PHOTOPERIODIC EFFECTS ON THE POSTJUVENAL MOLT OF THE EASTERN BLUEBIRD[1]

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Abstract. The postjuvenal (first prebasic) molt and its relationship to nesting and migration was studied in Eastern Bluebirds (*Sialia sialis*) in southeastern Michigan during 1972 to 1975. Experimental data were accumulated on birds observed in captivity to assess the effect of photoperiod on variability in the molt. Juveniles reared in spring molted between 18 July and 10 September and those reared in summer molted between 26 August and 16 October. Individual birds reared late in the season molted more rapidly and began the molt when younger after a shorter post-fledging period than birds hatched early in the season. Only juveniles hatched late in summer did not complete the molt before leaving the breeding grounds. Observations on captive birds indicated that the more rapid molt of late hatchlings was attributable to photoperiod at the beginning of the molt interacting with the age of the bird. Although some juveniles molted the rectrices and others did not, daylength at the onset of the molt was significantly shorter for captive birds that did not renew the rectrices than for those molting the rectrices ($P<0.01$). Modifications of the molt by late hatchlings, especially elimination of the rectrix molt, may represent bioenergetic adjustments to the reduction in time between hatching and the winter season.

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Recent studies have indicated that the avian molt is an adaptive process often having considerable intraspecific variation. Some black-billed magpies (*Pica pica*), for example, may begin molting before others have laid eggs (Holyoak, 1974). Several old world sylviids are known to begin the molt on the breeding grounds and, if food supplies dwindle, these species may arrest the molt until arriving on the wintering grounds (Pimm, 1973). Extent, speed, or timing of the molt is reported to vary geographically in several species (Davis, 1968; Garbutt and Middleton, 1974), and may even differ among juveniles of the same species living in the same locale (Ligon and White, 1974). The stimuli for molting in birds are not well documented (Wenstrom *et al*, 1972), although photoperiodism is suspected as one factor involved (Payne, 1972).

Like many passerines, the eastern bluebird undergoes a single annual molt (Dwight, 1900). The postjuvenal (first prebasic) molt is incomplete and excludes the primaries, secondaries, primary coverts, and alula. Pronounced individual differences in the molt of juvenal bluebirds were suspected early in a study of the breeding ecology of this species (Pinkowski, 1974a) because bluebirds have a lengthy breeding period (Peakall, 1970). Some young of summer broods are still in the nest when others, hatched in spring, have already begun to molt. Moreover, although Dwight (1900) and Bent (1949) state that the rectrices are molted in juvenal bluebirds, Webster (1973) found that sometimes the rectrices were not molted and concluded (personal communication) that the rectrices are not renewed in most juveniles in southern populations of *S. sialis* but are molted in the majority of birds in the north.

METHODS

The molt of Eastern Bluebirds near Washington, Macomb County, Michigan (42° 48' N, 82° 59' W) was studied during 1972 to 1975. Nests were found in both natural cavities and nest

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boxes (Pinkowski, 1976) and approximately 500 nestlings were color-banded. For comparative purposes only double-brooded pairs were included in the analysis. The first (spring) broods of 71 pairs studied fledged in late May or early June and the second (summer) broods fledged between mid-July and late August. Juveniles were easily sexed; females have a white edging on their outer rectrices and less blue on the remiges and rectrices than males (Pinkowski, 1974b). Thirty-five fledglings that remained in the study area were followed until their fall departure.

Premigratory flocks consisted of 5–30 individuals and included adults with diverse nesting histories and juveniles of various ages. Family groups usually remained together within one flock, but an occasional adult or fledgling was found apart from the main family unit. Distinguishing between the molt of the species and the molt of the individual was necessary but it was impossible to re-capture wild juvenal bluebirds in sufficient numbers to permit an analysis of molt conditions of individual birds. Molt status was easily observed through a high power spotting scope, however, and molting juveniles could be identified as such from a distance because of a marked difference in the juvenal and adult plumage (Bent, 1949). All birds were observed at least twice each week during 1973 to 1975 and once each week in 1972, the observations extending from early July until early November.

