TEMPORAL, SEX, AND POPULATION CHARACTERISTICS OF THE FIRST PREBASIC MOLT OF RED-WINGED BLACKBIRDS

By George M. Linz

Red-winged Blackbirds (*Agelaius phoeniceus*) begin their first prebasic (postjuvenal) molt in July. The duration of red-wing molt has been estimated quantitatively by regression analysis (Linz et al. 1983, Payne 1969) and qualitatively (Meanley and Bond 1970) by capturing numerous birds a single time. Using these techniques, information has been gathered on the relationship of molt and migration (Linz et al. 1983, Meanley and Bond 1970). Dunson (1965) and Payne (1969) studied the timing of red-wing molt in two nonmigratory, southern populations. Selander and Giller (1960) and Greenwood et al. (1983) reported on the percentage of each sex that undergoes complete first prebasic molt and first partial prealternate (prenuptial) molt, respectively.

First prebasic molt begins 45 to 60 d after leaving the nest (Meanley and Bond 1970). In North Dakota, red-wings generally fledge from early June to early August. Birds in more northern nesting areas (Canada) presumably fledge later than those in North Dakota. Birds that begin molt later in the season may grow more remiges concurrently than earlier molting birds (Dolnik and Gavrilov 1980, Evans 1966, Newton 1966).

Red-wings have sex-specific food habits (Linz et al. 1984, McNicol et al. 1982, Mott et al. 1972), often segregate into sex-specific flocks (Orians 1961, Smith and Bird 1969), have sex-specific roosting behavior (James et al. 1984, Weatherhead 1981), and have sex-specific migratory patterns (Allen 1914, Dolbeer 1982, James et al. 1984). Thus, outside of the breeding season, male and female red-wings appear to behave as though they are two distinct species.

I studied the progress of molt in hatching-year red-wings from two migratory populations in Cass County, North Dakota. My objectives were: (1) to test the hypothesis that later molting red-wings grow more remiges simultaneously than do earlier molting birds, (2) to determine if there are sex-specific differences in the first prebasic molt of red-wings, and (3) to determine differences in the phenology of molt in two late summer roosts. This information is used to make inferences about population movements and sex-specific migratory patterns.

STUDY SITES

I collected red-wings by shooting, decoy traps, cannon nets, and mist nets during the following times: Aug.-Oct. 1979 and June-Oct. 1980 in southwestern Cass County (Alice roost); Aug.-Oct. 1980, July-Oct. 1982, and July-mid-Sept. 1983 in east central Cass County (Harwood roost). Southwestern Cass County is on the eastern edge of the Drift Plains physiographic region (Stewart 1975). Numerous wetlands in this agricultural area provide both daytime resting sites and night roosts for blackbirds (Icterinae). The principal roost in this study area is located in the U.S. Fish and Wildlife Service Waterfowl Production Area at Alice (46°08'N, 97°04'W), which includes a 300 ha cattail (*Typha* spp.) marsh. At peak density, about 300,000 blackbirds roost in the marsh. Density varies from week to week during each season and from year to year. The Alice population consisted of adult males and females, secondyear males, and hatching-year males and females.

The Harwood roost is located 60 km east of the Drift Plains (46°51'N, 96°50'W) in the Agassiz Lake Plain. In contrast to the Drift Plains, the Agassiz Lake Plain has comparatively few wetlands (Stewart 1975). In autumn, the Harwood population consists of 5000 to 10,000 hatching-year birds. These birds roost in a cattail slough of approximately 10 ha.

METHODS

Plumages of red-wings have been described by Dwight (1900), Selander and Giller (1960), and Meanley and Bond (1970). All feathers are normally replaced during the first prebasic molt; however, some individuals may retain a few underwing coverts (Selander and Giller 1960). Primary remiges are replaced in sequence from 1 (innermost) through 9; the outer secondary remiges (1-6) are usually molted from outermost (1) to innermost (6). Secondary remiges begin to molt about the time primary 5 or 6 is dropped. All feather tracts complete molt at approximately the same time.

