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## FLIGHT FEATHER MOLT IN YELLOW-HEADED BLACKBIRDS (*XANTHOCEPHALUS XANTHOCEPHALUS*) IN NORTH DAKOTA

DANIEL J. TWEDT<sup>1,2,4</sup> AND GEORGE M. LINZ<sup>3</sup>

**ABSTRACT.**—Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*) in central North Dakota undergo prebasic molt or prejuvenile molt during late summer. Nestling Yellow-headed Blackbirds initiate a complete prejuvenile molt, grow their primary and secondary regimens in about 40 days, completing molt after they leave the nest by the first week in August. Remiges are not replaced during the subsequent preformative molt, being retained until the second prebasic molt. Nonlinear (logistic) regression of primary remex growth during definitive prebasic molts of Yellow-headed Blackbirds indicated 38 days were required to complete the linear phase of growth (between 10% and 90% of total primary length). Males added 19.5 mm/d and females added 15.7 mm/d to the total length of all primaries during this linear growth phase; an average of 4–5 mm per primary remex per day. Definitive prebasic molting of primary remiges in males and females was initiated in late June, after nesting and brood rearing were completed. Molts of Yellow-headed Blackbirds were completed by early September, before birds emigrated from North Dakota during mid-September. Because of their comparatively early completion of molt and emigration from the state, as well as their more diverse diet, agricultural depredation caused by Yellow-headed Blackbirds in North Dakota is likely less than that of Red-winged Blackbirds and Common Grackles. Received 16 September 2014. Accepted 27 March 2015.

**Key words:** blackbirds, crops, feathers, Icteridae, molt, North Dakota, *Xanthocephalus xanthocephalus*, Yellow-headed Blackbird.

Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*) breed in western and central North America (Twedt and Crawford 1995). The core of the Yellow-headed Blackbird breeding distribution is the Prairie Pothole Region of the northern Great Plains, where about 11.6 million birds nest (Peer et al. 2003). Trend analyses of North American Breeding Bird Survey data indicate that the continental population of Yellow-headed Blackbirds and the population within the Prairie Pothole Region have remained unchanged between 1966 and 2012 (Sauer et al. 2014).

Yellow-headed Blackbirds generally nest and roost in wetlands that contain dense growths of cattails (*Typha* spp.) and other emergent vegetation (e.g., *Scirpus* or *Phragmites* spp.). During late summer, mixed flocks of blackbirds, largely consisting of Red-winged Blackbirds (*Agelaius phoeniceus*), Common Grackles (*Quiscalus quiscula*), and Yellow-headed Blackbirds emanate from wetland roosts to feed in nearby ripening agricultural fields. These flocks are highly visible, as they often

number in the thousands, and thus draw the attention and ire of farmers. Although Red-winged Blackbirds and Common Grackles are responsible for the majority of the depredation to these crops, particularly sunflowers, Yellow-headed Blackbirds, which have a more diverse diet, also contribute to economic losses (Twedt et al. 1991, Homan et al. 1994, Peer et al. 2003).

Yellow-headed Blackbirds, like most blackbirds (Icteridae), exhibit a complex basic strategy (CBS) of molt cycles (Howell et al. 2003). Birds using this molt strategy initiate their first complete molt, the prejuvenile molt (first prebasic molt; Howell et al. 2003) as nestlings. Molt complexity arises after fledging, from an inserted first-cycle molt, termed a preformative molt, which is not repeated in subsequent molt cycles. For all North American blackbirds, except Yellow-headed Blackbird, the preformative molt is a complete molt wherein flight feathers (remiges) are typically replaced: a characteristic shared by only 27 of 288 North American species (Pyle 1997). Yellow-headed Blackbirds, on the other hand, have a more common partial or incomplete preformative molt (shared by 252 of 288 species), wherein they retain their juvenile flight feathers (remiges and rectrices) and only head and body feathers are molted (Pyle 1997). Thus, juvenile primary and secondary remiges are not molted until the second prebasic molt, which is a complete molt that typically commences at about one year of age. This complete

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definitive prebasic molt is repeated annually thereafter (Howell et al. 2003).

The prebasic molt of blackbirds is an energetically expensive process that coincides with late-summer flocking and likely influences the feeding ecology and migratory behavior of these blackbirds (Lustick 1970). Because the energetic demands of molt are contemporaneous with depredations to agriculture in the northern Great Plains (Linz et al. 2011, Klosterman et al. 2013), we undertook an assessment of molt biology of Yellow-headed Blackbirds to gain insight into how molt status may influence depredation of crops and affect migration. Focusing on the characteristics and phenology of flight feather molt of Yellow-headed Blackbirds in central North Dakota, our objectives were: (1) to determine the onset, rate, and progression of molt in Yellow-headed Blackbirds as assessed from primary and secondary remiges, and (2) to determine sex and age specific differences in molt phenology.

