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The American Goldfinch (Carduelis tristis) is unique among cardueline finches, being the only species known to acquire its dimorphic breeding (alternate) plumage through molt of the body feathers (Newton 1972:203). Additionally, the prolonged duration of both the post- and prenuptial molts (see below) of this species is unusual for a temperate zone passerine (Dorst 1974). Although Dwight (1900), Mundinger (1972) and Wiseman (1975) alluded to the molt of the goldfinch, it has not been recorded in detail. The goldfinch is well known for its late nesting (Tyler 1968, Immelman 1971, Mundinger 1972), the reason for which is not clear. Because molt is an integral part of the annual cycle, a detailed study of the process and its relationship to the other major events of the cycle might increase our understanding of the timing of events within that cycle, particularly as they relate to late nesting. The purpose of this paper is to detail the chronology of the molt as a first step in analyzing the integration of events in the annual cycle of the goldfinch (Middleton, unpubl.).

METHODS AND MATERIALS

Details of the natural sequence of molt throughout the year were obtained from 200 goldfinches collected for gonadal study between May 1967 and November 1970 and from 3,433 individuals which were banded in Guelph, Ontario, between mid-November and mid-May, 1970 to 1975. At capture, the feather tracts of each specimen were examined for signs of molt. Molt in the flight feathers was scored according to Evans (1966) and Newton (1966), and primary molt scores (Evans 1966, Newton 1966, 1967a) were used to plot the progression of the molt. Molt of the body feathers was based on the presence of pin feathers and new feathers in each pteryla.

The detailed chronology of the postnuptial molt was obtained from regular examination of 12 captive birds held in an outdoor aviary at the University of Guelph, Guelph, Ontario in 1971 (7 birds) and 1972 (6 birds). Before the molt period, these birds had been held in pairs in 1.82 m^3 breeding pens in natural goldfinch breeding habitats. During molt, the birds were exposed to the natural environment, and food and water were always available.

RESULTS

ADULTS: POSTNUPTIAL MOLT

The first molt of the entire feathering by individual birds followed their first breeding season. This was the postnuptial (second prebasic) molt by which an olivaceous winter (basic) plumage was acquired by both sexes. Molt started with the wings, then spread to the tail and body.

Wings. Molt of the remiges started with the primaries, which were replaced symmetrically on both sides from the innermost outwards (i.e., 1, 2....9). Usually two or three primaries were being replaced at one time.

Molt of the secondaries began at the time the third or fourth primaries were shed. Secondary eight was shed first, followed by nine and finally by seven. Their growth was rapid and was completed before the fifth secondary was shed. Secondaries one to six were molted from the outermost inwards (i.e., $1, 2, \ldots, 6$), and molt began at about the time the fourth or fifth primary was shed. Secondary growth was completed before the end of primary molt.

The greater primary coverts were each molted with their corresponding remex, while the secondary coverts were molted almost simultaneously at the start of molt of the secondaries. Innermost secondary coverts were shed slightly in advance of the outermost. Lesser and underwing coverts were molted at varying times during the primary molt and followed no recognizable pattern.

The three alular remiges were shed simultaneously when the fourth or fifth primary was shed. Their growth was rapid and was completed before the ninth primary was dropped.

Tail. Rectrices were molted simultaneously from each side in rapid succession. The pattern varied, but most commonly these feathers were molted from the center towards the sides (i.e., $1 \dots 6$). Tail molt coincided with the shedding of the fourth or fifth primary and was completed before primary molt ended.

Body. Body molt began on the head and gradually spread to all the body pterylae. Although body molt began with and reached its height during primary molt, its exact termination was difficult to determine because it tapered off gradually. Pin feathers were found on the head and throat along with remnants of the male's black cap as late as December and sometimes into January.

Although the body molt is more prolonged in this goldfinch than in other carduelines (Newton 1968a), heaviest body molt coincided with the wing molt. Primary molt scores suggest that postnuptial molt began



FIGURE 1. Primary molt scores for American Goldfinches at Guelph, Ontario, during postnuptial molt.

in the goldfinch population around mid-August and, apart from the body molt, was finished by late October to early November (Fig. 1). For the population as a whole, males molted about one week before the females. However, individuals varied considerably in the start of molt as some males began molting in early August whereas some late-nesting females did not molt until mid-September (Fig. 1). Although wing molt persisted in the population for about three months, data from the captives suggested that each bird required about 75 days to complete molt of the flight feathers. By contrast the body molt was spread over four months, each bird completing it in approximately 90 days (Table 1).

Because the breeding population leaves Guelph in November and is replaced by the overwintering birds (Middleton, unpubl.), it was impossible to follow the complete postnuptial molt in the breeding population. However, as the newly arrived winter birds were in a stage of molt similar to that of the departing summer birds, the timing of molt probably differed little between the two groups.