The birds were sexed, aged by plumage characteristics and presence or absence of the bursa of Fabricius (Payne 1969, Wright and Wright 1944), and assessed for stage of molt. Each primary and secondary of the right wing was assigned a score using a 5-point system similar to that of Bancroft and Woolfenden (1982), Evans (1966), Newton (1966), and Sealy (1979). A 0 was assigned an old feather, 1 a missing or small pin feather, 2 a feather up to $\frac{1}{3}$ grown, 3 up to $\frac{2}{3}$, 4 up to $\frac{3}{4}$ grown, and 5 a nearly complete or complete feather. In addition, in 1982 I measured the primaries of the right wing to the nearest millimeter from emergence from the skin to the tip.

I used linear regression analysis of both primary and secondary scores of molting red-wings against date to obtain a separate rate of molt for each set of remiges (Bancroft and Woolfenden 1982, Evans 1966, Linz et al. 1983, Newton 1966, Niles 1972, Payne 1969). Analysis of covariance was used to determine if the rates of molt differed between sexes, or locations, or among years. Duncan's multiple range test was used to determine whether or not the mean number of primaries growing simultaneously differed significantly among dates. I used a *t*-test to estimate whether the mean number of growing remiges differed between sexes. $P \leq 0.05$ was considered significant for all tests.



FIGURE 1. Hatching-year Red-winged Blackbirds captured in North Dakota during 1979, 1980, 1982, and 1983 were segregated by date of collection and according to the number of new primaries developed by each bird during first prebasic molt. The mean number of growing primaries by birds with the same number of new primaries is plotted versus time (numbers represent the number of new primaries).

RESULTS

Temporal differences in the number of remiges growing concurrently.— Red-wings were segregated by date of collection and according to the number of new primaries developed by each bird during first prebasic molt. The mean number of growing primaries by birds with the same number of new primaries were plotted versus time (Fig. 1). The same procedure was repeated with the secondaries.

Red-wings having 1 to 5 new primaries consistently averaged more growing primaries each successive 2-wk period. For example, during 29 July-11 Aug., birds collected with 2 new primaries averaged 2.7 growing primaries (n = 9, SE = 0.23, range = 1-3); from 23 Sept.-7 Oct., they averaged 4.1 growing primaries (n = 14, SE = 0.19, range = 3-5). All birds collected with 7 or 8 new primaries were growing their remaining primaries.

In comparison, only birds with one new secondary showed an increase in the number of growing secondaries each successive 2-wk period. Redwings with one new secondary during the period 12 Aug.-25 Aug. were growing 1.5 secondaries (n = 8, SE = 0.19, range 1-2); those collected with one new secondary during 21 Oct.-3 Nov. were growing 3.7 secondaries (n = 30, SE = 0.24, range = 1-5). Red-wings collected with 2 or 3 new secondaries showed no differences in the number of growing

Location	Year	Sex	n	Rate of primary feather growth (duration of molt in days)	Number of primaries growing concur- rently (SE)	Rate of secondary feather growth (duration of molt in days)	Number of secon- daries growing concur- rently (SE)
Alice	1979	Male	479	0.51 (88)	2.8 (0.05)	0.37 (81)	1.7 (0.06)
	1980	Male	395	0.43 (105)	3.3 (0.05)	0.29 (103)	2.1 (0.07)
		Female	378	0.38 (118)	2.9 (0.05)	0.28 (107)	2.1 (0.07)
Harwood	1980	Male	343	0.65 (69)	3.1 (0.05)	0.43 (70)	1.3 (0.07)
		Female	80	0.71 (63)	2.7 (0.12)	0.51 (59)	1.2 (0.12)
	1982	Male	322	0.65 (69)	3.2 (0.07)	0.35 (86)	1.2 (0.06)
		Female	283	0.62 (73)	2.7 (0.07)	0.34 (88)	1.0 (0.09)

TABLE 1. Rate of primary and secondary molt (points per day) and number of primaries and secondaries molted concurrently by hatching-year Red-winged Blackbirds at two roosts in North Dakota.

secondaries as the season progressed. Birds with 4 or 5 new secondaries were usually growing their remaining secondaries.

