J. Field Ornithol., 68(4):613–621

SEASONAL REPRODUCTIVE PATTERN OF WHITE-WINGED CROSSBILLS IN INTERIOR ALASKA

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Abstract.—It has been proposed that crossbills (*Loxia spp.*) are opportunistic breeders that time the onset of their reproductive cycle based on food availability rather than photoperiod, as is the case in most other bird species. Crossbills are able to nest throughout most of the year at middle latitudes, but the reproductive biology of these birds at high latitudes remains poorly known. A total of 469 White-winged Crossbills (*Loxia leucoptera*) was caught in Fairbanks, Alaska during a 2.5-yr period. Based on the proportion of juvenile birds in the sampled population, the proportion of adult females with a brood patch, and seasonal changes in adult male cloacal protuberance size, it appears that interior Alaska White-winged Crossbills breed only in spring and early summer. Timing of reproduction of crossbills breeding at high latitudes may be limited by environmental factors (potentially, ambient temperature and/or photoperiod) rather than by food availability.

PATRON REPRODUCTIVO ESTACIONAL DE *LOXIA LECOPTERA* EN EL INTERIOR DE ALASKA

Sinopsis.—Se ha propuesto que el género *Loxia* es de anidantes oportunistas que ajustan el inicio de su ciclo reproductivo en la disponibilidad de alimento más que en el fotoperiodo, como es el caso en la mayoría de las especies de aves Aves de este género pueden anidar a través de la mayor parte del año en latitudes medias, pero la biologia reproductiva de estas aves en latitudes altas permanece poco conocida. Un total de 46g individuos de *Loxia lecoptera* se capruraron en una sola estación en Fairbanks, Alaska en un periodo de 25 años. Basandose en la proporcion de aves juveniles la población muestreada, la proporción de nembras adultas con parcho reproductivo, y de los cambios estacionarios en el tamaño de la protuberancia cloacal de los machos, parece ser que en el interior de Alaska la especie anida solo durante la primavera y el verano temprano El tiempo de reproducción de *Loxia lecoptera* en latitudes altas puede estar limitado por factores ambientales (potencialidad, temperatura ambiental y/o fotoperíodo) más que por disponibilidad de alimento

In most bird species breeding at middle and high latitudes, increasing photoperiod in the spring plays an essential role in stimulating reproductive system development (Farner and Lewis 1973, Kubokawa et al. 1994, Sharp et al. 1986, Silverin 1994, Wingfield et al. 1980), and timing of reproduction occurs such that chances of survival of the offspring are maximal (Lack 1966). Timing of reproduction as well as photoinduced gonadal recrudescence rates can be modulated by nonphotoperiodic factors (e.g., food availability, mates, ambient temperature, and weather conditions; Silverin and Westin 1995, Wada 1993, Wingfield 1985a,b, Wingfield et al. 1982), but are otherwise relatively rigid, an adaptation to conditions in which the most favorable season to breed is presumably predictable.

In contrast, a few middle- and high-latitude species, in particular crossbills (Red Crossbill, *Loxia curvirostra*; White-winged Crossbill, *L. leucoptera*), are thought to breed opportunistically. Crossbills eat mainly conifer seeds (Newton 1972). The production of these seeds undergoes large and irregular annual and geographic fluctuations. Adequate food supply has been proposed to be the most important environmental factor used by crossbills to initiate breeding (Benkman 1990, 1992, Newton 1972). Accordingly, crossbill reproduction is presumed to be triggered not by photoperiod (Newton 1972, Tordoff and Dawson 1965), but by what would be considered to be supplementary cues (food) in other species. This hypothesis is supported by reports that crossbills can nest any month of the year, but mainly in spring and autumn, and infrequently between late November and December (Benkman 1992, Bent 1968, Godfrey 1986, Newton 1972). However, Hahn's (1995) detailed experimental studies on captive Red Crossbills (only one form which is not necessarily representative of Red Crossbills in New or Old World) showed that seasonal timing of reproduction in this species is controlled by photoperiod, with supplementary cues (food and social factors) playing an important modulatory role. Similarly, Tordoff and Dawson (1965) found that testicular growth initially occurs faster in Red Crossbills exposed to long than to short photoperiods.

