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TIMING, PATTERN, AND EXTENT OF FIRST PREBASIC MOLT OF WHITE-WINGED CROSSBILLS IN ALASKA

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Abstract.—The timing, pattern, and extent of the first prebasic wing molt of White-winged Crossbills (*Loxia leucoptera*) were determined during a 6-yr banding study in interior Alaska. Hatching-year birds were not caught in substantial numbers until May, and all crossbills molted from juvenal to first basic plumage between September and December. A subsample consisting of 65 males and 55 females in first basic plumage was used to determine the pattern and extent of wing covert molt. On average, birds molted three greater coverts (GC) and retained two juvenal medial coverts (MC) per wing. The number of molted GCs was negatively correlated with that of juvenal MCs. Twenty-three percent of the individuals molted no GC, and no crossbill replaced all these feathers. The pattern and extent of covert molt was similar in males and females and was symmetrical in 69% of the individuals, but differed by one or two feathers in the remaining birds. Males in first basic plumage and with partially red or pink contour feathers molted more GCs and retained fewer MCs than males without contour feathers of these colors, although both groups apparently were of the same age. Remex molt was found in only one bird, which also showed partial proximal secondaries (=tertial) replacement.

TEMPORADA, PATRÓN Y EXTENSIÓN DE LA PRIMERA MUDA PREBÁSICA DE *LOXIA LEUCOPTERA* EN ALASCA

Sinopsis.—Se determinó el tiempo, el patrón y la extensión de la primera muda prebásica de *Loxia leucoptera* durante un estudio de seis años en el interior de Alaska. No se atraparon aves de primer año de forma sustancial hasta mayo, y todas las aves mudaron del plumaje juvenil al primer plumaje básico entre septiembre y diciembre. Una submuestra de 65 machos y 55 hembras en primer plumaje básico se usó para determinar el patrón y extención de la muda de cubiertas del ala. En general, las aves mudaron tres cubiertas mayores (GC) y retuvieron dos cubiertas juveniles medias (MC) por ala. El número de GCs mudadas se correlacionó negativamente con las de MC juveniles. Veintitres prociento de los individuos no mudó GCs, y ningún ave reemplazó todas estas plumas. El patrón y la extensión de la muda de cubiertas fué similar en machos y hembras y fué simétrica en 69% de las aves, pero difirió por una o dos plumas en el resto de la muestra. Los machos en el primer plumaje básico y con plumas de contorno rosadas o parcialmente rojas mudaron más GCs y retuvieron menos MCs que machos sin plumas de contorno de estos colores, aunque ambos grupos aparentemente eran de la misma edad. Muda de remeras se halló en solo un ave, que también mostró reemplazamiento terciario parcial.

Considerable progress in our understanding of variations in molt patterns of European (Jenni and Winkler 1994) and North American (Pyle 1997a,b) passerines has been made in the recent past. During their first prebasic molt, most species replace only some feathers. In these species, molt limits (i.e., topographical boundaries between molted and retained juvenal feathers) can be particularly useful for determining age (Mulvihill

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1993, Pyle 1997a,b). However, there is a need for additional research on this topic. For example, many results were obtained from studies on a limited number of museum specimens. Identifying molt limits in these birds can be difficult because wings cannot be opened without risking damage. Further, some species show considerable but poorly understood variation in the extent of molt limits. Finally, published literature sometimes contains seemingly contradictory information on the timing and extent of molt within the same species.

Studies on White-winged Crossbills (*Loxia leucoptera*), a widespread species that lives primarily in northern conifer forests, illustrate this situation. Dwight (1900) and Bent (1968) reported that White-winged Crossbills acquire their first winter plumage by partial molt of the body, but not wing feathers. Similarly, Witherby (1943) stated that during first prebasic molt White-winged Crossbills of the Palearctic region (*Loxia l. bifasciata*) replace lesser and median, but not greater wing coverts. Also consistent with this conclusion, Newton (1972) described the fact that first-year birds can be distinguished from older birds in that they retain buff secondary coverts. In contrast, Svensson (1992) indicated that by late winter most first-year White-winged Crossbills have molted all wing coverts, although they retain juvenal proximal secondaries (=tertials). Cramp and Perrins (1994) proposed an intermediate situation. Accordingly, "advanced" birds retain at least outer greater coverts and all juvenal tertials, but "more retarded" birds retain many juvenal wing coverts. Finally, Pyle (1997a) determined the extent of first prebasic molt in 31 White-winged Crossbill museum specimens of unspecified origin. All birds had replaced some greater coverts, and 26% had molted all these feathers. The same percentage of individuals had molted at least one tertial.

