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IMPLICATIONS OF PREBASIC AND A PREVIOUSLY UNDESCRIBED PREALTERNATE MOLT FOR AGING RUSTY BLACKBIRDS

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Abstract. Aging birds often relies on differences in plumage between immatures and adults, and understanding these patterns can improve our ability to discern demographic patterns within populations. We investigated patterns of prebasic molt of the Rusty Blackbird (*Euphagus carolinus*) in fall at Whitehorse, Yukon Territory, and developed a new technique for aging based on characteristics of the head plumage acquired during prebasic molt. Furthermore, we investigated the possibility of a prealternate molt among wintering Rusty Blackbirds on the basis of captures in Mississippi and museum specimens from across the species' winter range. Finally, we examined how a prealternate molt might affect the aging of winter birds by plumage. Rusty Blackbirds completed their prebasic molt by the end of September, and immature birds had a more prominent eye ring and a paler chin than adults, allowing a reliable age determination. Previously, the Rusty Blackbird was thought to attain its breeding plumage through feather wear exclusively, but we discovered a partial prealternate molt in our examinations of live captures (76% molting) and museum specimens (59% molting). The prealternate molt was observed in all age and sex classes, was concentrated along the feather tracts of the head, and peaked in occurrence from mid-February to mid-March, when nearly 90% of birds were molting. Between mid-December and mid-February, the prealternate molt did not appear to interfere with aging birds in the hand by the pattern of the eye ring and chin in basic plumage. Age determination later in the spring, however, remains to be investigated.

Key words: *age determination*, Euphagus carolinus, *Icteridae*, *molt limit*, *prealternate molt*, *prebasic molt*, *Rusty Blackbird.*

Implicancias de la Muda Prebásica y de la Previamente No Descripta Muda Prealterna para Determinar la Edad de *Euphagus carolinus*

Resumen. La determinación de la edad de las aves a menudo se realiza a partir de diferencias de plumaje entre individuos inmaduros y adultos. Entender estos patrones puede mejorar nuestra capacidad de distinguir patrones demográficos dentro de las poblaciones. Investigamos patrones de muda prebásica de *Euphagus carolinus* durante el otoño en Whitehorse, Territorio Yukón, y desarrollamos una nueva técnica para determinar la edad basada en las características de las plumas de la cabeza adquiridas durante la muda prebásica. Además, investigamos la posibilidad de una muda prealterna entre individuos de *E. carolinus* invernantes basándonos en capturas en Mississippi y en especímenes de museo del rango de distribución de invierno de la especie. Finalmente, examinamos cómo una muda prealterna podría afectar la determinación de la edad de las aves invernales a partir del plumaje. *E. carolinus* completa su muda prebásica para fines de septiembre, y las aves inmaduras tienen un anillo ocular más prominente y una barbilla más pálida que los adultos, permitiendo una determinación confiable de la edad. Anteriormente, se pensaba que *E. carolinus* alcanzaba su plumaje nupcial exclusivamente a través de sus plumas, pero nosotros descubrimos una muda prealterna parcial en nuestros exámenes de capturas vivas (muda del 76%) y especimenes de museo (muda del 59%). La muda prealterna fue observada en todas las clases de edad y sexo, se concentró a lo largo del tracto de plumas de la cabeza, y tuvo su pico de ocurrencia desde mediados de febrero a mediados de marzo, cuando cerca del 90% de las aves estaban mudando. Entre mediados de diciembre y mediados de febrero, la muda prealterna no pareció interferir con las determinaciones de la edad de las aves en mano usando el patrón de plumaje básico del anillo ocular y la barbilla. No obstante, la determinación de la edad más adelante en la primavera, todavía queda por investigar.

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INTRODUCTION

In many passerines, juveniles undergo a partial or incomplete first prebasic molt in their year of hatching, while adults have a complete prebasic molt. In these species, young birds (<1 year old) in their first basic plumage can often be distinguished from adults (>1 year old) in basic plumage by molt limits, a visible contrast in appearance between the retained juvenal feathers and the adjacent feathers grown during the first prebasic molt (Pyle 1997). Many species have two distinct plumages, and the change from the basic (nonbreeding) to alternate (breeding) plumage (if any) is achieved by a partial prealternate molt that takes place before the reproductive season (Humphrey and Parkes 1959). A prealternate molt can complicate the process of distinguishing young and adult birds (Mulvihill 1999).