Sex and interpopulation differences in molt.—The molt scores of the 9 primaries and 6 secondaries of 2280 molting hatching-year red-wings (males only in 1979) were analyzed (Table 1). Rate of primary and secondary molt did not differ between sexes at Harwood or Alice. Molt scores of both sexes increased significantly faster in the Harwood population than in the Alice population. Furthermore, the percentage of molting birds tended to be higher at Alice than at Harwood (Fig. 2).

In 1980 and 1982 males grew more primaries simultaneously than did females. The number of primaries grown simultaneously by each sex did not differ between Alice and Harwood in 1980 and 1982. Males collected at Alice in 1979, however, were growing fewer primaries than those collected in 1980 and 1982.

The sexes differed only slightly in the number of growing secondaries. Males and females at Alice grew more secondaries concurrently than those at Harwood. The number of secondaries grown simultaneously by males differed among years at Alice but not at Harwood.

In 1982 the rate of primary growth at Harwood, as determined by regression analysis, was 11.9 mm/d for males and 9.4 mm/d for females. Thus each growing primary of males and females grew a mean of 3.7 mm (11.9 mm/3.2 growing primaries) and 3.5 mm (9.4 mm/2.7 growing primaries)/d, respectively.

DISCUSSION

Number of remiges growing concurrently.—Dolnik and Gavrilov (1980) concluded that Chaffinches (Fringilla coelebs) that begin molt early in the season tend to replace feathers at a slower rate than those that begin molt late in the season. Similarly, my data show that hatching-year red-



FIGURE 2. The percentage of hatching-year Red-winged Blackbirds molting Aug.-Oct. (1979, 1980, 1982) in 2 populations located near Alice (n = 1166) and Harwood (n = 1314), North Dakota.

wings that began molt in July and August grew fewer primaries concurrently than those that began molt in September or later (Fig. 1). Assuming that (1) the growth of individual primaries is independent of normal environmental factors (Chilgren 1978), (2) regardless of size, individual primaries take a similar amount of time to complete growth (Dhondt 1973, Evans 1966, Newton 1966, Seel 1976), and (3) there is little variation in the length of time required by corresponding feathers of different birds to complete growth (Mewaldt and King 1978); the average number of growing feathers will be proportional to the rate of molt (Snow 1965). If this is true, hatching-year red-wings vary greatly in duration of molt. For example, in this study, birds with 2 new primaries had a mean of 3.1 growing primaries, with a range of 2-5. In accordance with Snow (1965), birds growing two primaries would molt 1/3 slower than average and those birds growing five primaries would molt 60% faster than average. This tends to synchronize molt within the population.

Synchronization of molt within the population enables the birds to migrate as a group without great disparity in individual flying ability. On the other hand, birds growing many flight feathers concurrently must meet additional energy costs and may be more susceptible to predation. A late nesting season, and hence a delayed molt, may reduce the survival rate of hatching-year red-wings and thus act as a natural population regulator.

Comparison of sexes.—Molt of the remiges of hatching-year male and female red-wings proceeds at a similar rate. Since the linear dimensions of male red-wings are about 18% longer than those of females (Powers 1970), the males must grow more remiges per day than females to maintain the same rate of molt. Males could increase their rate of molt by (1) growing individual remiges faster, (2) growing more remiges simultaneously (Evans 1966, Newton 1966), or (3) a combination of the two. Males grew each individual primary only 5% faster (3.5 mm/d/growing remex-3.7 mm/d/growing remex) than did the females, which is insufficient for the males to maintain the same rate of molt as the females. However, males as a population grew significantly more remiges concurrently than females in my study area. Thus the population data indicate that males synchronize molt with females by a combination of growing individual remiges faster and by growing more remiges simultaneously than females. A capture/recapture study of a large number of males and females would clarify their molt strategies.