One factor that potentially complicates studies on crossbills in general is that these birds can breed during most of the year in parts of their range (Bent 1968, Newton 1972, Godfrey 1986, Benkman 1992), whereas most other temperate and high-latitude species reproduce seasonally. As a result of their extended annual reproductive period, crossbills at many stages of development and molt may be present over a large portion of the year at a given location (Benkman 1992). White-winged Crossbills breeding in the northern part of the species' range (interior Alaska), however, exhibit a seasonal reproductive pattern (Deviche 1997). In this population, females with an incubation patch and young in complete juvenal plumage occur mostly between April and July and between May and August, respectively. Studying this population offers the possibility to examine the timing, duration, extent, and pattern of prebasic molt without the potentially confounding influence of an unusually long breeding period as may be the case at lower latitudes.

METHODS

I mist-netted hatching-year/second-year (HY/SY) White-winged Crossbills at a single location in Fairbanks, Alaska (64°50′N, 147°50′W) between May 1993 and January 1999 (see Deviche 1997 for details on capture methods). No HY birds were caught January–March, and only one bird of this age category was mist-netted in April. Because there was no indication of year-to-year differences in first prebasic molt timing (for molt terminology, see Humphrey and Parkes 1959, Thompson and Leu 1994, Jenni and Winkler 1994) data were combined across years.

To study the pattern and extent of first prebasic molt, I used data collected for birds that were caught between December 1994 and May 1995 (n = 63) and between November 1998 and January 1999 (n = 66). Birds caught between April and October were not included in this analysis because they were either in complete juvenal plumage or were molting greater and/or median coverts (see Results). I also excluded four birds that could not be sexed (see below) and five birds for which incomplete data were collected or that were still undergoing wing molt at the time of capture. Some birds caught in November–mid-December were not molting wing feathers any longer, but were still undergoing light contour feather growth (see Results). Data collected for these birds were retained. The final sample used to study first prebasic molt pattern and extent consisted of 65 males and 55 females.

I measured the right wing chord of each bird to the nearest 1 mm and weighed each bird to the nearest 0.1 g. I counted the number of molted (adult, i.e., first basic) greater coverts (GC) and of retained (juvenal) median coverts (MC) and noted the position of each molted or retained feather from distal to proximal (GC_1–GC_{10} or MC_1–MC_8, Jenni and Winkler 1994) for each wing separately. Juvenal MCs were generally located distally. Mean values for the left and right wings of each individual were calculated and are presented here. If the position or number of replaced GCs or the number of juvenal MCs differed between the left and right wings of an individual (see Results), corresponding mean values were calculated and used for statistical analyses. I also examined whether any remex had been replaced. Birds were banded and released at the capture site. All data are presented as medians ±½ interquartile intervals (Nicholson et al. 1997), except body masses (means ± standard deviations).

The sex of birds in juvenal plumage could not be determined. Whenever possible, the sex of birds that were undergoing or had completed first prebasic molt was inferred from plumage color (Svensson 1992, Cramp and Perrins 1994, Pyle 1997b). Females are generally dull olive-green without red, orange, or yellow (except lower back and rump) whereas males have at least partly red, pink, orange, and/or yellow contour plumage. The validity of this criterion was confirmed by examination of specimens of known sex that were collected from the same population and deposited at The University of Alaska Museum and by necropsy of birds that were brought into captivity for physiological investigations (personal observations). Before statistical analyses, males were divided into two groups based on whether their contour plumage (flanks, head, lower back, and rump) was at least partly red-pink (n = 25) or of a different color or color combination (n = 40).