ADULTS: PRENUPTIAL MOLT

The prenuptial (prealternate) molt was restricted to the replacement of the body feathers only, which resulted in the acquisition of the dimorphic breeding (alternate) plumage. The first signs of this molt occurred in late January when isolated pin feathers reappeared on the throat and head. This resulted in a

TABLE 1. Incidence of molt in American Goldfinch populations at Guelph, Ontario. Pooled data for 1968-1975.

Time period	Adult male		First-year male		Female	
	N	% Molting	N	% Molting	N	% Molting
Jan. 1–15 16–31	41 106	$\begin{array}{c} 2.4\\ 13.5\end{array}$	$\frac{162}{368}$	$\begin{array}{c} 21.0\\ 26.1 \end{array}$	90 252	14.4 7.5
Feb. 1–15 16–28	67 37	14.9 16.2	273 237	$29.3 \\ 37.6$	191 160	16.2 19.4
Mar. 1–15 16–31	29 26	$20.7 \\ 73.1$	$\begin{array}{c} 117 \\ 106 \end{array}$	$\begin{array}{c} 46.2\\ 85.8\end{array}$	87 70	$\begin{array}{c} 16.1 \\ 67.1 \end{array}$
Apr. 1–15 16–30	$\begin{array}{c} 13\\14\end{array}$	100.0 100.0	105 73	98.1 100.0	$\frac{56}{19}$	87.5 100.0
May 1–15 16–31	3 10	100.0 70.0	32	100.0	9 6	100.0 83.0
June 1–15 16–30	17 13	58.8 92.0	20 17	$\begin{array}{c} 75.0\\ 82.4 \end{array}$	$\begin{array}{c} 30\\ 26 \end{array}$	87.7 96.2
July 1–15 16–31	10 8	60.0 0.0	6 2	50.0 0.0	$\frac{1}{7}$	0.0 0.0
Aug. 1–15 16–31	9 2	0.0 50.0	2	50.0	$egin{array}{c} 6 \ 4 \end{array}$	0.0 25.0
Sept. 1–15 16–30	9 *5	88.9 100.0	1 1	100.0 100.0	10 *6	20.0 100.0
Oct. 1–15 16–31	*5 *5	100.0 100.0			*6 *6	100.0 100.0
Nov. 1–15 16–30	27 33	92.6 97.0	21 34	95.2 97.1	$\begin{array}{c} 16 \\ 51 \end{array}$	100.0 98.0
Dec. 1–15 16–31	16 12	81.3 16.7	12 37	83.3 16.2	$\begin{array}{c} 18 \\ 43 \end{array}$	77.8 48.8

* Data from captive birds only.

gradual increase of yellow on the throat and the reappearance of the black cap in males. The number of pin feathers on the face and head increased in late February, and the first pin feathers on the body proper appeared with regularity in the second week of March. By the second half of March all birds were molting heavily. Heavy molt persisted through April and May and gradually tapered to its end in late June to early July (Table 1). At Guelph, the first males in a predominantly yellow plumage regularly appeared in the second week of April, when the pin feathers on the dorsal and ventral tracts began to open. However, these birds were still molting heavily.

Because the birds that overwinter in Guelph leave the area in mid-May, when they are still in heavy molt, I could not follow the complete prenuptial molt of the winter population. However, the birds that were arriving in the breeding areas were also in heavy molt during late May and early June, and their molt persisted into July. This information again suggests that the timing of the molt was not markedly different in the two populations. Data from the captive birds showed that between three and four months were required by each bird to complete the prenuptial molt, which agreed with the data from the wild birds.

IMMATURES

The sequence of molts through which immature goldfinches passed was basically similar to that described by Dwight (1900), with a few notable differences. The postjuvenal (first prebasic) molt, although restricted to the body, did include the upper and lower tail coverts, but not the wing coverts. This molt, which coincided with the adult postnuptial molt, was prolonged. The postjuvenal molt began in September, reached its peak in October and November, and tapered off gradually. Within this period the early-reared nestlings began to molt before those reared late in the season. Pin feathers persisted on the throat and head into January. As a result of the postjuvenal molt, sex identification of the immature birds became possible by mid-November. Males assumed a gradually intensifying yellow throat color while females retained a much paler yellow. This method of sex identification was verified by gonadal examination and subsequent retrapping of birds banded as immatures.

The end of the postjuvenal molt and the start of the prenuptial (first prealternate)

molt was difficult to determine because isolated pin feathers were found on the throat and head region of many immature birds during late January and February. By late February and early March, the number of pin feathers had increased markedly in the head region, and the black cap began to appear in the males. As with the adults, heavy body molt started with marked regularity during the second week of March. From this point on, the timing and progression of the molt was similar to that already described for the adults, except that the secondary coverts of the immatures were replaced as a unit during the latter half of April. Their replacement was rapid and resembled that for the adult birds during postnuptial molt.

With the completion of the prenuptial molt, the immature birds assumed their first breeding plumage which was similar to that of the adults. However, birds in their first breeding season could still be separated from adult birds because the former retained their drab olivaceous lesser wing coverts and scapular feathers, and young males showed a white flash on the bases of the primary feathers (Middleton 1974).