## METHODS

*Study Area.*—We assessed molt status of Yellow-headed Blackbirds from central North Dakota, primarily Benson and Wells counties but also some from the adjacent counties of Eddy, Nelson, Pierce, and Ramsey. This area is primarily agricultural and contains numerous wetlands (Ralston et al. 2007). Nelms et al. (1994) estimated the regional breeding population at 19.3 Yellow-headed Blackbird pairs per square kilometer. This area of central North Dakota is also in the migratory corridor of Yellow-headed Blackbirds that breed in more northern latitudes (Royall et al. 1971).

Standard feather and molt designations follow those of Humphrey and Parkes (1959) as modified by Howell et al. (2003) and Howell and Pyle (2015) and Wolfe et al. (2014). Male and female Yellow-headed Blackbirds in basic plumage were captured from 27 May to 4 June 1987, whereas birds in juvenile, formative, or basic plumage were captured from 1 July to 18 September 1987 and from 12 June to 12 September 1988. We captured birds using decoy traps and mist nets, or collected birds via shooting. After recording their molt status, captured birds were banded (permit # 08567, US Department of Agriculture, Wildlife Services, National Wildlife Research Center) and released. We only measured birds in juvenile plumage after they had fledged, not as nestlings.

We recorded the feather identification number of growing or missing primary feathers ( $P_1$ – $P_9$ ) and the length (mm) of all new, growing, or missing primaries until all primaries were fully-grown. If all primaries were fully-grown, we recorded the length of  $P_1$  (proximal) and  $P_9$  (distal), and for a random selection of individuals, we recorded the length of all primaries. Lengths of unmeasured fully-grown primaries,  $P_2$  through  $P_8$ , were estimated from  $P_1$  and  $P_9$  via multivariate regression. We considered the onset of molt to be the loss of  $P_1$ , and primary molt was considered complete when  $P_9$  was fully-grown. Primary remex length was also measured repeatedly on captive Yellow-headed Blackbirds, that were maintained as decoys with ad libitum food (poultry feed and mixed grains) and water, within large ( $3 \times 9$  m) traps.

We recorded the status of each secondary feather ( $S_1$ – $S_8$ ) as: 1 for an old feather, 2 for a missing feather, 3 for a growing feather, or 4 for a new complete feather. Molt of secondaries commenced with the loss of any secondary and was completed when all secondaries were fully-grown.

Prejuvenile molt of Yellow-headed Blackbirds begins while they are still in the nest (Ammann 1938, Twedt 1990). However, we only measured and recorded remex lengths after birds had fledged. Preformative molt of Yellow-headed Blackbirds occurs after fledging but it is a partial molt wherein juvenile primary and secondary remiges are retained. Thus, we considered prejuvenile molt of primary and secondary remiges to be complete when all feathers within each of these tracts, respectively, were fully grown.

Males undergoing prejuvenile molt were aged as hatching-year (HY), males undergoing second prebasic molt were aged as second-year (SY), whereas males undergoing subsequent definitive ( $\geq 3$ rd) prebasic molt were aged as after second-year (ASY) unless all remiges had been shed during the molt; in which case, we could not distinguish SY males from ASY males so they were categorized as AHY males. We aged females undergoing prejuvenile molt as HY and females undergoing definitive prebasic molt as AHY. We used Student's *t*-tests to compare the number of growing or missing primary remiges and secondary remiges between sex and age classes.

Nonlinear (logistic) regression of primary length against time was used to obtain age-sex specific growth curves for each primary remex during