The age of crossbills caught before early December was determined

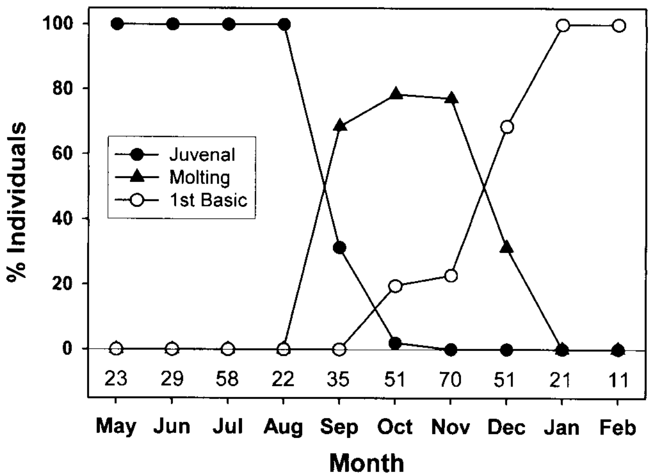

FIGURE 1. Seasonal changes in the proportions of hatching-year (May–December) and second-year (January and February) White-winged Crossbills (*Loxia leucoptera*) found to be either in juvenal plumage (Juvenal), molting into first basic plumage (Molting), or in complete first basic plumage (1st Basic) at Fairbanks, Alaska, 1993–1999. Numbers above the horizontal axis indicate the numbers of birds caught during each month.

based on skull ossification (Pyle 1997b). I ranked the degree of skull ossification on a scale ranging from 0 (no ossification) to 3 (skull fully ossified). Ossification was complete in most birds by mid-December. At that point, HY/SY crossbills were separated from older (AHY/ASY) birds using a combination of plumage characteristics (Svensson 1992, Cramp and Perrins 1994, Pyle 1997b). Many HY/SY birds that have completed first prebasic molt retain some juvenal (streaked, dark brown-grey) feathers on the head, back, and/or flanks. In addition, the tertials of HY/SY birds usually have small white or buff tips and an extensive buff-white fringe whereas older birds have white tertial tips without pale fringe. Finally, many HY/SY birds retain one, or more often, several juvenal under-tail coverts. These feathers have buff-colored margins and dark brown centers whereas older birds (especially males) have under-tail coverts with black centers and broad white margins that are sometimes tinged pink (males only).

Nonparametric statistical tests were performed as described by Siegel (1956) and Winkler and Hays (1975). Statistical significance level was in all cases set at $\alpha = 0.05$.

RESULTS

Timing of first prebasic molt.—All HY crossbills caught before September were in complete juvenal plumage (Fig. 1) and had unossified or partially ossified skulls. First prebasic molt started in September, continued until December in at least some individuals, and was without exception completed by January.