The occurrence and extent of prealternate molt of closely related species and even subspecies can differ considerably (e.g., Lanyon 1975, Banks 1978), possibly in relation to differences in ecology, migratory behavior, or energetic constraints (Banks 1978, Greenwood et al. 1983, Mulvihill and Rimmer 1997). Moreover, age and sex classes within a population can show different degrees of prealternate molt (e.g., Selander 1958), which may be linked to different reproductive strategies (Pyle and Howell 2004). New World blackbirds (Icteridae) cover a large spectrum of variation in the occurrence of prealternate molt, ranging from never, as in the Shiny Cowbird (*Molothrus bonariensis*; Lowther and Post 1999) to frequent, occurring in just one age-sex class, as in the Great-tailed Grackles (*Quiscalus mexicanus*; Selander 1958), in all but one age-sex class, as in the Red-winged Blackbird (*Agelaius phoeniceus*; Humphrey and Parkes 1959), or all age-sex classes, as in the Bronzed Cowbird (*Molothrus aeneus*; Lowther 1995). In all of these cases, the prealternate molt is partial, involving contour feathers and coverts to varying degrees, but not flight feathers.

The Rusty Blackbird (*Euphagus carolinus*) has experienced a severe population decline (Niven et al. 2004, Sauer et al. 2008). Many aspects of its biology are poorly known (Avery 1995), and reasons for the decline are unclear (Greenberg and Droege 1999, 2003). Research on demographic patterns associated with the decline have been hampered by the lack of reliable plumage criteria for determining the age (first year versus adult) of birds observed or captured, particularly in the winter range. A thorough knowledge of molt patterns would further assist researchers in selecting appropriate feathers for linking breeding and wintering populations with stable isotopes (Larson and Hobson 2009) or in determining seasonal exposures to contaminants, such as methylmercury (Evers et al. 2005). Unfortunately, the timing and extent of the Rusty Blackbird's prebasic molt is poorly documented, and it is unknown whether hatch-year birds undergo a partial or complete first prebasic molt. This information is necessary for development of accurate plumage-based methods of age determination. Furthermore, it has been thought that the species lacks a prealternate molt and therefore attains its summer plumage exclusively by wear of the rusty feather edges (Avery 1995, Pyle 1997). However, during our field work on wintering Rusty Blackbirds in Mississippi, we regularly found individuals undergoing varying degrees of head and body molt.

In this study we examined the prebasic and prealternate molts of the Rusty Blackbird to document the timing and extent of each molt and determine whether there are consistent patterns in plumage that could be used to age birds in both plumages. Specifically, we first document a previously undescribed prealternate molt of the Rusty Blackbird from our examinations of wintering birds that we captured in Mississippi and museum specimens collected from across the species' winter range. We then examined fall migrants captured in the Yukon Territory to determine the extent of the prebasic molt and to identify consistent and discernable differences in the first and adult basic plumage among birds of known age. Finally, we determined whether feather wear and the prealternate molt obscured our ability to discern the age-related differences in plumage that we identified in birds in fresh basic plumage in the fall.

METHODS

Between December and March, 2005–2009, we captured 224 Rusty Blackbirds in mist nets at 14 sites in the species' core winter range in the lower Mississippi Alluvial Valley (Niven et al. 2004) around Greenville, Mississippi (33° 27.3′ N, 91° 2.1′ W) and examined each bird for evidence of prealternate molt. Four sites were located in pecan orchards, four in fragments of bottomland forest along creeks, and six in larger patches of bottomland forest (Leroy Percy State Park, Delta National Forest, Yazoo National Wildlife Refuge, Panther Swamp National Wildlife Refuge). We also examined 139 museum specimens provided by the Mississippi Museum of Natural Science, Jackson, University of Mississippi, Oxford, the National Museum of Natural History, Washington, D.C., and the Academy of Natural Sciences, Philadelphia. These specimens were collected from throughout the species' winter range between October and May, 1844–1971 (median 1940, 25% percentile 1920, 75% percentile 1954), except for two specimens collected in 1986 and one in 2000.

In each captured bird and museum specimen we assessed body molt by blowing through the contour feathers and coverts and searching for newly emerged pin feathers. Following Berthold et al. (1970), we categorized feather tracts into 19 patches, except we included the eye ring with the cheek patch and merged the belly and flank patches. For each captured bird we assigned each feather patch to one of four categories of molt intensity: 0, no molt; 1, <33% of the patch in molt; 2, 33–67% of the patch in molt; 3, >67% of the patch in molt. For the museum specimens, we only recorded the number of patches in molt and not molt intensity or which particular patches were in molt.

For age and sex determination during winters 2005–2008, we followed Pyle (1997). We used the presence of visible molt limits along the underwing coverts to distinguish birds that were younger than one year (young) from birds that were older than one year (adult). However, these molt limits were not always easy to detect so in addition we inspected the bills and legs of all birds for age-related marks of wear. Specifically, the bill of young birds has a smooth surface and no marks or scars, particularly around the nares, and fleshy gapes may still be visible in the winter. Likewise, the leg scales of young birds are smooth, relatively shiny, very dark, and lack a second or third layer of visible scales. Claws of young birds are smooth and shiny (G. Hofmann, pers. comm.). In most cases, our evaluations of molt limits and wear of the bare parts resulted in the same age classification. However, in four birds (three females, one male) the underwing coverts showed no molt limits (indicating adult birds), whereas the legs and bill showed nearly no wear. After thorough inspection of the underwing coverts and legs and bill we categorized three of the birds as adults (according the underwing pattern) and one as young female (according to the leg and bill wear).

