NOTES ON THE MOLT SCHEDULE OF THE PLAIN TITMOUSE

By KEITH L. DIXON

The position of the molt in the annual cycle in birds is of interest in relation to the demands for energy for other essential activities. As a rule the inception of molt is delayed until breeding has been completed, so that events that are physiologically incompatible do not overlap (see Farner, 1958:18, and Miller, 1961:153). Exceptions may be found in the tropics, but in at least some of these cases, molt follows the period when the majority of individuals breed (Miller, 1955). An apparent contradiction to this principle came to my attention with the discovery that Plain Titmice (*Parus inornatus*) were undergoing molt while feeding fledglings in mid-June. This discovery led to an examination of the timing and progress of molt in marked individuals whose breeding histories were known.

MATERIALS AND METHODS

Progress of molt was observed in titmice live-trapped incidental to other objectives at the Hastings Natural History Reservation in Monterey County, California, from June 21 through August 20, 1959. Thirteen records of nine immature individuals and 28 records of 11 adults were obtained in this interval. These data were augmented by examination of 10 adults and four immatures taken as specimens within three miles of Hastings Reservation between May 29 and August 3, 1959, and by study in the Museum of Vertebrate Zoology of nine adults and 11 immature specimens taken during the molting period in Monterey, San Benito, San Luis Obispo and Contra Costa counties. Thus the postjuvenal molt is documented by 28 records and the annual molt by 47.

In the examination of living birds reliance was placed on the extent of molt of the remiges, since Baldwin (1953:326) found that their replacement provided "the most stable criterion" of the progress of annual molt. A series of arbitrary stages of the annual molt was recognized (table 1) based largely on the pattern of molt in the flight feathers in the schedule utilized by Pitelka (1945:245) for the Scrub Jay (*Aphelocoma coerulescens*).

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RESULTS

Postjuvenal molt.—This molt apparently involves replacement of the entire body plumage, all the rectrices, the proximal secondaries and all the greater secondary coverts. Rarely, the outermost primaries and their coverts may be renewed. The most extensive replacement noted was in an immature male (Mus. Vert. Zool. no. 88946), skull-aged by C. G. Sibley, and taken 3¼ miles southwest of Danville, Contra Costa County, September 1, 1940. It had renewed the five proximal secondaries and primaries 9 and 10 in both wings. Apparently the replacement of all rectrices and the three proximal secondaries is the rule in immature titmice in the Coast Ranges of central California. The postjuvenal molt in the Tufted Titmouse of the *Parus bicolor* complex in Kansas and Texas is comparable in extent (Dixon, 1955:130–131), although this condition may not obtain in other species groups of the genus. A similar pattern of postjuvenal molt occurs in the Great Tit, *Parus major* (Witherby *et al.*, 1943:249; Vaurie, 1950:33). The latter author remarked that this molt was "peculiar," and he found no evidence of replacement of rectrices in any other Eurasian titmouse.

TABLE 1

MOLT STAGES RECOGNIZED IN ADULT PLAIN TITMICE

Stage	Primaries	Secondaries
1	1, 2 dropped or breaking sheaths	
2	3 nearly full-length; 5–10 old	
3	1–4 full-grown; 6– or 7–10 old	8 new; 1 dropped
4	7– or 8–10 old	7 one-half grown; 1, 2 partly grown
5	9–10 old	4–6 old; 7–9 fully grown
6	9 replaced; 10 old	5–6 old
7	10 new, short	6 old or emerging
8		6 partly grown

Molt was not detected in juvenal Plain Titmice taken on June 25 and 27, 1959, but three live-trapped at Hastings Reservation, July 15 to 18, were molting feathers of the ventral and crural tracts. Inception of molt of the capital tract was observed in another individual on July 22. Replacement of proximal secondaries was noted in a specimen taken three miles east of the Reservation on August 2, and central rectrices and proximal secondaries were being renewed in four juveniles trapped between August 13 and 19. Two others trapped in this interval retained a full complement of juvenal rectrices. Two of four specimens from San Luis Obispo County, September 14 to 16, 1947, had completed the molt of the rectrices, and the lateral rectrices of the other two were nearly full length. A female (Calif. Acad. Sci. no. 55894), taken at Hayward, Alameda County, on September 23, 1898, appears to represent a late hatching date since only the two proximal secondaries have been renewed, and all rectrices are sheathed. Thus the duration of the postjuvenal molt apparently exceeds two months, approximating the interval required in the Scrub Jay in the same region (Pitelka, 1945:236) and in the Andean Sparrow, *Zonotrichia capensis* (Miller, 1961:158). However, the remiges are not replaced in most individuals of these species.