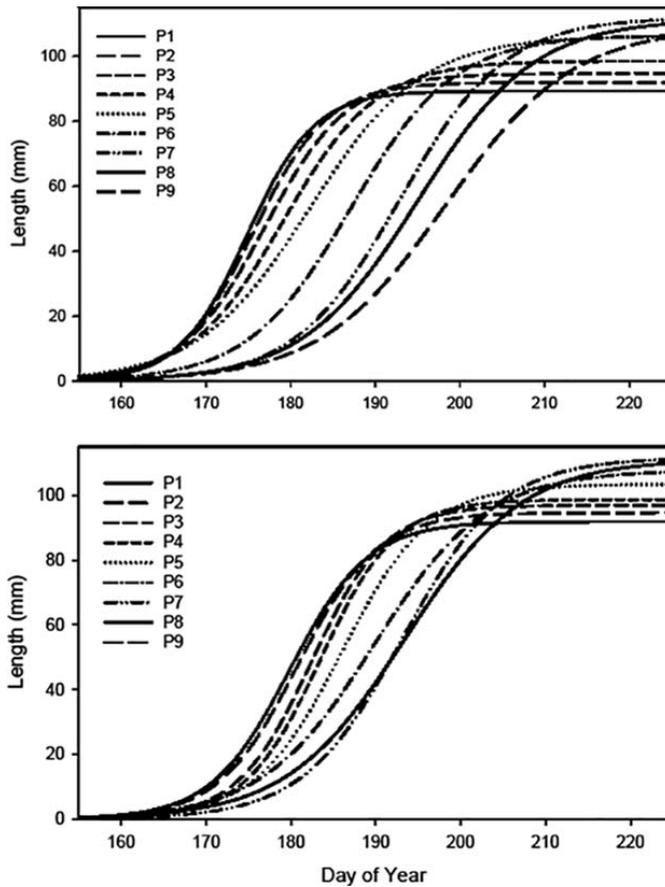


FIG. 1. Growth curves determined from logistic regressions for primary regimes P<sub>1</sub> (left) sequentially through P<sub>9</sub> (right) for second-year (SY; Fig. 1-upper) and after second-year (ASY; Fig. 1-lower) male Yellow-headed Blackbirds in central North Dakota between 1 June and 15 September. Age could not be assigned after all remiges were shed; thus, curves for P<sub>7</sub>–P<sub>9</sub> also include data for adult males of undetermined age (after hatching-year, AHY).

definitive prebasic molt for males and females and during 2nd prebasic molt for males as:

$$\text{Length (mm)} = \frac{A}{1 + Be^{[K_L(t_i - t_0)]}}$$

where  $K_L$  is the logistic growth constant,  $A$  is the asymptotic maximum length,  $B$  is the curve displacement,  $t_i$  is time (day of year), and  $t_0$  is the day of year of initial primary loss. We obtained our initial estimates of  $t_0$  from plots of primary length against time. The estimated regression parameters ( $A$ ,  $B$ , and  $K$ ) were then iteratively used to predict the onset of primary molt ( $t_0$ ) for individual birds. We then used the mean predicted  $t_0$  in regressions to obtain final parameter estimates.

The asymptotic end points of logistic regressions render estimates near their extremities suspect; therefore, as suggested by Ricklefs (1967), we determined the time interval ( $t_{10-90}$ ) required for growth for 10% to 90% of the asymptotic total length. Yellow-headed Blackbirds molt and replace their primaries sequentially from P<sub>1</sub> through P<sub>9</sub>. We used chi-square goodness of fit tests to compare observed age-sex specific growth rates of P<sub>1</sub> through P<sub>9</sub> with predicted growth rates from regression equations. We restricted comparison to between 10% and 90% of the asymptotic maximum length. Separate comparisons of growth rates were made for each primary. Statistical analyses were performed using SAS software (SAS Institute Inc., Cary, NC, USA).

TABLE 1. Mean number ( $\pm$  SE) of growing or missing primary and secondary remiges during juvenile molt in hatching-year (HY), second prebasic molt in second-year (SY), and definitive prebasic molt in after second-year (ASY) or after hatching-year (AHY) Yellow-headed Blackbirds from central North Dakota.

Sex	Age	N <sup>a</sup>	Primaries	N <sup>b</sup>	Secondaries
Female	HY	70	3.47 $\pm$ 0.34	58	6.50 $\pm$ 0.33
	AHY	404	3.54 $\pm$ 0.09	453	4.20 $\pm$ 0.10
Male	HY	122	3.62 $\pm$ 0.26	121	7.12 $\pm$ 0.19
	SY <sup>c</sup>	234	4.56 $\pm$ 0.09	188	3.47 $\pm$ 0.10
	ASY <sup>c</sup>	250	4.71 $\pm$ 0.10	203	3.31 $\pm$ 0.10
	AHY	922	3.51 $\pm$ 0.06	927	3.96 $\pm$ 0.06

<sup>a</sup> Number of birds molting  $\geq 1$  primary remex.

<sup>b</sup> Number of birds molting  $\geq 1$  secondary remex.

<sup>c</sup> Ages could not be separated after molt of all primary remiges, thus SY and ASY males are included in AHY.

## RESULTS

**Prejuvenile Molt.**—Some fledged individuals of both sexes had completed growth of juvenile primary remiges on 2 July. Growth of juvenile secondary remiges was first observed completed on 24 June for males and 1 July for females. By the first week of August, >90% of HY males and females had completed molt of primary remiges (Fig. 1). Numbers of growing primary remiges during prejuvenile molt did not differ significantly between sexes ( $T_{190} = 0.36$ ,  $P = 0.72$ ; Table 1). Similarly, the numbers of growing secondary remiges did not differ between sexes ( $T_{177} = 1.74$ ,  $P = 0.08$ ; Table 1).

**Prebasic Molt.**—The first observed loss of  $P_1$  occurred on 22 June for males and on 24 June for females. Females and males were first observed with all basic plumage primary remiges completely grown on 18 and 19 August, respectively.

Secondary remiges molted from the extremities,  $S_1$  and  $S_8$ , toward the center, with  $S_3$  or  $S_4$  being the last secondary remex replaced. The first observed loss of a secondary occurred on 24 June in females and on 2 July in males. On 3 August females were first observed with completely grown, basic-plumage, secondary remiges, whereas the first males were observed with fully grown basic-plumage, secondary remiges on 18 August.