We captured fall migrant Rusty Blackbirds in mist nets from 9 August to 4 October, 2006–2009, in Whitehorse, Yukon Territory, Canada (60° 45.0′ N, 135° 9.4′ W). We determined age of each bird as either hatch year (young) or after hatch year (adult) by the extent of skull pneumatization, which is completed in young birds by the end of October (Pyle 1997). We found that in the fall the molt limits along the median underwing coverts (Pyle 1997) could be consistently seen in young males but were usually not visible in young females. We, therefore, tested the consistency of subtle differences between young and adult birds in plumage color around the eye and chin. We photographed the faces of birds aged by skull pneumatization and presented each photograph to six naïve observers who were instructed to score the extent of each bird's pale eye-ring into one of four categories: 0 = absent; 1 = thin, dull, and indistinct; 2 = moderate width, bright, and distinct; and 3 = thick, bright, and almost complete. We provided sample photographs to illustrate each score. We also noted the color of the chin feathers. To emphasize that we were assessing age-related differences among birds in fresh basic plumage, we assessed the molt stage of each of 623 birds by first determining the molt status of each primary feather, then, following Newton (1966), calculating an overall primary-molt score for each bird. A completed primary molt is indicated by a score of 225.

Because the basic plumage of nonbreeding birds is subject to wear and possibly prealternate molt, we tested whether the differences in head plumage between birds in fresh first and adult basic plumage were still discernable in winter 2008–2009. We first aged the winter birds by the underwing coverts and wear marks on the bill and legs, then scored them for the head-plumage characteristics established from birds of known age in the fall.

STATISTICAL ANALYSES

For the winter field data ($n = 224$ birds) we used hierarchical log-linear analysis and compared the proportion of birds that were in prealternate molt by season (divided into three 30-day periods from mid-December to mid-March), age, and sex. To select the final model we used a backward-elimination procedure in which we fit a saturated model, sequentially assessed the chi-squared values among effects of an equivalent order (starting with highest-order effects first), and then eliminated in each step the effect with the smallest nonsignificant ($P \geq 0.05$) change in the chi-squared value. The only terms that remain in the final model are (1) those that result in a significant ($P < 0.05$) change in chi-squared value when removed and (2) any associated lower-order effects when an interaction effect is retained (Wuensch 2006).

We further examined the overall molt intensity of those field-captured birds that were in prealternate molt ($n = 170$). We calculated overall molt intensity as the sum of molt intensity of all feather patches divided by 19, the total number of patches. We further explored the pattern of molt on the head versus the rest of the body by summing the intensities on the chin, throat, cheek, side of neck, forehead, crown, and back of head (subsumed as head molt) and also for the remaining patches of body feathers (subsumed as body molt). These data were not normally distributed so we used nonparametric tests. Specifically, we compared the intensity of molt in feather patches with a Friedman test. We tested for differences in molt intensity between the head and body with a Wilcoxon test. We tested for variation in molt intensity among the three 30-day periods with a Kruskal–Wallis test. We ran the tests for all patches combined as well as for head and body patches separately.

For the museum specimens ($n = 139$ birds) we compared the proportion of birds in prealternate molt by sex and 30-day period from mid-October to mid-May (season) with a hierarchical log-linear analysis. We did not test for an age effect because the tags of <33% of the museum specimens had age information. We also assessed molt intensity among those museum specimens that showed signs of prealternate molt ($n = 82$). Here, we measured molt intensity as the number of patches showing molt and tested its variation by season with a Kruskal–Wallis test.

Finally, we compared the number of birds in prealternate molt in the contemporary field samples from Mississippi ($n = 224$) to that in a subsample of older museum specimens ($n = 96$) for the period December–March, which was covered by both samples. We used the hierarchical log-linear model with the backwards-elimination procedure described above to test for variation in the proportion of birds in molt relative to season (mid-December to mid-March) and sample origin (field vs. museum). Furthermore, we used a Mann–Whitney test to compare the number of patches in molt (molt intensity) from December to March in molting birds in the field ($n = 170$) to that in museum specimens ($n = 63$).

For the fall data, we compared the eye-ring scores of young and adult birds with a chi-squared test ($n = 68$ from photographs). We ran all statistical analyses in SPSS version 15.0 (SPSS 2006). We set the level of significance for statistical tests at $P < 0.05$ and present all means ± SE.