Annual molt.—The sequence of annual or complete molt does not differ from that reported for *Parus bicolor* (Dixon, 1955:129–130), and it appears typical for most passerines. Molt begins with the first (innermost) primary, and molt of the first (outermost) and eighth secondaries follows after five or six primaries have been dropped. Molt of the rectrices begins shortly after replacement of the secondaries begins, and it is completed as a rule before secondaries 5 and 6 are dropped. The full growth of secondary 6 marks termination of the molt.

The progress of this molt in west-central Californian populations is plotted in figure 1, and that for individuals that were retrapped is indicated by connecting lines in figure 2. The data presented in both figures indicate that molt in this population begins in the first half of June. This observation is of particular interest in relation to the breeding histories of several of the individuals concerned.

The brood of pair T (fig. 2) still occupied the nest on May 19, and juveniles still begged aggressively on June 1. Female T retained only the distal five primaries when examined on June 21. Conceivably her wing molt may have begun as early as June 1. Her mate had not dropped primary 4 on June 22. On June 10 female T appeared to have lost all her rectrices; these were fully grown but sheathed on July 13, and they had not been molted by August 20. Presumably the simultaneous, early replacement was to suffice for the ensuing year, and it may explain why her mate "overtook" her in molt stage by mid-July, as shown in figure 2.

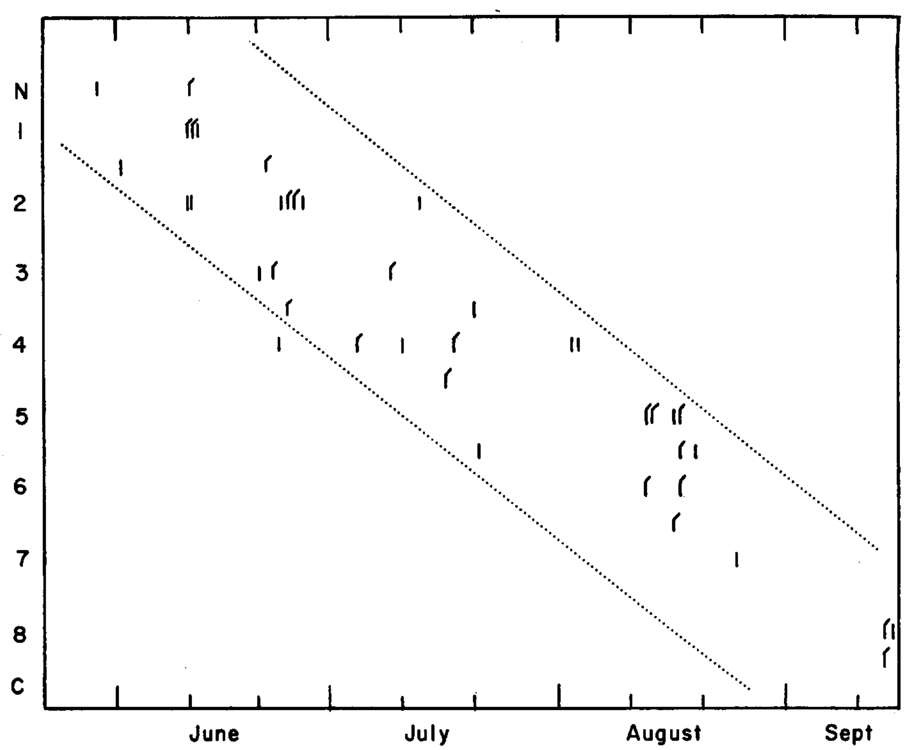

Fig. 1. Schedule of annual molt in Plain Titmice (*Parus inornatus*) from west-central California based principally upon flight feathers. Males are represented by a projection at upper end of vertical lines. N = no molt in evidence; C = molt completed.

Female U was in stage 2 (primary 3 one-half grown) on June 24, one month after her brood left the nest. Her mate's molt stage was comparable on that date, and both birds were in the same stage on August 13.