Males undergoing second prebasic molt tended to initiate molt about a week earlier than males undergoing definitive prebasic molt, with ~90% of SY males undergoing molt by mid-July (Fig. 1). Females exhibited a more erratic pattern of prebasic molt initiation. Some females had completed prebasic molt by early August, whereas

other birds had yet to initiate prebasic molt at that time (Fig. 2). Yet by early August, ~90% of the female population was undergoing prebasic molt. Thus, by the first week of September, the proportion of females having completed prebasic molt approximated the proportion of males that had completed prebasic molt (Fig. 2).

For males undergoing second prebasic molt (SY males) and males undergoing subsequent (definitive) prebasic molt (ASY males), neither the numbers of growing or missing primary remiges ( $T_{482} = 1.07$ ,  $P = 0.28$ ) nor secondary remiges ( $T_{389} = 1.12$ ,  $P = 0.26$ ) differed between these age classes (Table 1).

The numbers of growing or missing primary remiges during prebasic molt did not differ significantly between sexes ( $T_{1324} = 0.29$ ,  $P = 0.78$ , Table 1). We noted a maximum of eight primaries, on the same wing, were concurrently growing or missing on AHY birds. However, females had more growing or missing secondary remiges than did males ( $T_{1378} = 2.11$ ,  $P = 0.04$  Table 1).

**Rate of Molt.**—Logistic regression estimates indicated the onset of primary molt ( $t_0$ ) occurred 5 days earlier for females than for males (Table 2). The rate of growth among primaries appeared to follow a different pattern in males than in females. In SY (Fig. 1-upper) and ASY (Fig. 1-lower) males, later molting primaries ( $P_6$ – $P_9$ ) tended to grow more slowly than early molting primaries ( $P_1$ – $P_5$ ). The opposite occurred in AHY females (Fig. 2), where later molting primaries ( $P_6$ – $P_9$ ) grew more rapidly than early molting primaries. Regression estimates for all primaries indicated growth rates slowed as each primary neared completion.

Captive birds exhibited arrested or suspended molt (Freed and Cann 2012), but we found that once a feather was lost, it re-grew to completion. Growth rates of individual primaries for males as estimated from regression equations from free-living birds did not differ from growth rates of primaries from SY males ( $\chi^2 = 7.25$ ,  $df = 27$ ,  $P = 0.99$ ) and AHY males ( $\chi^2 = 18.19$ ,  $df = 30$ ,  $P = 0.95$ ) in captivity. For AHY females, growth rates of primaries estimated from regression equations differed from the observed growth rate of captive females ( $\chi^2 = 79.92$ ,  $df = 57$ ,  $P = 0.02$ ): observed growth rates of early molting primaries ( $P_1$ – $P_4$ ) significantly underestimated the observed growth rates of captive females ( $\chi^2 > 12.6$ ,  $df \geq 5$ ,  $P < 0.05$ ), whereas observed growth rates of later molting primaries ( $P_5$ – $P_9$ ) adequately fit the observed

TABLE 2. Estimated logistic regression coefficients ( $\pm$  asymptotic SE) for growth of primary remiges (P1–P9) in adult [second-year (SY), after secondyear (ASY), and after hatching-year (AHY)] Yellow-headed Blackbirds from central North Dakota, with estimated day of year growth commenced ( $t_0 \pm$  SD), and the time (days) required for growth from 10% to 90% of their asymptotes ( $t_{10-90}$ ).