RESULTS

We captured a total of 224 birds in Mississippi, including 43 young males, 69 adult males, 39 young females, and 73 adult females. We found evidence of prealternate molt in 76% of these birds (Fig. 1). The backwards-elimination procedure removed all third- and fourth-order effects from the saturated model describing the proportion of field-captured birds in prealternate molt. The final hierarchical log-linear model included the effects of season × molt and season × age, including all lower-order effects of these variables (Table 1), and had reasonable goodness of fit ($\chi^2_{15} = 9.0$, $P = 0.88$). This model indicates that the proportion of birds in prealternate molt increased through the season (season × molt $\chi^2_2 = 6.7$, $P = 0.04$; Table 1) and was highest (0.86) from mid-February to mid-March (Fig. 1). The interaction between season and age (season × age $\chi^2_2 = 6.5$, $P = 0.04$; Table 1) indicates that the prevalence of age classes in the samples varied by season. Likewise, the number of birds sampled varied by category for the main factor effects season ($\chi^2_2 = 24.2$, $P < 0.001$), age ($\chi^2_2 = 16.3$, $P < 0.001$), and molt ($\chi^2_2 = 44.4$, $P < 0.001$) such that more birds were captured early in the winter (Fig. 1), fewer young ($n = 82$) than old ($n = 142$) birds were captured, and more birds were in molt than not (see above). We did not find that the proportion of birds in molt was related to either the sex (0.73 of males and females each were in molt; sex × molt, $\chi^2_2 = 0.003$, $P = 0.96$) or age of the birds (0.74 of young and 0.70 of adults in molt; age × molt, $\chi^2_2 = 0.4$, $P = 0.41$; Table 1).

TABLE 1. Relationship between the proportion of wintering Rusty Blackbirds in prealternate molt and their age, sex, and season of capture in Greenville, Mississippi, 2005–2009. We distinguished two age classes (younger and older than one year) and divided the winter into three 1-month periods starting mid December. The hierarchical log-linear analysis first generates a saturated model with all variables included. The effects in the final model are based on a backwards-elimination approach that retained only those effects from the saturated model that resulted in a significant change in the chi-squared value when removed. When an interaction term was retained, all lower-order effects were also retained (Wuensch 2006). For the saturated model, partial associations are adjusted for all other effects in the model and are shown for all factors and their interactions.

Effects	df	χ^2	P
In final model			
Season × molt	2	6.7	0.04
Season × age	2	6.5	0.04
Season	2	24.2	<0.001
Molt	1	44.4	<0.001
Age	1	16.3	<0.001
Not in final model			
Season × sex × molt	2	3.8	0.15
Season × age × molt	2	0.3	0.86
Sex × age × molt	1	<0.01	1.00
Season × sex × age	2	3.6	0.16
Sex × molt	1	<0.01	0.96
Age × molt	1	0.7	0.41
Sex × age	1	0.3	0.56
Season × sex	2	0.2	0.92

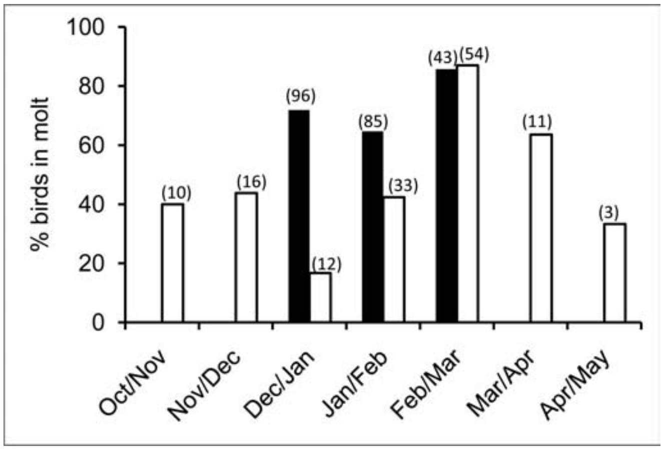

FIGURE 1. Percentage of Rusty Blackbirds in molt through the winter, based on field captures in Mississippi, 2005–2009 (black bars) and museum specimens collected across the species' winter range, 1844–2000 (white bars). Each 30-day period of the season starts at the middle of each month; numbers of birds sampled are indicated above each bar.

Among the 170 birds in prealternate molt that we captured in Mississippi, molt was not evenly distributed among feather patches (Friedman test, $\chi^2_{18} = 701.1$, $P < 0.001$). It was far more frequent on the cheek patch (69% of molting birds) than on any other patch (≤19% of molting birds; Fig. 2). Other feather patches with considerable molt included in descending order the chin, crown, flank, side of neck, and throat (13–19% of molting birds; Fig. 2). On average, birds molted more intensely around the head ($\bar{x} = 2.0 \pm 0.2$) than on the body ($\bar{x} = 1.3 \pm 0.2$; Wilcoxon $z = -4.0$, $P < 0.001$). Also overall molt intensity increased over the season (Kruskal–Wallis test $\chi^2_2 = 14.8$, $P = 0.001$) because of an increase in molt intensity on the head (Kruskal–Wallis test, $\chi^2_2 = 20.9$, $P < 0.001$) but not the body (Kruskal–Wallis test, $\chi^2_2 = 1.6$, $P = 0.46$).