The brood of pair W left the nest on May 31. The male's molt stage on June 25 was comparable to that of the pair cited previously, but the female's molt lagged somewhat, with primary 4 emerging from its sheath on July 13.

Male V was the only individual known to be undergoing its first annual molt (skull-aged in preceding autumn). He had not been successful in rearing a brood.

The mate of female Z disappeared about the time the brood fledged, but the burden of rearing the six nestlings did not appear to retard her molt unduly.

An adult female taken by me 4 miles east of Jamesburg, Monterey County, June 11, 1959, was foraging for her begging fledglings. She had replaced three primaries. Other adults taken at the same area on that date were in a comparable stage of molt.

DISCUSSION

In none of the cases in which nesting dates were known did the molt begin until the fledglings were about two weeks out of the nest. By this stage the fledglings clearly are foraging for themselves (Dixon, 1949:128), although feeding of juveniles a week beyond that stage was witnessed at Berkeley, California, on May 30, 1947. Thus the overlap in molting and nesting does not appear critical in terms of additional energy demands on the parents.

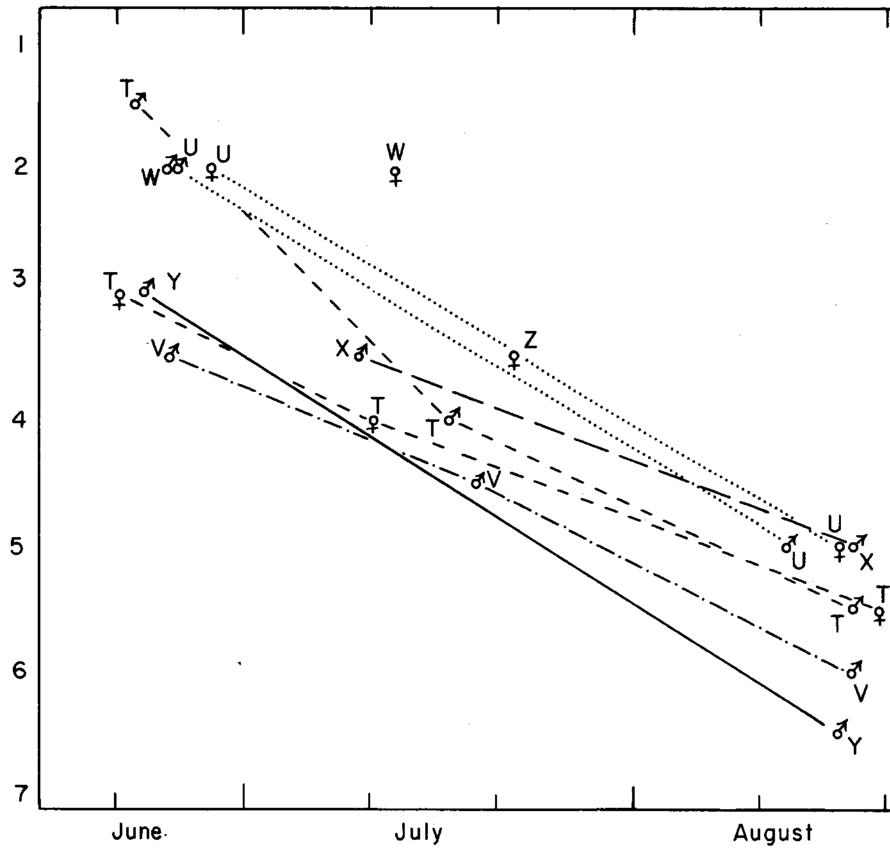

Fig. 2. Progress of molt in nine adult Plain Titmice live-trapped in the interval from June 21 to August 20, 1959. See text for discussion.

A scattering of data on inception of molt from other years indicates that the schedule in 1959 represented no significant departure from the norm for populations in west-central California. One specimen taken in San Benito County had dropped primary 3 on June 1, 1936, and another, taken on July 23, 1939, retained only two old secondaries and the distalmost primary. The extent of replacement of the rectrices in four color-banded adults retrapped at Berkeley, August 17 to 19, 1947, would place these individuals in molt stages 4 to 6; this schedule accords fairly well with that plotted in figure 1. However, since the three broods of these adults were fledged in the period from May 1 to May 9, the onset of molt may have followed nesting by a greater interval than in the population at Hastings Reservation in 1959.