Bluebird juveniles obtained as nestlings in southeastern Michigan were studied in captivity from 1969 to 1974. Seven juveniles obtained from the study area from mid-June to mid-August were followed through the molt; these birds entered the aviaries at daylength regimes identical to those they previously experienced in the wild. Five pairs of captive birds allowed to breed in captivity at various photoperiods successfully raised young (Pinkowski, 1975), 18 of which were also used in the molt analysis. Only one brood of juveniles (2–4 birds) was kept in each cage at any time. Cages measuring approximately 8 cu m were illuminated by two 100 watt incandescent bulbs. Natural light was excluded from the aviary rooms. Daylength (length of time the aviaries were illuminated) was altered by automatic timers so that changes in the daylight period in the aviaries coincided with natural changes except that daylength changes in the aviaries were always in 15-minute decrements. Only 24 hr photocycles were employed. Maximum daylength was 16 hrs (LD 16:8) and the minimum was 8 hrs (LD 8:16).

Diet was kept as constant as possible for the captive birds and consisted of insects purchased locally (mealworms, *Tenebrio* sp., and house crickets, *Acheta domesticus*) or caught in various traps (often frozen for later use). Fruit, mostly black cherry (*Prunus serotina*) and staghorn sumac (*Rhus typhina*), occasionally was offered and water was always available. Temperature was maintained at approximately 14 to 17°C. Seven birds observed until after molt initiation were released before molt completion because of limitations of food supply and space in the aviaries. Other captive birds survived beyond molt completion and most were eventually released into the wild. Except for one randomly-selected bird I did not wish to dis-

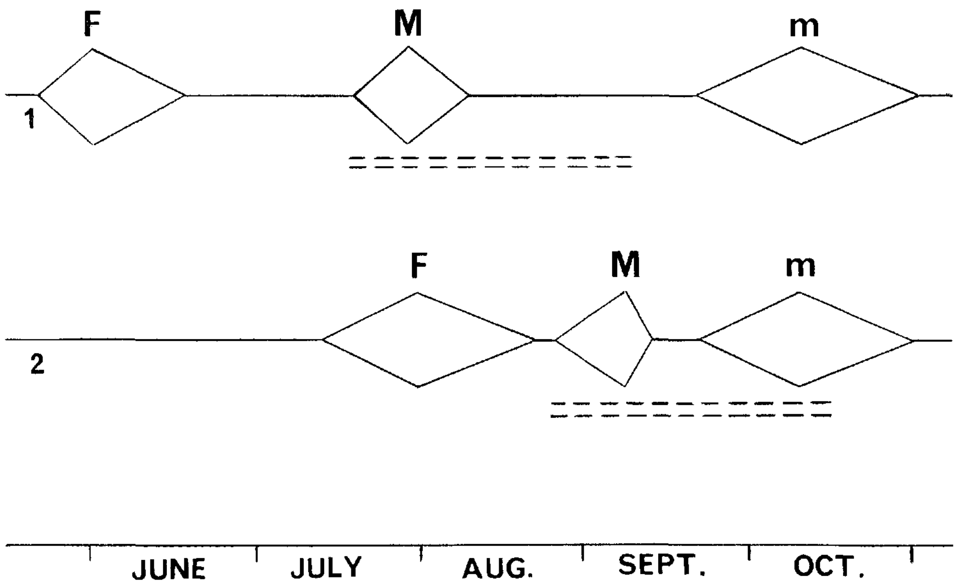

FIGURE 1. Diagramatic scheme showing the temporal relationship of fledging (F), molting (M), and migration (m) in first (1) and second (2) broods of juvenal Eastern Bluebirds. The vertical diagonal of each kite indicates the mean date for initiation of the activity, the horizontal diagonal indicates the range of initiation dates, and the dashed lines represent molting individuals. Sample sizes are given in the text.

turb, all 18 juveniles followed through the molt were caught and examined once each week to determine the progress and extent of the molt.

RESULTS

Molting juveniles were observed in the study area over a 91-day period from 18 July to 16 October. Juveniles reared in spring began the molt in mid-to-late July, when 2 to 3 months old, and completed the molt by early or mid-September (range of molting dates = 18 July–10 September, n = 23). Young reared in summer began molting in late August to mid-September, when less than 2 months old (range of molting dates ± 26 August–16 October, n = 12). Thus, young of spring broods begin the molt at an older age and after a longer post-fledging period than young of summer broods (fig. 1), and in early September some juveniles reared in spring have completed the molt and other hatched in late summer have not yet begun molting.