Sex	Age	Primary	Asymptote A	Growth constant $K_L$	Displacement $B^a$	Day of year $t_0$	Days $t_{10-90}$
Female	AHY	P <sub>1</sub>	73.24 $\pm$ 1.22	0.113 $\pm$ 0.010	4.62 $\pm$ 0.40	159 $\pm$ 17	38.8
		P <sub>2</sub>	75.75 $\pm$ 1.27	0.114 $\pm$ 0.010	3.99 $\pm$ 0.35	165 $\pm$ 17	38.6
		P <sub>3</sub>	78.46 $\pm$ 1.31	0.113 $\pm$ 0.010	4.37 $\pm$ 0.38	162 $\pm$ 17	39.2
		P <sub>4</sub>	81.42 $\pm$ 1.35	0.113 $\pm$ 0.010	4.27 $\pm$ 0.37	165 $\pm$ 17	38.2
		P <sub>5</sub>	83.09 $\pm$ 0.00 <sup>a</sup>	0.122 $\pm$ 0.00 <sup>a</sup>	3.83 $\pm$ 0.00 <sup>a</sup>	170 $\pm$ 15	36.1
		P <sub>6</sub>	90.56 $\pm$ 1.22	0.143 $\pm$ 0.011	4.88 $\pm$ 0.36	174 $\pm$ 13	30.7
		P <sub>7</sub>	90.30 $\pm$ 1.08	0.158 $\pm$ 0.011	3.76 $\pm$ 0.25	188 $\pm$ 12	27.8
		P <sub>8</sub>	89.00 $\pm$ 1.05	0.157 $\pm$ 0.011	4.92 $\pm$ 0.25	189 $\pm$ 19	27.9
		P <sub>9</sub>	86.08 $\pm$ 1.19	0.149 $\pm$ 0.010	3.30 $\pm$ 0.20	194 $\pm$ 14	29.5
Male	SY	P <sub>1</sub>	89.33 $\pm$ 1.27	0.250 $\pm$ 0.019	4.26 $\pm$ 0.31	169 $\pm$ 7	17.6
		P <sub>2</sub>	91.99 $\pm$ 1.50	0.228 $\pm$ 0.018	3.56 $\pm$ 0.28	170 $\pm$ 7	19.3
		P <sub>3</sub>	94.75 $\pm$ 0.97	0.203 $\pm$ 0.035	3.33 $\pm$ 0.54	171 $\pm$ 7	21.7
		P <sub>4</sub>	98.62 $\pm$ 1.96	0.181 $\pm$ 0.014	3.02 $\pm$ 0.23	173 $\pm$ 7	24.2
		P <sub>5</sub>	106.27 $\pm$ 3.38	0.151 $\pm$ 0.012	2.97 $\pm$ 0.21	175 $\pm$ 7	29.0
		P <sub>6</sub>	106.50 $\pm$ 5.07	0.164 $\pm$ 0.016	3.78 $\pm$ 0.30	179 $\pm$ 7	26.8
	SY and AHY	P <sub>7</sub>	111.99 $\pm$ 0.49	0.161 $\pm$ 0.006	4.21 $\pm$ 0.16	184 $\pm$ 8	27.3
		P <sub>8</sub>	111.45 $\pm$ 0.70	0.146 $\pm$ 0.006	4.35 $\pm$ 0.17	185 $\pm$ 9	30.1
		P <sub>9</sub>	109.11 $\pm$ 0.95	0.133 $\pm$ 0.006	3.99 $\pm$ 0.17	188 $\pm$ 11	32.9
Male	ASY	P <sub>1</sub>	91.90 $\pm$ 2.00	0.216 $\pm$ 0.019	4.38 $\pm$ 0.37	173 $\pm$ 14	20.4
		P <sub>2</sub>	94.65 $\pm$ 2.14	0.214 $\pm$ 0.019	4.24 $\pm$ 0.37	174 $\pm$ 14	20.5
		P <sub>3</sub>	96.96 $\pm$ 2.09	0.229 $\pm$ 0.021	4.32 $\pm$ 0.38	176 $\pm$ 12	19.2
		P <sub>4</sub>	98.66 $\pm$ 2.19	0.226 $\pm$ 0.020	4.32 $\pm$ 0.27	177 $\pm$ 11	19.5
		P <sub>5</sub>	103.37 $\pm$ 2.45	0.195 $\pm$ 0.016	3.93 $\pm$ 0.31	179 $\pm$ 9	22.5
		P <sub>6</sub>	107.71 $\pm$ 3.24	0.151 $\pm$ 0.014	3.78 $\pm$ 0.32	181 $\pm$ 10	29.2
	ASY and AHY	P <sub>7</sub>	111.55 $\pm$ 0.56	0.171 $\pm$ 0.007	4.78 $\pm$ 0.20	184 $\pm$ 9	25.7
		P <sub>8</sub>	111.14 $\pm$ 0.80	0.144 $\pm$ 0.007	4.47 $\pm$ 0.21	183 $\pm$ 11	30.5
		P <sub>9</sub>	108.34 $\pm$ 1.01	0.137 $\pm$ 0.007	4.14 $\pm$ 0.21	188 $\pm$ 11	32.0

<sup>a</sup> standard error not estimable.

growth rates of primaries from captive females ( $\chi^2 < 4.6$ ,  $df \geq 3$ ,  $P > 0.20$ ).

## DISCUSSION

*Juvenile Plumage.*—Juvenile plumage is acquired by a complete prejuvenile molt (Humphrey and Parkes 1959) which begins when the nestlings are  $\sim 2$  days old and is completed in about 40 days when fledged birds are independent. Formative plumage (Howell et al. 2003) is acquired by a partial preformative molt. The preformative molt includes replacement of some of the head and body feathers; however, neither primary nor secondary remiges are replaced (Ammann 1938, Twedt and Crawford 1995). We found fledged birds of both sexes with complete sets of fully grown juvenile primary remiges on 2 July and  $>90\%$  of all HY birds had completed prejuvenile molt of primary remiges by the first week of August (Fig. 1). As the linear dimensions of

male remiges are about 20% longer than female remiges (Twedt 1990) and the numbers of growing remiges are essentially the same between sexes (Table 1), we surmise the males grow  $\sim 20\%$  more feather per day than do females. These rates resulted in synchronization of molt between sexes within the HY population.