Analysis of molt patterns of the 139 museum specimens resulted in a model including the effects molt × season and sex with all lower-order effects of these variables (goodness of

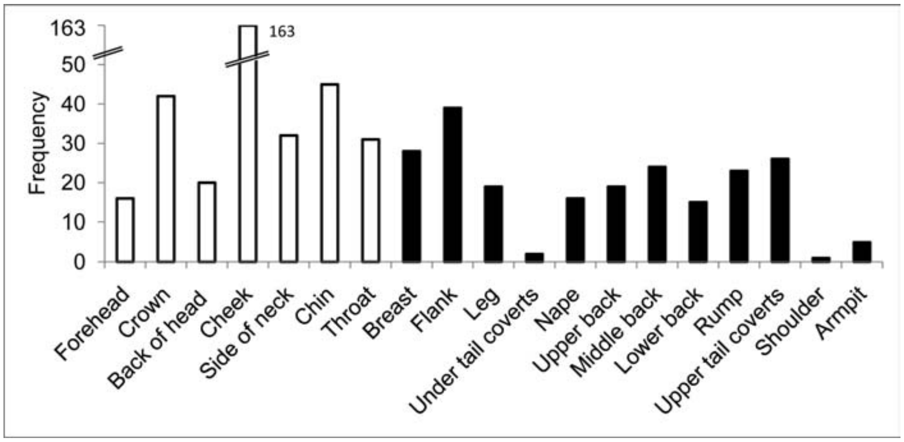

FIGURE 2. Occurrence of molt by feather patch among 170 molting Rusty Blackbirds captured in Mississippi, 2005–2009. White and black bars indicate feather patches on the head and the rest of the body, respectively.

fit $\chi^2_{13} = 12.3$, $P = 0.5$; Table 2). The museum specimens covered a wider seasonal range (mid-October to mid-May) than the field data from Mississippi and included a higher proportion of birds in molt from mid-February to mid-March (0.87 of birds in molt) and from mid-March to mid-April (0.64 of birds in molt) than earlier in the winter season (molt × season, $\chi^2_6 = 37.1$, $P < 0.001$, Fig. 1, Table 2). The proportion of birds in molt did not vary by sex (sex × molt, $\chi^2_1 = 0.05$, $P = 0.83$). There was a bias of males (68%) in the total sample (sex $\chi^2_1 = 17.65$, $P < 0.001$). In contrast to the field data from Mississippi, in the museum specimens molt intensity (measured as the number of patches with molt) among molting birds ($n = 82$) did not change through the season (Kruskal–Wallis test $\chi^2_6 = 7.1$, $P = 0.31$; Fig. 3). Seasons combined, the specimens showed molt in an average of 2.7 ± 0.22 patches.

TABLE 2. Relationship between the proportion of Rusty Blackbirds in prealternate molt and their sex and season of sampling in museum specimens collected from 1844 to 2000. We divided the winter into three 1-month periods starting mid December. See Table 1 for an explanation of the hierarchical log-linear model approach. For the saturated model, partial associations are adjusted for all other effects in the model and are shown for all factors and their interactions.

Effects	df	χ^2	P
In final model			
Season × molt	2	37.1	<0.001
Sex	2	17.7	<0.001
Season	2	84.5	<0.001
Molt	1	4.5	0.03
Not in final model			
Sex × molt	2	9.7	0.14
Season × sex	2	0.3	0.86

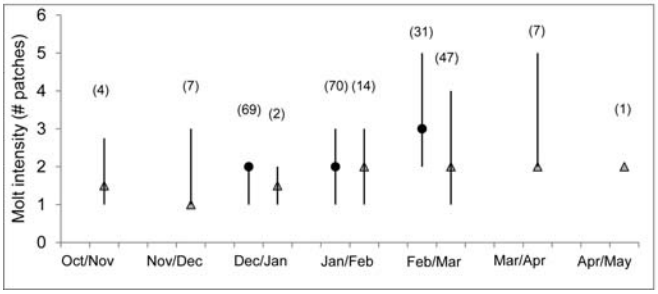

FIGURE 3. Median number of feather patches in active molt by season among wintering Rusty Blackbirds captured in Mississippi, December–March, 2005–2009 (black circles; sample size of molting birds in parentheses) and collected for museum specimens across the species' winter range (gray triangles), October–May, 1844–2000. Bars indicate the quartiles of molt intensity (number of patches in molt).