Juveniles reared in summer completed the molt more rapidly than those reared in spring despite the similarity in the length of time over which molting individuals of spring and summer broods were observed (55 and 52 days, respectively). Variance of fledging dates for summer broods was greater (128.8 days) than for spring broods (49.0 days) [$F = 2.6$, $P < 0.01$] and accounted for a greater portion of range in molting dates of summer broods because molt initiation depended on fledging date. The earliest young fledged molted from mid-July to early September (approximately 10 weeks) whereas the latest young fledged molted from early September to mid-October (6 weeks).

Except for aerial feeders, the majority of small, north temperate, migratory passerines molt on the breeding grounds (Rohwer, 1971). All bluebird juveniles hatched in spring appeared to complete the molt before departing in the fall (fig. 1). Juveniles hatched in late summer, however, sometimes left the breeding grounds before completing the molt; most of these birds probably departed to begin the fall migration but a few moved into lowlands that are typical habitats of bluebirds in the non-breeding periods. Molting juveniles, however, occasionally entered the study area during fall; many of these were, judging from their molt status, reared in summer. Thus most, but not all, juveniles molt prior to fall migration and the exceptions involve mostly birds reared in summer (see Kingerly, 1973).

Observations were made on captive juveniles to test the hypothesis that the tendency of late hatchlings to begin the molt at a younger age is under photoperiodic control. The results (fig. 2)

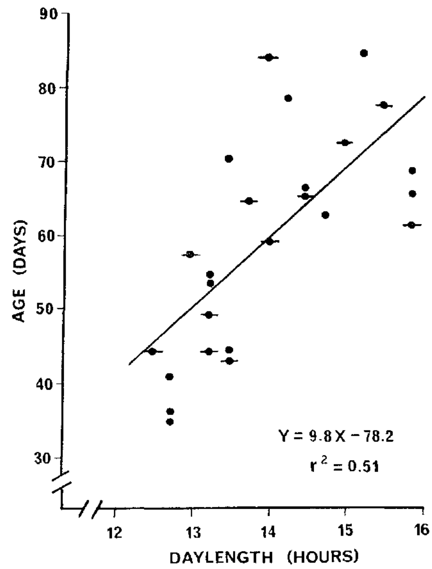

FIGURE 2. Relationship between daylength and the age of 25 captive juvenal Eastern Bluebirds at the start of the molt. In each case the daylength was decreasing when the molt began. Solid circles represent females and circles with horizontal bars represent males.

show positive correlation between daylength and age at onset of the molt. The slope of the regression line is significantly different from 0 [$F = 23.7$, $P < 0.001$] and the 95% confidence interval was 5.6 and 14.0. For all birds sampled the molt began at ages of 35 to 84 days ($\bar{X} = 59 \pm 14.4$). The beginning of the molt of the two birds under 40 days old occurred less than a week after they attained independence.

For captive birds observed through molt completion the time required to complete the molt varied from 35 to 96 days. The mean duration of the molt was 50.5±12.4 days. The slope of the regression line (fig. 3) for duration of the molt plotted on daylength at the onset of molt differed significantly from 0 [$F = 15.8$, $P < 0.005$] and the 95% confidence interval was 3.2 and 10.5. No significant regression was noted, however, when duration of molt was plotted on daylength at the completion of the molt. Captive males began the molt at virtually the same daylength ($\bar{X} = 14.0 \pm 1.1$ hr; $n = 12$) as females ($\bar{X} = 14.1 \pm 1.2$; $n = 13$). Duration of the molt was also not significantly different for males ($\bar{X} = 52.8 \pm 10.0$ days) compared to females ($\bar{X} = 58.2 \pm 18.9$ days).

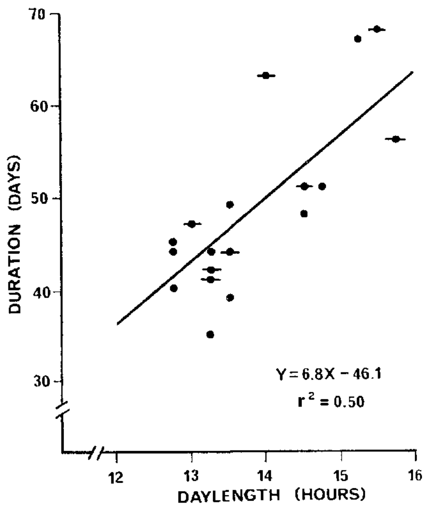

FIGURE 3. Relationship between daylength at the start of the molt and duration of the molt in 18 captive Eastern Bluebirds. Solid circles represent females and circles with horizontal bars represent males.