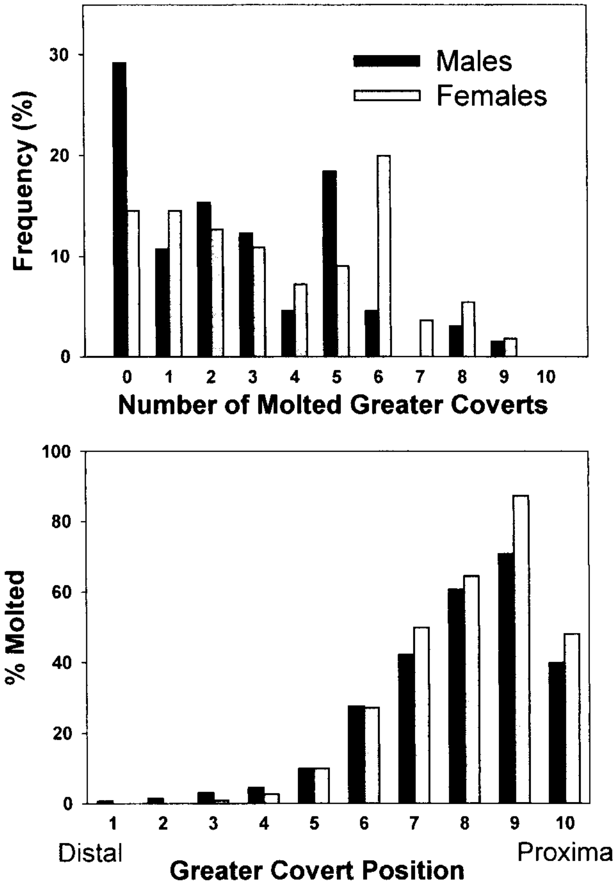

FIGURE 2. Frequency (% sampled individuals) of greater covert molt (upper panel) and percentages of males and females that molted greater coverts as a function of the covert position on the wing (lower panel) for HY/SY White-winged Crossbills at Fairbanks, Alaska, 1993–1999.

Pattern and extent of first prebasic molt.—During first prebasic molt, birds replaced, on average, three (±2) GCs and retained two (±2) juvenal MCs. No bird molted any primary or secondary, but one red-colored male caught in November had replaced two tertials on each wing. Twenty-three percent of the birds retained all juvenal GCs (Fig. 2). The remaining individuals replaced a variable number of GCs, but no bird molted all these feathers. Males and females molted similar numbers of GCs and retained similar numbers of juvenal MCs (Mann-Whitney rank sum tests: $Ps > 0.3$). A similar proportion of males and females molted various numbers of GCs (Kolmogorov-Smirnov two-tailed test: $P = 0.1$; Fig. 2). In both sexes, the frequency of GC_{1-9} replacement increased from the

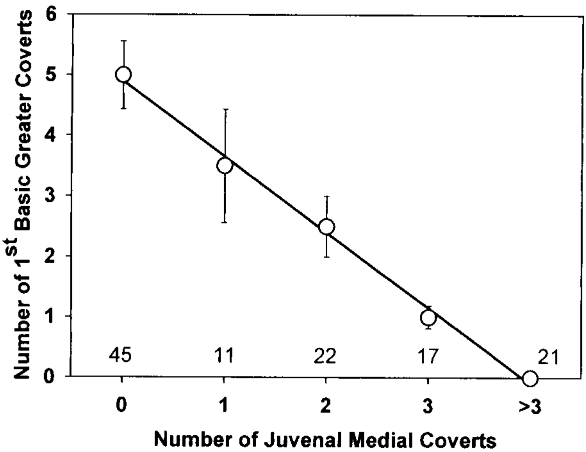

FIGURE 3. Relationship between the number of retained juvenal coverts and of molted greater coverts (medians ± ½ interquartile interval) of HY/SY White-winged Crossbills at Fairbanks, Alaska. Figures above the horizontal axis refer to the number of individuals used for calculations.

distal to the proximal part of the wing (Fig. 2). For example, less than 5% and 60–90% of the individuals replaced GC_{1-4} and GC_{8-9}, respectively.

The number of molted GCs was similar in birds caught in November (3 ± 2; n = 33), December (2 ± 2; n = 49), January (3 ± 2; n = 21), and February–May (3 ± 1; n = 17; Kruskal-Wallis: $P > 0.1$). GC molt was symmetrical in 69% of the birds but the number and/or position of molted GCs differed by one feather in 28% of the crossbills and by two feathers in the remaining three percent of the birds. There was a highly significant negative correlation between the number of molted GCs and of retained juvenal MCs (Fig. 3; $r = -0.76$, $n = 116$, $P < 0.001$).

Males with a partially red-pink plumage and males of a different color had similar body masses and identical wing lengths (Fig. 4). Males of either type caught between November and mid-December also had identical degrees of skull ossification. The extent of covert molt was, however, dependent on overall plumage color. Partially red-pink males replaced on average more GCs and retained less juvenal MCs than males without red-pink in their plumage (Mann-Whitney rank sum tests: $Ps < 0.001$). HY/SY males had shorter wings than older (AHY/ASY) males caught during the same period (n = 14; 88 ± 1 mm; Mann-Whitney rank sum test: $P < 0.001$), but young and older males had similar body masses (AHY/ASY males: 28.0 ± 1.3 g; $P > 0.5$).