For combined museum and field data, the backwards-elimination procedure did not eliminate any of the seven effects from the saturated hierarchical log-linear model describing the proportion of birds in prealternate molt relative to the full-factorial effects of season, sample origin, and molt. This model confirmed that the proportion of birds in molt increased through the season (molt × season, $\chi^2_2 = 31.2$, $P < 0.001$; Table 3; Fig. 1) and was highest from mid-February to mid-March (0.87 of birds in molt). However, the seasonal pattern of the field and museum samples also differed (season × origin × molt: $\chi^2_2 = 7.9$, $P = 0.02$): the proportion of birds in prealternate molt from mid-December to mid-February was lower in the museum (0.36 of birds in molt) than in the field sample (0.69 birds in molt; Fig. 1). The field and museum samples differed in sampling effort (origin $\chi^2_1 = 50.3$, $P < 0.001$) and were also not evenly distributed across the season (origin × season $\chi^2_2 = 58.7$, $P < 0.001$; see Fig. 1). However, molt intensity, measured as average number of patches in molt, in the

TABLE 3. Relationship between proportion of wintering Rusty Blackbirds in prealternate molt and season of sampling (three 1-month periods starting mid-December) and sample origin (field captures from 2005 to 2009 versus museum specimens from 1844 to 2000). See Table 1 for an explanation of the hierarchical log-linear model approach. For the saturated model, partial associations are adjusted for all other effects in the model and are shown for all factors and their interactions.

Effect	df	χ^2	*P*
Origin × molt	1	11.1	0.001
Season × molt	2	31.2	<0.001
Molt	1	50.3	<0.001
Origin × season	2	58.7	<0.001
Origin	1	50.3	<0.001
Season	2	2.3	0.33

field samples ($\bar{x} = 2.4 \pm 0.2$) did not differ from that in the museum samples ($\bar{x} = 2.7 \pm 0.3$; Kruskal-Wallis test, $\chi^2 = -1.2$, $n = 233$, $P = 0.23$; Fig. 3).

In fall in the Yukon Territory, the 623 birds we captured and scored for molt had a mean overall primary-molt score of 217.6 ± 0.9. We also examined tails and upper wing coverts for retained feathers, finding none, although this examination was not systematic. Young birds had pale eye-rings more prominent than those of adults. For males, all young birds ($n = 21$) had eye-ring scores of 1–3, while all adults ($n = 14$) scored 0 (no pale eye-ring). For females, 23 of 24 young birds scored 2–3 and one had a score of 1, while all adults ($n = 9$) scored 0–1. The difference between young birds and adults in the proportion of birds with eye-ring scores of 0, 1, and 2–3 was highly significant ($n = 68$, $\chi^2_2 = 56.6$, $P < 0.001$). We noted that adults tended to have darker chins than young birds, although we did not quantify this consistently.

Finally, we assessed whether the pale eye ring and chin that we observed among young birds during fall was still discernable in winter. In winter 2008–2009, we captured and aged 26 Rusty Blackbirds, including eight adult males, five young males, five adult females, and eight young females. Although the sample size was quite small, we did find consistency between age determinations based on underwing coverts and head plumage. Birds that we classified as young according to molt limits in the underwing coverts ($n = 11$ birds) always displayed (1) a few pale feathers around the eye and (2) light beige (young males) or nearly whitish (young females) feathers on the chin at the base of the bill; adults had black (adult males) or darker beige (adult females) chin feathers. In 15 birds lacking observable molt limits in the underwing coverts we noted two with a few light feathers left around the eye. We reclassified these birds as young because they may have previously molted all of their juvenile underwing coverts in the fall (Pyle 1997).

DISCUSSION

Both field captures and museum specimens of wintering Rusty Blackbirds clearly show the existence of a previously undescribed partial prealternate molt. Throughout the winter season and the winter range, 69% of the 363 birds that we examined were replacing at least some body feathers when captured or collected. Furthermore, the proportion of birds in molt increased over the winter with a peak from mid-February to mid-March of nearly 90% of the birds in molt. This prealternate molt was particularly prominent around the head. The widespread occurrence of the prealternate molt in museum specimens of the Rusty Blackbird indicates that prealternate molt is common for the species and not restricted to our study area in Mississippi.

The frequency, timing, and extent of the Rusty Blackbird's prealternate molt is similar to that of other temperate-zone icterids and songbirds in general. First, the age and sex classes seem to be equally likely to undergo prealternate molt, which corresponds to the pattern of prealternate molt suspected in the closely related Brewer's Blackbird (*Euphagus cyanocephalus*; Martin 2002) and Boat-tailed Grackle (*Quiscalus major*; Post et al. 1996). Second, a peak of molt in the end of the winter and early spring (February–April) is characteristic of many species (e.g., Lanyon 1975, Miskiman 1980, Combs and Fredrickson 1995, Post et al. 1996, Johnson and Peer 2001, and Martin 2002). Third, the prealternate molt of the Rusty Blackbird is most often concentrated around the head. Among blackbirds this pattern is documented for Brewer's Blackbird (Martin 2002), Boat-tailed Grackle (Post et al. 1996), Great-tailed Grackle (Johnson and Peer 2001), Bronzed and Brown-headed Cowbirds (*Molothrus ater*; Lowther 1993, 1995), suggesting an important role of the head plumage in courtship display and mate choice (Hohman et al. 1997). In addition, a change of plumage color through the wearing of feather tips, which occurs over most of the body of a Rusty Blackbird, may not function well for the fine feathering around the face and bill.