Other investigators have noted sex-specific molt strategies in red-wings. Selander and Giller (1960) provided evidence that a higher percentage of female red-wings undergo complete first prebasic molt than males. Greenwood et al. (1983) found that females are more likely to have a prealternate molt than males. Since there are pronounced behavioral differences between the sexes during migration (i.e., sex-specific migration patterns, roosting behavior, and food habits), it may be more important for an individual to synchronize molt with other individuals of the same sex than with individuals of the opposite sex.

Interpopulation differences in phenology of molt.—Weatherhead and Bider (1979) and Weatherhead (1981) found that the number of birds using a particular roost may vary from day to day and from year to year. Furthermore, the rate of population increase varies between roosts (Weatherhead 1981). I attribute the differences in the estimated duration of molt between the Alice and Harwood populations to the amount of immigration and emigration exhibited by the population. The Alice population is located along a major migration route and consisted of many feeding flocks of hatching-year and after hatching-year red-wings. The Harwood population is located 60 km east of the Drift Plains and the associated migration route. This population appeared to consist of a single flock of hatching-year birds.

Red-wings normally remain within 200 km of their breeding area until molt is complete (Dolbeer 1978, 1982). Dolbeer's analysis of banding returns, however, indicates that birds nesting in western Canada and New England may migrate during August and September. Molt would not be complete during the earlier part of this period. Meanley and Bond (1970) suggest that primaries 8 and 9 must be at least ²/₃ grown before Red-winged Blackbirds will migrate from the Patuxent, Maryland area. Throughout the period of molt, the percentage of molting birds remained higher at Alice than at Harwood (Fig. 2). Apparently, flocks of redwings leave the Alice area upon completion of molt and flocks consisting of birds less advanced in molt arrive from the north during the same period (Linz et al. 1983). The Harwood population may be less dynamic than the Alice population with fewer birds moving into or out of the area. That is, birds that have completed molt may tend to stay with the flock. I suggest that if environmental conditions are favorable, birds that have completed molt early may remain with the flock, thus maintaining flock integrity. On the other hand, individual red-wings may leave Harwood upon completion of molt and be replaced by birds in a similar stage of molt.

SUMMARY

In summary, (1) individuals that begin molt earlier in the season grow fewer remiges concurrently than those that begin molt later, (2) apparently first prebasic molt of red-wings is synchronized within and between sexes, and (3) the amount of turnover in a migratory population using a roost varies between roosts (i.e., roosts are more or less dynamic).

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LITERATURE CITED

- ALLEN, A. A. 1914. The Red-winged Blackbird: a study in the ecology of a cat-tail marsh. Proc. Linn. Soc. NY 24-25:43-128.
- BANCROFT, G. T., AND G. E. WOOLFENDEN. 1982. The molt of Scrub Jays and Blue Jays in Florida. Ornithological Monographs No. 29. viii + 51 pp.
- CHILGREN, J. D. 1978. Effects of photoperiod and temperature on postnuptial molt in captive White-crowned Sparrows. Condor 80:222-229.
- DHONDT, A. A. 1973. Postjuvenile and postnuptial moult in a Belgian population of Great Tits, *Parus major*, with some data on captive birds. Gerfaut 63:187-209.
- DOLBEER, R. A. 1978. Movement and migration patterns of Red-winged Blackbirds: a continental overview. Bird-Banding 49:17-34.
- -----. 1982. Migration patterns for age and sex classes of blackbirds and starlings. J. Field Ornithol. 53:28-46.
- DOLNIK, V. R., AND V. M. GAVRILOV. 1980. Photoperiod control the molt cycle in the Chaffinch (Fringilla coelebs). Auk 97:50-62.
- DUNSON, W. A. 1965. Physiological aspects of the onset of molt in the Red-winged Blackbird. Condor 67:265-269.
- DWIGHT, J. 1900. The sequence of plumages and moults of the passerine birds of New York. Ann. New York Acad. Sci. 13:73-360.
- EVANS, P. R. 1966. Autumn movements, moult and measurements of the Lesser Redpoll, Carduelis flammea carbaret. Ibis 108:183-216.
- GREENWOOD, H., P. J. WEATHERHEAD, AND R. D. TITMAN. 1983. A new age- and sexspecific molt scheme for the Red-winged Blackbird. Condor 85:104-105.