During the first week of August, nearly 90% of HY Yellow-headed Blackbirds had completed molt, while Red-winged Blackbirds were at this time just initiating their preformative molt. In Red-winged Blackbirds, the preformative molt may be a complete molt wherein all feathers, including remiges, are regenerated (Selander and Giller 1960). As a consequence, in a study at Cass County, North Dakota roost sites, Linz and Fox (1983) did not find HY Red-winged Blackbirds with completed preformative molt until 18 September. Many HY Red-winged Blackbirds do not complete preformative molt until the first

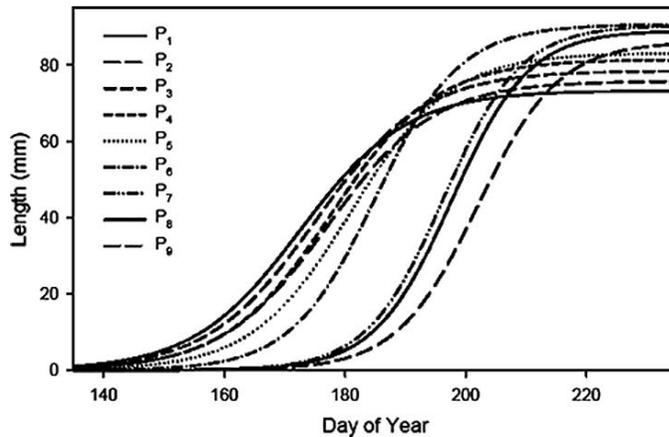


FIG. 2. Growth curves determined from logistic regressions for primary regimens  $P_1$  (left) sequentially through  $P_9$  (right) for after hatching-year (AHY) female Yellow-headed Blackbirds in central North Dakota between 1 June and 15 September.

week in October (Linz 1986). Indeed, on 14 October, >70% of HY Red-winged Blackbirds at study roosts were molting (Linz and Fox 1983). This marked temporal difference in completion of molt between HY Yellow-headed Blackbirds and HY Red-winged Blackbirds likely influences the timing of emigration from our study area, with Yellow-headed Blackbirds leaving several weeks before Red-winged Blackbirds.

*Definitive Basic Plumage.*—Definitive basic plumage (Howell and Pyle 2015) of Yellow-headed Blackbirds is acquired by a complete definitive prebasic molt that begins in North Dakota in mid- to late June and is completed by late August. By early September, nearly all Yellow-headed Blackbirds were aerodynamically, and probably energetically, prepared for migration. Indeed, emigration took place *en masse* during early September, such that by mid-September few Yellow-headed Blackbirds remained in our study area. This exodus of Yellow-headed Blackbirds occurred despite the continued availability of abundant food in unharvested sunflower fields and the continued presence of large numbers of Red-winged Blackbirds and Common Grackles in the study area well into October.

We recognize growth rates from birds in suspended or arrested molt may be atypical; however, we think it is useful to compare primary growth rates from captive birds with predicted growth rates from our logistic regressions on free-ranging birds. Thus, discrepancies between growth rates of captive females and our regression models for  $P_1$  through  $P_4$ , constructed from measurements on

free-living birds, were not unexpected. Arrested molt in captive birds resulted in fewer primaries growing simultaneously than during normal molt. Thus, more energy may be devoted to the growth of fewer primaries, resulting in a higher growth rate (Rohwer et al. 2009). Arrested molt was not a factor after  $P_9$  was shed; therefore, the growth rates of  $P_5$  through  $P_9$  were not impacted by arrested molt. More primaries grow concurrently during the early stages of molt (before completion of  $P_1$ ) than during the latter stages of molt (after  $P_1$  was complete) such that individuals in arrested molt are likely to be growing fewer primaries than those undergoing normal molt (Twedt 1990). This is contrary to Snow (1965), who found that individuals molting different numbers of primaries did so at rates proportional to the number of growing.

Although we found no evidence of differing numbers of growing primary remiges between sexes in free-ranging birds, we did detect sex-specific trends in the rate of growth among the sequence of growing primary remiges. Females were erratic in initiating molt, possibly coinciding with termination of nesting or brood rearing (White et al. 1991), but they tended to grow their later molting primary remiges ( $P_6$ – $P_9$ ) at more rapid rates than did males. Similarly, we found female Yellow-headed Blackbirds grew more secondary remiges simultaneously than did males. This increased rapidity of molt may allow females, even those initiating molt later in the summer, to complete molt in synchrony with males, whose later molting primaries grew at a slower rate.

Differences in growth rate, together with the lesser total length of female primary remiges, resulted in both males and females growing between 10% and 90% of their total primary remiges length in about 38 days. Males added 19.5 mm/d and females added 15.7 mm/d to the total length of all primaries during this linear growth phase. This equates to an average per-primary growth rate of 4.4 mm per day for females and 5.5 mm per day for males, which is similar to the 4–5 mm per primary remex per day reported for molt in other species (Dawson 2003, Mallet-Rodrigues 2012).