Surprisingly, when we compared the historic and the current samples between December and February, we found a lower percentage of molt in the historic sample, whereas we found no such differences between February and March. The apparent delay of molt among the older specimens may be caused by two factors. First, historic samples were collected over a large latitudinal range, the timing of molt may vary along a north–south gradient (Williamson and Emison 1971, Ryder and Rimmer 2003). For example, it may be that birds wintering farther north initiate prealternate molt later, as they have more time before migrating to the breeding range than do birds wintering farther south. Alternatively, the food supply is likely to improve earlier in the south, and this may allow birds to achieve body condition for molt more quickly. Second, a general increase in average temperature since most specimens were collected may have favored earlier molt in the recent sample. Indeed, average temperatures in December in Greenville, Mississippi, increased by 0.9 °C from the 1940s (the average date of collection of the specimens) to the present (TuTiempo.net 2010).

A technique to determine the age of Rusty Blackbirds in the field without capture and examination in the hand would contribute considerably to studies of the demography, habitat distribution, and migration strategies of the species. Our study clearly demonstrates that Rusty Blackbirds in fresh basic plumage can be reliably identified as in their year of hatching or older by the presence of a pronounced pale eye-ring. In addition, it is likely that a lighter chin characterizes young birds as well. We further tested the efficacy of this facial pattern for aging wintering birds from December to early February after both wear and molt may have intervened. Some of the light feathers around the eye (the eye-ring) and the throat near the base of the bill in young birds appeared to persist into late winter and worked well for aging birds in the hand in winter. However, these findings require further confirmation as only 26 birds were available in winter 2008–2009 when we first used this method. The last birds were captured on 20 February, among them was a young bird which still showed these characteristic plumage patterns. Whether age determination by head plumage is still possible in the spring has to be tested further, because the number of birds in molt increased considerably after mid-February. The described patterns could be discerned under close examination in the hand during winter, but the differences are often too subtle to be observed reliably without capture and inspection by someone familiar with the patterns. Initial attempts by CMH in Mississippi indicate that identification of age in the field is possible from the coloration of the throat when the bird is close by, well visible, and well lit on the throat.

Although the Rusty Blackbird's pronounced prealternate head molt has the potential to impede age determination later in spring, it may allow back-tracking of breeding birds to their winter sites by stable-isotope ratios (Hobson 2005). Selection of feathers around the head that lack rusty edges may aid in identifying feathers grown in the winter range and help to establish connectivity between breeding and wintering populations (Hobson et al. 2010). Furthermore, the same feathers collected during spring migration or on the breeding ground can also be used to assess winter exposures to contaminants such as methylmercury (Evers et al. 2005).

In conclusion, in winter the Rusty Blackbird undergoes a partial prealternate molt, particularly around the head. Historic samples from museums indicate that this prealternate molt is widespread and common throughout the winter range. This molt does not seem to interfere with age determination based on the pattern of basic plumage on the head until at least mid-February. The study also shows topics requiring further research. First, the new technique needs further validation by being applied together with the traditional technique. Second, more research is needed to determine whether age-related differences in head plumage persist into spring. Third, because of the size of our sample we did not investigate timing of molt along a latitudinal gradient, but this relationship could, in conjunction with climatic data, give important information about changes in environmental conditions over time and their implications for the Rusty Blackbird's molt. Last, the function of the prealternate molt requires further investigation as it may be related to performance on the breeding ground and therefore under sexual selection.

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LITERATURE CITED

Avery, M. L. 1995. Rusty Blackbird (*Euphagus carolinus*), no. 200. *In* A. Poole and F. Gill [eds.], The birds of North America. Academy of Natural Sciences, Philadelphia.

Banks, R. C. 1978. Prealternate molt in nuthatches. Auk 95:179–181.

Berthold, P., E. Gwinner, and H. Klein. 1970. Vergleichende Untersuchung der Jugendentwicklung eines ausgepraegten Zugvogels, *Sylvia borin*, und eines weniger ausgepraegten Zugvogels, *S. atricapilla*. Vogelwarte 25:297–331.

Combs, D. L., and L. H. Fredrickson. 1995. Molt chronology of male Mallards wintering in Missouri. Wilson Bulletin 107:359–365.

Evers, D. C., N. M. Burgess, L. Champoux, B. Hoskins, A. Major, W. M. Goodale, R. J. Taylor, R. Poppenga, and T. Daigle. 2005. Patterns and interpretation of mercury exposure in freshwater avian communities in northeastern North America. Ecotoxicology 14:193–221.

Greenberg, R., and S. Droege. 1999. On the decline of the Rusty Blackbird and the use of ornithological literature to document long-term population trends. Conservation Biology 13:553–559.

Greenberg, R., and S. Droege. 2003. Rusty Blackbird: troubled bird of the boreal bog. Bird Conservation, June 2003.