DISCUSSION

Previous studies suggested that White-winged Crossbills have a longer annual breeding period than most other species living at similar latitudes (Bent 1968, Newton 1972, Godfrey 1986, Benkman 1992). While crossbills

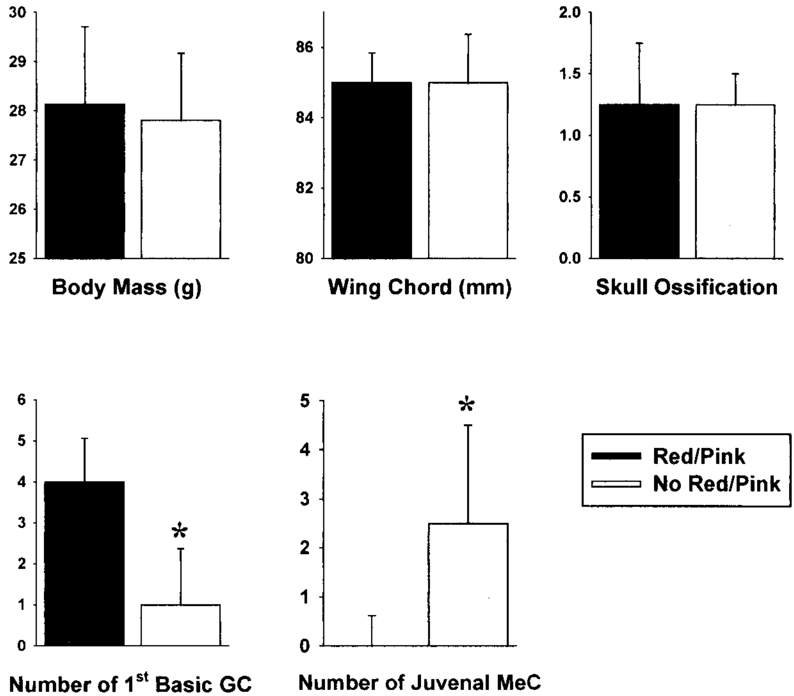

FIGURE 4. Body mass (mean ± standard deviation), wing chord, degree of skull ossification (median ± ½ interquartile interval), number of molted (adult) greater coverts (GC), and number of retained (juvenal) medial coverts (MeC) of HY/SY male White-winged Crossbills with or without red/pink contour feathers. *: $P < 0.001$, Mann-Whitney rank sum test comparing the two groups of males. See legend of Figure 1 for additional comments.

may reproduce during most of the year at middle latitudes when their preferred food (conifer seeds) is sufficiently abundant, this does not appear to be the case in interior Alaska (Deviche 1997). In this region, crossbills apparently reproduce seasonally and only during spring and summer. The present investigation establishes that another aspect of the biology of interior Alaska crossbills (i.e., the timing of first prebasic molt) is likewise highly seasonal. All HY birds molted between September and December, although birds of this age category were present in the area starting in May.

Crossbills have relatively extended stages of development compared to other small passerines (Benkman 1992, Cramp and Perrins 1994). Likewise, some individuals presumably initiated first prebasic molt when at least 160 d old (difference between April and September). This situation, if correct, contrasts with that reported for many European passerines of similar size that begin and complete first prebasic molt when less than 60 d old and at the age of 90–130 d, respectively (Jenni and Winkler 1994).

Godfrey (1986) and Cramp and Perrins (1994) also stated that White-winged Crossbills start first prebasic molt shortly after fledging. In a frugivorous passerine (*Phainopepla nitens*), plumage maturation was delayed by dietary protein limitation (Thompson and Walsberg, 1992). Similarly, factors related to the specialized diet (conifer seeds) of crossbills may constrain their developmental rate and dictate the timing of their first prebasic molt initiation.