We found that age-sex differences in Yellow-headed Blackbird prebasic molt phenology exist between SY males, ASY males, and AHY females. Variation in the onset of prebasic molt may be related to the duration of or participation in breeding activities. As documented for many north-temperature passerines (Mewaldt and King 1978), including other Icterids (Selander 1958, Payne 1969, Sealy 1979, Linz et al. 1983), Yellow-headed Blackbirds do not appear to undertake prebasic molt until they have completed nesting. Male Yellow-headed Blackbirds may be polygynous: Males often do not breed until their third summer and males have a reduced parental role compared to the females (Patterson et al. 1980). We found that the relative timing of onset of prebasic molt among males was related to the presumed degree of participation each age class had in nesting activities. That is, SY males (generally nonbreeding) began molt before ASY males (Fig. 1). This relationship of prebasic molt and nesting activity is similar to that reported for Red-winged Blackbirds (Linz et al. 1983). The difference in phenology of prebasic molt between SY and ASY males suggests that males may congregate in separate, age specific, groups after the nesting season. Although some breeding male and female Yellow-headed Blackbirds initiate prebasic molt concurrently, in this North Dakota population a larger proportion of males than females initiated molt early. This difference may be attributed to the reduced role of males in rearing young, or the greater heterogeneity of prebasic molt initiation among females may be due to some females reneesting (Dolbeer 1976) or late-nesting (Crawford 1977).

It appeared that molt (prejuvenile and prebasic), along with its underlying physiological changes, was complete or nearly complete before emigration of Yellow-headed Blackbirds from central North Dakota in September. This lends support to the argument advanced by Linz et al. (1983) that local

Red-winged Blackbirds migrated from their study area after completion of preformative or prebasic molt and that continued prevalence of molting birds in the population was due to immigration from more northern latitudes. On the other hand, the morphologically based predictions of Twedt et al. (1994) indicated that a high proportion of local-breeding Yellow-headed Blackbirds remained in this study area despite immigration of birds from more northern breeding areas. Perhaps this apparent difference in migration patterns between these species can be attributed to differences in molt phenology.

Previous research suggested diet influences the extent of depredation on crops that is inflicted by blackbird species, such that the more varied diet of Yellow-headed Blackbirds resulted in fewer depredations than those due to Red-winged Blackbirds and Common Grackles (Twedt et al. 1991, Peer et al. 2003). We conclude that the comparatively early completion of molt and emigration of Yellow-headed Blackbirds from North Dakota essentially removes Yellow-headed Blackbirds from late season depredations and further reduces the impact of this species on agriculture in this region.

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#### LITERATURE CITED

- AMMANN, G. A. 1938. The life-history and distribution of the Yellow-headed Blackbird. Dissertation. University of Michigan, Ann Arbor, USA.
- CRAWFORD, R. D. 1977. Breeding biology of year-old and older female Red-winged and Yellow-headed blackbirds. *Wilson Bulletin* 89:73–80.
- DAWSON, A. 2003. A detailed analysis of primary feather moult in the common starling, *Sturnus vulgaris* – new feather mass increases at a constant rate. *Ibis* 145: E69–E76.