Even though the period of the annual molt in the population of the Plain Titmouse studied does not intrude appreciably upon the period of fledgling dependency, it begins earlier in calendar date than is the case in most passerines. For example, Miller (1928: 411) indicates that comparable molt in the Loggerhead Shrike (*Lanius ludovicianus*) begins about July 1. There are, however, a few examples of species in which molt follows fledging closely. In the Rook (*Corvus frugilegus*) in southwestern England, Marshall and Coombs (1957:555, 558) reported the onset of annual molt early in May, soon after the departure of the most advanced broods from their nests. Eaton (1957:23), in a study of a migratory species, the Northern Waterthrush (*Seiurus noveboracensis*) in New York, stated that "even before the young became independent the adults started to molt." Inception of annual molt in populations of the Scrub Jay of central coastal California may begin in the first half of June (Pitelka, 1945:247), but presumably this molt follows nesting by a greater interval than that reported for the titmouse. The most pronounced intrusion of molt on the nesting cycle of a species of temperate latitudes is that reported for the Clark Nutcracker (*Nucifraga columbiana*) by Mewaldt (1958). In some individuals the molt of the primaries was found to begin at the time of ovulation. However, the rate of molt in this species is slower than that of most other passerines.

The duration of the annual molt in the population of Plain Titmice here is estimated to exceed three months, and it appears to be similar to that of other species of the genus. The period of molt in *Parus major* in Britain is reported by Witherby *et al.* (1943:249) to occupy the months from August to October. Likewise the duration of molt is comparable to that for Californian populations of two other non-migratory species, the House Finch (*Carpodacus mexicanus*), about 90 days as reported by Michener and Michener (1940), and the Scrub Jay, three months as reported by Pitelka (1945). However, the termination of the molt in these species falls somewhat later than the mid-September period judged to obtain in the titmouse. Thus it appears that the duration of the molt in the Plain Titmouse is of an order expected for a sedentary species in its latitude, but the molt has been shifted to occupy the earliest period compatible with other events of the annual cycle.

TABLE 2

VOLUME OF ARTHROPODS IN CC. PER 100 GM. OF OAK FOLIAGE

Date	Volume cc. per 100 gm. dry oak foliage*
April	
16–17	0.33
27–28	0.82
May	
2– 3	0.47
9–11	0.58
22–23	0.28
June	
1	0.10*
11–12	0.14*
26–27	0.21*

* No compensation for incomplete drying of foliage.

One advantage that a population might obtain in having the inception of its molt advanced would be to avail itself of a richer food supply. Samples of arthropods taken from oak foliage at Hastings Reservation in the spring of 1959 lend little support to this possibility. Terminal twigs were enclosed in paper bags and removed from the trees, and the anaesthetized arthropods were removed and preserved. The volume of arthropod material in each sample was measured by displacement, and this volume related to the weight of leaves (air dried for two months or more) in that sample. The data (table 2) show that abundance declined after mid-May. Thus, the molt began several weeks after the peak of arthropod abundance in 1959. Further, lepidopterous larvae were insignificant in volume after May 22. The food items available in the molt period are smaller but more numerous than the moth larvae prevalent in May, but their abundance presumably is adequate for the situation wherein each individual (adult and juvenile) is foraging for itself.

It appears, however, that conditions at the termination of the molt period may be more critical to the population. A parallel to the adjustment of the molt and testis cycles of the Anna Hummingbird (*Calypte anna*) to the dry season, as pointed out by Williamson (1956:356), seems plausible. Williamson's climatic data for Berkeley (p. 363) indicate that the warmest month (September) falls at the end of the dry season. Data for three other stations of long-term record (Salinas, Hollister, King City) of the Coast Ranges show a similar pattern, with September being one of the four warmest months. Conceivably arthropod food supplies would be less dependable as the dry season progressed, and, hence, early completion of the molt would be advantageous. The fact that the molt of both adults and immatures is essentially complete by mid-September supports the view that selection favors the earlier time schedule. Such an adjustment would be more easily effected than an increase in the rate of molt. The fact that there is an adjustment supports Pitelka's (1958:48) contention that molt as well as nesting must be tailored to local conditions.

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Hastings Natural History Reservation, Carmel Valley, California, and *Department of Zoology, Utah State University, Logan, Utah, June 30, 1961.*