- JAMES, F. C., R. T. ENGSTROM, AND C. NESMITH. 1984. Inferences about population movements of Red-winged Blackbirds from morphological data. Am. Midl. Nat. 111: 319-331.
- LINZ, G. M., S. B. BOLIN, AND J. F. CASSEL. 1983. Postnuptial and postjuvenal molts of Red-winged Blackbirds in Cass County, North Dakota. Auk 100:206-209.
- LINZ, G. M., D. L. VAKOCH, J. F. CASSEL, AND R. B. CARLSON. 1984. Food of Redwinged Blackbirds (Agelaius phoeniceus) in sunflower fields and corn fields. Can. Field-Nat. 98:38-44.
- McNICOL, D. K., R. J. ROBERTSON, AND P. J. WEATHERHEAD. 1982. Seasonal, habitat, and sex-specific food habits of Red-winged Blackbirds; implications for agriculture. Can. J. Zool. 60:3282-3289.
- MEANLEY, B. AND G. M. BOND. 1970. Molts and plumages of the Red-winged Blackbird with particular reference to fall migration. Bird-Banding 41:22-27.
- MEWALDT, L. R., AND J. R. KING. 1978. Latitudinal variation in prenuptial molt in wintering Gambel's White-crowned Sparrows. N. Am. Bird Bander 3:138-144.
- MOTT, D. F., R. R. WEST, J. W. WEST, AND J. L. GUARINO. 1972. Food of the Redwinged Blackbird in Brown County, South Dakota. J. Wildl. Manage. 36:983-987.
- NEWTON, I. 1966. The moult of the Bullfinch Pyrrhula pyrrhula. Ibis 108:41-67.
- NILES, D. M. 1972. Molt cycles of Purple Martins (Progne subis). Condor 74:61-71.
- ORIANS, G. H. 1961. The ecology of blackbird (Agelaius) social systems. Ecol. Monogr. 31:285-312.
- PAYNE, R. B. 1969. Breeding seasons and reproductive physiology of Tricolored Blackbirds and Red-winged Blackbirds. Univ. Calif. Publ. Zool. 90.
- POWERS, D. M. 1970. Geographic variation of Red-winged Blackbirds in central North America. Univ. Kans. Mus. Nat. Hist. Misc. Publ. 19:1-83.
- SEALY, S. G. 1979. Prebasic molt of the Northern Oriole. Can. J. Zool. 57:1473-1478.
- SEEL, D. C. 1976. Moult in five species of Corvidae in Britain. Ibis 118:491-536.
- SELANDER, R. K., AND D. R. GILLER. 1960. First-year plumages of the Brown-headed Cowbird and Red-winged Blackbird. Condor 62:202-214.
- SMITH, L. B. AND R. D. BIRD. 1969. Autumn flocking habits of the Red-winged Blackbird in southern Manitoba. Can. Field-Nat. 83:40-47.
- SNOW, D. W. 1965. The molt enquiry. Fourth report. Bird Study 12:135-142.
- STEWART, R. E. 1975. Breeding birds of North Dakota. Tri-College Center for Environmental Studies, Fargo, North Dakota.
- WEATHERHEAD, P. J., AND J. R. BIDER. 1979. Management options for blackbird problems in agriculture. Phytoprotection 60:145-155.
- ——. 1981. The dynamics of Red-winged Blackbird populations at four late summer roosts in Quebec. J. Field Ornithol. 52:222-227.
- WRIGHT, P. L., AND M. H. WRIGHT. 1944. The reproductive cycle of the male Redwinged Blackbird. Condor 46:46-59.

Colorado Cooperative Wildlife Research Unit, Colorado State University, Fort Collins, Colorado 80523 (Send reprint requests to: Denver Wildlife Research Center, Bldg 16, Denver Federal Center, Denver, Colorado 80225-0266). Received 25 Apr. 1985; accepted 22 Dec. 1985.