Some authors suggested that the first prebasic molt of White-winged Crossbills does not include replacement of wing feathers (Bent 1968, Newton 1972). Other studies, however, found this molt to include replacement of some wing coverts and, in a small proportion of individuals, also of some tertials (Cramp and Perrins 1994, Pyle 1997a,b). The present investigation supports the latter conclusion in that most individuals replaced some GCs and most MCs, but partial tertial replacement occurred only in one bird. Although the pattern of wing molt in this study was qualitatively similar to that described by Pyle (1997a), the extent of wing molt was less than that reported by that author. Pyle found that some GCs were replaced during the first prebasic molt in *all* the individuals that he examined. Twenty-six percent of the birds also replaced all these feathers and at least one tertial. In contrast, 23% of the crossbills that I sampled replaced *no* GC, *no* bird molted all these feathers, and only one individual showed partial tertial replacement. Although the dates of collection and sex of the specimens examined by Pyle (1997a) were not reported, these variables are unlikely to account for differences in molt extent between that author's and the present data.

Detailed comparative studies found that the timing, duration, and extent of first prebasic molt in passerines depend on numerous factors and can differ intraspecifically (Jenni and Winkler 1994, Pyle 1997a, Hussell 1998). In particular, this molt is often less extensive, possibly because of a later onset and/or earlier cessation, in northern than southern populations of the same species (Mulvihill and Winstead 1997). Interior Alaska is located in the northern part of the White-winged Crossbill distribution (Benkman 1992, Cramp and Perrins 1994). Thus, differences between Pyle's (1997a) and the present results may reflect the fact that the extent of first prebasic molt in this species decreases with increasing latitude and the specimens examined by Pyle (1997a) were obtained at a lower latitude than interior Alaska. Additional studies on crossbills sampled at various latitudes are warranted to evaluate this hypothesis and to elucidate the physiological mechanisms involved.

In White-winged Crossbills, the extent of GC and MC molt were correlated. The extent of covert molt in males also was correlated with plumage color. Hatching-year/SY males with partially red-pink contour feathers molted more extensively (i.e., replaced more GCs and retained fewer MCs) than other males of the same age cohort. This difference was specific to molt, as the two male types were morphologically similar in terms of wing lengths and body masses, suggesting that they belonged to the same population. In some regions White-winged Crossbills may show a "split molt" pattern (Newton 1972, Pyle 1997b). Accordingly, males that molt in April–June develop a yellow or orange plumage whereas males that molt later acquire red feathers. Males sampled during this study did not conform to this pattern because they acquired plumage of various colors (red, pink, orange, yellow, or a mixture thereof) during first prebasic molt, although they all molted during the same season. There was, therefore, no apparent relationship between when molt began and first basic plumage color. Males that acquired a red-pink basic plumage also had the same degree of skull ossification as males that developed a plumage without red or pink. Assuming that degree of ossification is age-dependent (Jenni and Winkler 1994), this result suggests that males of different colors were of similar age and basic plumage color was, therefore, not age-related.

Other authors have observed that the color of the first basic plumage in male White-winged Crossbills is highly variable (Newton 1972, Cramp and Perrins 1994). During molt into definitive adult plumage, males become predominantly pink-red irrespective of their first basic plumage color (Cramp and Perrins 1994). In addition, wild caught, initially red-feathered males molt into yellow plumage in captivity (Newton 1972; personal observations). Taken together, these observations indicate that contour feather color in male White-winged Crossbills is not determined genetically and suggest that this color depends on the availability of specific dietary components as is the case in other species (House Finch, *Carpodacus mexicanus,* Hill 1993). This conclusion is supported by the fact that in crossbills (*Loxia* spp.) and Pine Grosbeaks (*Pinicola enucleator*), feather color is controlled by the presence of carotenoid pigments obtained from dietary sources (Stradi et al. 1996). Males of different colors, but belonging to the same age class and molting in the same region, may differ in subtle ways with regard to aspects of their diet and/or to their absorption, metabolism or deposition of feather pigments. Additional studies are warranted to elucidate whether and how one or several of these factors control phenotypic variability in plumage color and, correlatively, the extent of molt within a same free-living population.

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