Greenwood, H., P. J. Weatherhead, and R. D. Titman. 1983. A new age- and sex-specific molt scheme for the Red-winged Blackbird. Condor 85:104–105.

Hobson, K. A. 2005. Stable isotopes and the determination of avian migratory connectivity and seasonal interactions. Auk 122:1037–1048.

Hohman, W. L., S. W. Manley, and D. Richard. 1997. Relative costs of prebasic and prealternate molts for male Blue-winged Teal. Condor 99:543–548.

Humphrey, P. S., and K. C. Parkes. 1959. An approach to the study of molts and plumages. Auk 76:1–31.

Johnson, K., and B. D. Peer. 2001. Great-tailed Grackle (*Quiscalus mexicanus*), no. 576. *In* A. Poole and F. Gill [eds.], The birds of North America. Academy of Natural Sciences, Philadelphia.

Lanyon, W. E. 1975. Evidence of an incomplete prealternate molt in some South American *Myiarchus* flycatchers. Condor 77:511.

Larson, K. W., and K. A. Hobson. 2009. Assignment to breeding and wintering grounds using stable isotopes: a comment on lessons learned by Rocque et al. Journal of Ornithology 150:709–712.

Lowther, P. E. 1993. Brown-headed Cowbird (*Molothrus ater*), no. 47. *In* A. Poole and F. Gill [eds.], The birds of North America. Academy of Natural Sciences, Philadelphia.

Lowther, P. E. 1995. Bronzed Cowbird (*Molothrus aeneus*), no. 144. *In* A. Poole and F. Gill [eds.], The birds of North America. Academy of Natural Sciences, Philadelphia.

Lowther, P., and W. Post. 1999. Shiny Cowbird (*Molothrus bonariensis*), no. 399. *In* A. Poole and F. Gills [eds.], The birds of North America. Birds of North America, Inc., Philadelphia.

Martin, S. G. 2002. Brewer's Blackbird (*Euphagus cyanocephalus*), no. 616. *In* A. Poole and F. Gill [eds.], The birds of North America. Birds of North America, Inc., Philadelphia.

Miskiman, M. 1980. Red-winged Blackbirds: I. Age-related epaulet color changes in captive females. Ohio Journal of Science 80:232–235.

Mulvihill, R. S. 1999. Using wing molt to age passerines. North American Bird Bander 18:1–10.

Mulvihill, R. S., and C. C. Rimmer. 1997. Timing and extent of the molts of adult Red-eyed Vireos on their breeding and wintering grounds. Condor 99:73–82.

Newton, I. 1966. The moult of the bullfinch *Pyrrhula pyrrhula*. Ibis 108:41–67.

Niven, D. K., J. R. Sauer, G. S. Butcher, and W. A. Link. 2004. Christmas bird count provides insights into population change in land birds that breed in the boreal forest. American Birds 58:10–20.

Post, W., J. P. Poston, and G. T. Bancroft. 1996. Boat-tailed Grackle (*Quiscalus major*), no. 207. *In* A. Poole and F. Gill [eds.], The birds of North America. Academy of Natural Sciences, Philadelphia.

Pyle, P. 1997. Identification guide to North American birds, part 1: Columbidae to Ploceidae. Slate Creek Press, Bolinas, CA.

Pyle, P., and S. N. G. Howell. 2004. Ornamental plume development and the "prealternate molts" of herons and egrets. Wilson Bulletin 116:287–292.

Ryder, T. B., and C. C. Rimmer. 2003. Latitudinal variation in the definitive prebasic molt of Yellow Warblers. Wilson Bulletin 115:325–332.

Sauer, J. R., J. E. Hines, and J. Fallon [online]. 2008. The North American Breeding Bird Survey, results and analysis 1966–2007, version 5.15.2008. U.S. Geological Survey, Patuxent Wildlife Research Center, Laurel, MD. <http://www.mbr-pwrc.usgs.gov/bbs/bbs.html> (3 June 2010).

Selander, R. K. 1958. Age determination and molt in the Boat-tailed Grackle. Condor 60:355–376.

SPSS. 2006. SPSS Base 15.0 user's guide. SPSS, Inc., Chicago.

TuTiempo.net [online]. 2010. Historical weather: Greenville, Greenville Municipal Airport, Mississippi, USA. <http://www.tutiempo.net/en/Climate/Greenville_Greenville_Municipal_Airport/12-1999/722356.htm> (13 May 2010).

Williamson, F. S. L., and W. B. Emison. 1971. Variation in the timing of breeding and molt of the Lapland Longspur (*Calcarius lapponicus*) in Alaska, with relation to differences in latitude. BioScience 21:701–707.

Wuensch, K. L. [online]. 2006. Three-way hierarchical log-linear analysis: positive assortative mating. <core.ecu.edu/psyc/wuenschk/MV/LogLin/Log3H.doc> (16 April 2009).