analysis within sex not conducted because sexes did not differ ($P > 0.05$).
[b] Means with different letters significantly different ($P < 0.05$; Tukey-Kramer multiple comparison).

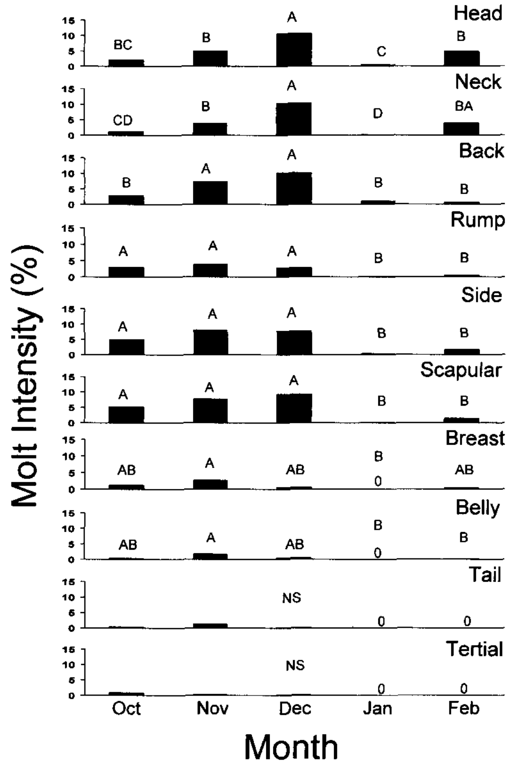

FIGURE 1. Mean percentage of molting feathers (PIN; pinfeathers/total feathers) within 10 feather groups of American Coots collected from October 1992–February 1993 at Guntersville Reservoir, Alabama. Means within feather groups with different letters differ significantly ($P < 0.05$; Tukey-Kramer multiple comparisons).

WINTER MOLT CHRONOLOGY

Timing of molt in birds varies between taxa, and is related to ecological factors such as the timing of other important annual-cycle events (Mewaldt and King 1978). Similar to coots in the present study, fall/winter molt intensity was lowest in January for male Mallards in Missouri (Combs and Fredrickson 1995), Gadwalls (*Anas strepera*) in Louisiana (Paulus 1984), Northern Pintails (*Anas acuta*) in California (Miller 1984), and Greater Scaups (*Aythya marilandica*) in Quebec (Billard and Humphrey 1972). Early completion of prealternate molt in male Gadwalls, Black Ducks (*Anas rubripes*), and American Wigeons (*Anas americana*) is thought to be associated with early pairing in these species (Paulus 1983, Hepp and Hair 1984, Wishart 1985). If early pairing results in improved access to food (Paulus 1983, Hepp and Hair 1984), then there may be selection for attaining prealternate plumage as early as possible for males of species that pair in fall and early winter.

However, species such as coots, Northern Pintails, and Greater Scaups, which do not pair until late winter or spring (Alisauskas and Arnold 1994, Baldassarre and Bolen 1994), also exhibit a similar pattern of reduced molt intensity during mid winter. For these birds, suspension or completion of molt prior to January probably is associated with reduced ambient temperatures and food availability typically experienced in mid winter. Molting during the coldest time of the year may be maladaptive because the insulatory capacity of plumage is positively related to its thickness (Calder and King 1974). Also, coots and many ducks experience low food availability and lowest lipid reserves during mid winter (Baldassarre and Bolen 1994, McKnight 1998). Reduction of molt intensity at this time may function to minimize overlap of nutritionally demanding events (King 1974).

MOLT INTENSITY AMONG FEATHER GROUPS

Molt was most intense in the head, neck, back, side, and scapular regions, whereas tail and tertial molt was relatively light (< 5%) or absent throughout fall and winter (Fig. 1). This may be expected for migratory species which undergo wing and tail molt immediately following the breeding season (Gullion 1953), because flight feathers must be fully grown (or nearly so) for efficient flight during fall migration. Molt also was consistently light in breast and belly feathers throughout fall and winter. Because coots spend much of their time in water (Alisauskas and Arnold 1994, McKnight and Hepp 1998), selection may be particularly strong for maximizing insulation during winter in body regions, such as the breast and belly, that are in constant contact with the water (de Vries and van Eerden 1995).