The physical appearance of the immature and adult plumages mentioned above are adequately described elsewhere (Dwight 1900, Chapman 1912, Forbush 1929, Godfrey 1966, Tyler 1968).

DISCUSSION

With the exception of the prolonged body molt, the postnuptial molt of the American Goldfinch resembles that of other cardueline finches (Evans 1966, Newton 1966, 1967a, 1968a, 1972, Middleton 1969) and passerines in general (Stresemann and Stresemann 1966). The time taken to complete wing molt fell within the spread found by Newton (1968a) for several British finches and was similar to the molt period of the European Goldfinch (*Carduelis carduelis*) in Australia (Middleton 1969).

Although the chronology of the molt and many of the data on timing were obtained from the 13 captive birds, the results should not have been greatly affected; Newton (1969) and Morton and Welton (1973) found little difference in timing of the molt between captive birds and wild populations. As found for some species, the time required to complete a molt may vary in different parts of the range. This may partly explain the differing times recorded for the postnuptial molt at Guelph, in New York (Mundinger 1972), and in Ohio (Wiseman 1975). However, molt was not the major concern of the latter studies. The tendency for males to molt before females was noted by Wiseman (1975) and is common to various passerine species (Bell 1970, Niles 1972, Morton and Welton 1973, Verbeek 1973). This may result from the slightly earlier degeneration of the testes than of the ovaries (Middleton, unpubl.).

Because other cardueline species acquire the breeding aspect through abrasion (Newton 1972), the prenuptial molt of the body plumage is unique to the American Goldfinch. As a result, this goldfinch is probably the most strikingly dimorphic of the carduelines during the breeding season. Thus it has gained all the advantages of seasonal dimorphism discussed by Hamilton and Barth (1962) and Welty (1975). But this does not explain why the goldfinch is the only cardueline to produce a dimorphic breeding plumage through body molt. Apparently the goldfinch is the only cardueline with sufficient time in its annual cycle to complete a body molt before nesting. In the evolution of late nesting the species eventually incorporated a prenuptial molt into its annual cycle. However, the energetic demands of such a molt may preclude the simultaneous development of the gonads. Thus the prenuptial body molt may now function as one of the physiological mechanisms that ensures the late timing of the constituent phases of the gonadal cycle discussed by Mundinger (1972). Additionally, the prenuptial molt may have provided the possibility of developing a less dense summer plumage, which could be advantageous to a species restricted to breeding in open habitat in the hottest summer months.

The prolonged body molt characteristic of both post- and prenuptial molts of the goldfinch at Guelph, was longer than observed by either Mundinger (1972) or Wiseman (1975) and is uncharacteristic of a temperate zone passerine (Dorst 1974). Body molt in the goldfinch barely overlaps with breeding but does occur during the migratory period in both autumn and spring (Middleton, unpubl.). Generally, it is accepted that the molt is more rapid in strongly migratory species than in residents (Newton 1969, Morton and Welton 1973). However, the time required by the American Goldfinch for its molts is longer than for other migratory finches (Newton 1968a, Wolf 1969). Newton (1968b) showed that the Bullfinch (Pyrrhula pyrrhula), a resident species in Britain, maintains its body condition and fat levels, and does not

incur a long-term protein debt during molt. He therefore suggested that molt is not a time of hardship and deprivation for this species as has been suggested for birds in general (Payne 1972). In addition, the molt of the Bullfinch is long when compared to other carduelines (Newton 1968a). This may have been related to its its diet as the longest molt periods of British carduelines (Newton 1968a) were characteristic of those with the most highly granivorous diets (Newton 1967b).

Because the American Goldfinch is almost exclusively granivorous, even during the breeding season (Middleton, unpubl.), the prolongation of body molt may permit the protein demands of molt to be met on a seed diet. This would be particularly important during prenuptial molt in March-May when natural food supplies are at their lowest and when decreased plumage insulation, at a time of unpredictable weather, would create an additional energetic demand (Lustick 1970). Furthermore, prolongation of the body molt at a suppressed rate would also distribute the energy demands of molt over a protracted period, and thus avoid a restricted period of high energy demand. Both mechanisms could be particularly important to a seed-eating species such as the American Goldfinch.

SUMMARY

The annual molt was studied in 3,633 American Goldfinches collected for gonadal study or banding between 1967 and 1975, and from 13 captive birds used for breeding in 1971 and 1972. The postnuptial molt is similar to that described for most cardueline finches and for passerines in general. However the goldfinch proved unique among carduelines in the acquisition of its breeding plumage by a prenuptial body molt. In addition, the prolonged period required to complete both the prenuptial and postnuptial body molts is unusual for a temperate zone passerine. The presence of the prenuptial molt may have some relationship to late nesting by the goldfinch. The prolonged body molts may be necessary adaptations which permit the highly granivorous goldfinch to meet the energetic demands of molt.

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