Nine of 17 captive birds (52.9%) from 8 different broods sampled for tail molt renewed the rectrices. In each case either all or none of the rectrices were renewed. On two occasions young molting the rectrices and young not molting the rectrices were from the same brood, and in both cases all males in the brood molted the rectrices and all females did not. Altogether, 6 males and 3 females molted the rectrices and 3 males and 5 females did not. Thus there was some evidence that males renew the rectrices more often than females but the sample was too small to draw definitive conclusions.

Daylength at the onset of the molt differed significantly for birds molting and not molting the rectrices ($P < 0.01$), averaging 15.1±0.8 hrs (range = 13.75–16.0 hrs) and 13.7±0.6 hrs (range = 13.25–14.75 hrs) for the two groups, respectively. No significant difference, however, was found in daylength at the completion of the molt for the two groups. Birds molting the rectrices required a longer time ($\bar{X} = 66.3 \pm 13.9$ days; range = 51–96) to complete the molt than did the birds not molting the rectrices ($\bar{X} \pm 44.8 = 4.2$ days; range ± 39–51) and the difference was highly significant ($P < 0.001$).

DISCUSSION

Although stress, dietary requirements, or other factors relating to captivity are thought to influence feather replacement in some species (Woehler, 1953, cited by Davis, 1968), other studies indicate no difference in the molt of wild and captive birds (Zwickel and Lance, 1966; Davis, 1968; Garbutt and Middleton, 1974). Results, demonstrated in a study of the molt of captive birds, do not describe precisely the molt of birds in the wild but suggest plausible explanations for some of the variation observed in the molt of birds under natural conditions (Payne, 1972).

Late hatchlings of multi-brooded passerines may undergo an abbreviated postjuvenal molt compared to early hatchlings (Michener and Michener, 1940; Davis, 1957; Scott, 1967). Also, young that fledge later are typically several weeks younger at the onset of the molt and take less time to complete the molt than birds fledged earlier (Ligon and White, 1974; Pearson, 1975). Seasonal adjustments in timing, extent, and speed of the molt exist in the eastern bluebird and apparently are under the control of photoperiod interacting with the age of the bird.

Daylength at the onset of the molt evidently determines the rate and extent of the molt in bluebird juveniles. Daylength and changes in the photoperiod after the onset of the molt appear not to be important, but additional experimental data would clarify the role of photocycles after the molt is initiated. Although a partial tail molt has been reported (Reese, 1975) among some multi-brooded species such as the cardinal (*Cardinalis cardinalis*), partial tail molt was not observed in our study of bluebirds and was not mentioned by Webster (1973).

Pitelka (1958) suggests that molt timing in the Steller's jay (*Cyanocitta stelleri*) is related to the period of peak food supplies; presumably because of the increased energy demands associated with feather replacement (see Lustick, 1970). A similar situation may exist among bluebirds hatched early in the season. Insect biomass increases during summer and is maximum in late August to early September in northcentral states (Johnston, 1967) and fruits consumed by bluebirds are abundant at that time. Late August is within the molting period of early hatchlings, but late hatchlings molt later, at a more rapid rate, and at a time when frosts are not uncommon and insect biomass may be temporarily depleted. Moreover, a shorter daylength in late September and October permits less time for foraging.

The postjuvenal molt of late hatchlings of multi-brooded species may be less extensive to compensate for food reduction and increased energy demands associated with a later, more rapid molt. Because of a shorter post-fledging period, late hatchlings have experienced relatively little feather wear. Survival value of more extensive feather renewal by late hatchlings would presumably be less than that accrued from the energy and time conserved by a more rapid, less extensive molt.

Time and energy demands placed on late hatchlings would be reduced if these birds could molt and migrate on overlapping schedules or occupy the breeding locale on a year-round basis. That some late bluebird hatchlings apparently molt and migrate at the same time may be possible because none of the flight feathers (remiges and rectrices) are renewed by these birds. Yearlings hatched late in the season predominate among the few bluebirds remaining in the study area each winter (see Pinkowski, 1974a), which suggests that they also predominate among the non-migrants. Non-migrants are occupying marginal wintering areas and in the event of stresses associated with a "hard" winter, they would be the first to be eliminated (Rohwer, 1971). Thus, late bluebird hatchlings are at a bioenergetic disadvantage compared to early hatchlings and modifications of the late hatchling's molt may partially offset the bioenergetic demands placed on young reared late in the season.

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