NUTRITIONAL COSTS OF MOLT

Although temporal variation in Total Molt Score and %MOLT was similar, values for Total Molt Score were twice as large as those for %MOLT. These differences may have important effects on nutritional interpretation of molt intensity. For example, the Total Molt Score value in December corresponds to roughly 8% molt. However, when expressed as percentage of total feather mass undergoing molt (%MOLT), the value falls to 3%. The disparity exists for two reasons. First, wing (excluding tertials) and leg feathers account for 24 and 5% of total feather mass, respectively, and were not sampled in the present study. Hence, the maximum Total Molt Score value of 100 does not include a substantial portion of total feather mass. Second, dry mass of feathers varied among regions. For example, back feathers comprised 10% of total feather mass, whereas head feathers constituted < 2%. If each of these regions contained 50% pinfeathers (therefore, identical Total Molt Scores), then molting back feathers would account for 5% of total feather mass, whereas pinfeathers in the head region would account for < 1%. Hence, expressing molt intensity as a percentage of total feather mass (%MOLT) resulted in a pattern of temporal variation identical to Total Molt Score, but yielded a more biologically relevant value which potentially allows for better estimation of nutrient costs.

Compared to other nutrient-intensive events such as egg formation, wing molt, and migration, 3.3% molt in December appears small. However, increased nutrient requirements are not the only costs associated with molt. Thermal conductance increases during molt due to disruption of plumage insulation, and increased evaporative heat loss through engorged blood quills and increases in body water turnover (Murphy 1996). Reduced plumage thickness may result in increased thermoregulatory costs (Blackmore 1969), especially for birds molting head feathers, because a disproportionate amount of heat is lost through the head (Calder and King 1974). This may be particularly important to aquatic birds, such as coots, that submerse the head in cold water while diving (de Vries and van Eerden 1995). Although, there is little evidence of significant heat loss due to thermoregulatory inefficiency during molt (Murphy 1996), it is important to note that birds in these studies were not exposed to cold temperatures or immersion.

Replacing feathers during fall and winter could have important nutritional implications, depending on food quality and availability (Miller 1986). Evaluation of the nutritional significance of molt depends on the interaction between nutrient requirements and intake. Using the equation for basal metabolic rate (BMR) from Prince (1979; BMR = $87 \cdot \text{body mass}^{0.734}$), and adjustments for activity and thermoregulation (Prince 1979, S. K. McKnight, unpubl. data), daily energy expenditure (DEE) of coots in December was estimated at 141.7 kcal day^{-1}. Digestible energy in the diet in December was 2.4 kcal g^{-1} (S. K. McKnight, unpubl. data). Dividing 141.7 kcal day^{-1} by 2.4 kcal g^{-1} yields 59.0 g of food day^{-1} needed to satisfy energy requirements. This is similar to 52.2 g day^{-1} estimated for wintering Eurasian Coots (*Fulica atra*) consuming submersed vegetation (*Ruppia cirrhosa*) in the Camargue, France (Verhoeven 1980). Assuming a cost of 29.9 kcal g^{-1} of growing feathers (estimated for Northern Shovelers [*Anas clypeata*], body mass = 0.495 kg; Murphy 1996), molt in December accounted for an additional energetic cost of 6.6 kcal day^{-1} (2.7 g food day^{-1}) for coots in the present study (excluding unknown costs of increased thermoregulation; see above). Although we have no estimates of intake rate, this 5% increase in food consumption likely was not excessive because food was relatively abundant in December (McKnight and Hepp 1998).

Total protein costs of molt can be high due to the high protein content of feathers (Murphy 1996). However, daily protein costs may be reduced by extending the duration of molt. For male Canvasbacks (*Aythya valisineria*), postreproductive molt was extended over six months, allowing them to meet protein requirements from an herbivorous diet without selecting protein-rich foods (Thompson and Drobney 1997). For coots in the present study, protein composition of the diet in December was 17.6% (S. K. McKnight, unpubl. data). Even with liberal estimates of plumage mass and feather growth (8 mm day^{-1}), estimated food intake needed to satisfy daily protein requirements was only 13.1 g food day^{-1}. Hence, at least four times as much food was required to satisfy DEE than to meet daily protein requirements in December, when protein costs were highest. Barring deficiencies in specific amino acids in the diet (i.e., Murphy and King 1987), coots at Guntersville Reservoir probably met total protein costs simply by satisfying daily energy requirements. We conclude that because of adequate protein and energy content of the diet, and relatively low molt intensity, molt resulted in minimal additional nutrient costs for coots in this study.

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