- DOLBEER, R. A. 1976. Reproductive rate and temporal spacing of nesting of Red-winged Blackbirds in upland habitat. *Auk* 93:343–355.
- FREED, L. A. AND R. L. CANN. 2012. Changes in timing, duration, and symmetry of molt of Hawaiian forest birds. *PLoS One* 7:e29834. doi:10.1371/journal.pone.0029834
- HOMAN, H. J., G. M. LINZ, W. J. BLEIER, AND R. B. CARLSON. 1994. Dietary comparisons of adult male Common Grackles, Red-winged Blackbirds, and Yellow-headed Blackbirds in north central North Dakota. *Prairie Naturalist* 26:273–281.
- HOWELL, S. N. G., C. CORBEN, P. PYLE, AND D. I. ROGERS. 2003. The first basic problem: a review of molt and plumage homologies. *Condor* 105:635–653.
- HOWELL, S. N. G. AND P. PYLE. 2015. Use of “definitive” and other terms in molt nomenclature: a response to Wolfe et al. (2014). *Auk: Ornithological Advances* 132: 365–369.
- HUMPHREY, P. S. AND K. C. PARKES. 1959. An approach to the study of molts and plumages. *Auk* 76:1–31.
- KLOSTERMAN, M. E., G. M. LINZ, A. A. SLOWIK, AND H. J. HOMAN. 2013. Comparisons between blackbird damage to corn and sunflower in North Dakota. *Crop Protection* 53:1–5.
- LINZ, G. M. 1986. Temporal, sex, and population characteristics of the first prebasic molt of Red-winged Blackbirds. *Journal of Field Ornithology* 57:91–98.
- LINZ, G. M., S. B. BOLIN, AND J. F. CASSEL. 1983. Postnuptial and postjuvinal molts of Red-winged Blackbirds in Cass County, North Dakota. *Auk* 100:206–209.
- LINZ, G. M. AND G. FOX. 1983. Food habits and molt of Red-winged Blackbirds in relation to sunflower and corn depredation. *Bird Control Seminar Proceedings* 9:167–180. <http://digitalcommons.unl.edu/icwdmbirdcontrol/278> (accessed DD Month YYYY).
- LINZ, G. M., H. J. HOMAN, S. J. WERNER, H. M. HAGY, AND W. J. BLEIER. 2011. Assessment of bird-management strategies to protect sunflowers. *BioScience* 61:960–970.
- LUSTICK, S. 1970. Energy requirements of molt in cowbirds. *Auk* 87:742–746.
- MALLET-RODRIGUES, F. 2012. Replacement and growth of primary feathers in captive Rock Pigeons, *Columba livia* (Aves: Columbidae). *Zoologia* 29:121–125.
- MEWALDT, L. R. AND J. R. KING. 1978. Latitudinal variation of postnuptial molt in Pacific Coast White-crowned Sparrows. *Auk* 95:168–174.
- NELMS, C. O., W. J. BLEIER, D. L. OTIS, AND G. M. LINZ. 1994. Population estimates of breeding blackbirds in North Dakota, 1967, 1981–1982, and 1990. *American Midland Naturalist* 132:256–263.
- PATTERSON, C. B., W. J. ERCKMANN, AND G. H. ORIAN. 1980. An experimental study of parental investment and polygyny in male blackbirds. *American Naturalist* 116: 757–769.
- PAYNE, R. B. 1969. Breeding seasons and reproductive physiology of Tricolored Blackbirds and Red-winged Blackbirds. University of California Publications in Zoology 90:1–137.
- PEER, B. D., H. J. HOMAN, G. M. LINZ, AND W. J. BLEIER. 2003. Impact of blackbird damage to sunflower: bioenergetic and economic models. *Ecological Applications* 13:248–256.
- PYLE, P. 1997. Molt limits in North American passerines. *North American Bird Bander* 22:49–89.
- RALSTON, S. T., G. M. LINZ, W. J. BLEIER, AND H. J. HOMAN. 2007. Cattail distribution and abundance in North Dakota. *Journal of Aquatic Plant Management* 45: 21–24.
- RICKLEFS, R. E. 1967. A graphical method of fitting equations to growth curves. *Ecology* 48:978–983.
- ROHWER, S., R. E. RICKLEFS, V. G. ROHWER, AND M. M. COPPLE. 2009. Allometry of the duration of flight feather molt in birds. *PLoS Biology* 7:e1000132. doi:10.1371/journal.pbio.1000132
- ROYALL JR., W. C., J. L. GUARINO, J. W. DE GRAZIO, AND A. GAMMELL. 1971. Migration of banded Yellow-headed Blackbirds. *Condor* 73:100–106.
- SAUER, J. R., J. E. HINES, J. E. FALLON, K. L. PARDECK, D. J. ZIOLKOWSKI JR., AND W. A. LINK. 2014. The North American Breeding Bird Survey, results and analysis 1966–2012. Version 02.19.2014. USGS, Patuxent Wildlife Research Center, Laurel, Maryland, USA. <http://www.mbr-pwrc.usgs.gov/bbs> (accessed 10 June 2014).
- SEALY, S. G. 1979. Prebasic molt of the Northern Oriole. *Canadian Journal of Zoology*. 57:1473–1478.
- SELANDER, R. K. 1958. Age determination and molt in the Boat-tailed Grackle. *Condor* 60:355–376.
- SELANDER, R. K. AND D. R. GILLER. 1960. First-year plumages of the Brown-headed Cowbird and Redwinged Blackbird. *Condor* 62:202–214.
- SNOW, D. W. 1965. The moult enquiry: fourth report, June 1965. *Bird Study* 12:135–142.
- TWEDT, D. J. 1990. Diet, molt and geographic variation of Yellow-headed Blackbirds, *Xanthocephalus xanthocephalus*. Dissertation. North Dakota State University, Fargo, USA.
- TWEDT, D. J., W. J. BLEIER, AND G. M. LINZ. 1991. Geographic and temporal variation in the diet of Yellow-headed Blackbirds. *Condor* 93:975–986.
- TWEDT, D. J., W. J. BLEIER, AND G. M. LINZ. 1994. Geographic variation in Yellow-headed Blackbirds from the northern Great Plains. *Condor* 96:1030–1036.
- TWEDT, D. J. AND R. D. CRAWFORD. 1995. Yellow-headed Blackbird (*Xanthocephalus xanthocephalus*). The birds of North America online. Number 192.
- WHITE, D. W., E. D. KENNEDY, AND P. C. STOFFER. 1991. Feather regrowth in female European Starlings rearing broods of different sizes. *Auk* 108:889–895.
- WOLFE, J. D., E. I. JOHNSON, AND R. S. TERRILL. 2014. Searching for consensus in molt terminology 11 years after Howell et al.’s “first basic problem.” *Auk* 131: 371–377.