Indications that White-winged Crossbills can reproduce outside the breeding season used by most other passerine species have been obtained mostly at middle latitudes (Bent 1968). Although the species is widespread in northern coniferous forests (Benkman 1992, Godfrey 1986), its biology at high latitudes is poorly known. This study examines variables associated with breeding in a natural population of White-winged Crossbills. Data were collected over a 2.5-yr period at a site located near the northern limit of the North American breeding range. The study area is characterized by large seasonal changes in ambient temperature and in photoperiod, which varies between less than 4 h in winter to nearly 22 h in summer.

METHODS

Bird capture.—A total of 469 White-winged Crossbills was captured on an opportunistic basis between January 1993 and August 1995 at a site near Fairbanks, Alaska (64°50′N, 147°50′W). All birds were caught between 0600 and 1900 h (AST) at a single location situated in an upland mature spruce (*Picea glauca* and *P. mariana*) and birch (*Betula papyrifera*) forest. Birds were attracted into a mist net by placing one or two live caged decoy males next to the net.

Bird handling and data collection.—Birds were removed from the net within minutes of capture, and a blood sample (max. 600 μl) was collected from an alar vein of some individuals for future analysis of circulating hormone concentrations. The body mass (BM) of all birds was measured to the nearest 0.1 g and corrected for the amount of blood removed. Contour feather molt intensity was ranked from 0 (no molt) to 3 (heavy molt involving most body areas), and degree of skull pneumatization was determined following Pyle et al. (1987). For males, I measured the cloacal protuberance (CP) width to the nearest 0.1 mm with calipers. In other male passerine birds, the CP is an androgen-sensitive secondary sex characteristic, and its seasonal development correlates with the overall activity of the reproductive system (Deviche 1995, Morton et al. 1990, Schwabl and Farner 1989). For females, I quantified the presence and development of a brood patch as follows: (0) no brood patch; (1) abdominal feathers lost, but skin not thickened or fluid-filled; (2) fully developed brood patch, including highly vascularized and thickened, fluid-filled abdominal skin; (3) brood patch regressed; abdominal skin grayish and wrinkled (Pyle et al. 1987). After data collection and age and sex determination were completed (see below), most birds were banded and released at the capture site. Some individuals were held in captivity for behavioral and physiological investigations.

Age and sex determination.—Juveniles were defined as those non-molting individuals that were in heavily streaked, brownish juvenal plumage (Cramp and Perrins 1994, Pyle et al. 1987, Svensson 1992). It has been reported that this plumage is worn only for a short time after leaving the nest (Godfrey 1986). The skulls of these birds were generally unpneumatized to partially pneumatized, and their sex was not determined. Immature birds were either undergoing contour feather molt from juvenal to basic plumage or had completed this molt, but had a partially pneumatized skull. Such birds were caught in September (2), October (12), November (33), and December (12). Finally, adults were individuals having completed molt from juvenal to first basic plumage, and with a completely pneumatized skull. Whenever possible, the sex of these birds was determined using a combination of previously described criteria (plumage coloration, CP width, and presence of a brood patch; Cramp and Perrins 1994, Pyle et al. 1987, Svensson 1992).

Data analysis.—Unless otherwise specified, data collected for the 2.5 yr of the study were combined and organized by calendar month. For each month, I computed the proportion of juvenile birds caught relative to the total number of birds caught during the same period. Seasonal changes in female reproductive status were analyzed by calculating the proportion of adult females without and with (stages 1–3 combined) a brood patch for each month separately. Relatively few adult females were caught between August and December (the monthly maximum was two adult females caught in August), so that data obtained for this period are not included in the analysis. Proportions of juveniles and of females with a brood patch were calculated only if at least ten birds (ages and sexes combined) and ten adult females, respectively, were caught during the period considered. Seven and nine adult females were caught in March and April, respectively, and data collected for these two months were combined. Changes in proportions from one month to the next were analyzed using χ^2-tests. When 20% of the expected values of a contingency table were less than five, data were analyzed using a two-tailed Fisher exact probability test. In the case of the proportion of females with a brood patch, statistical significance level was set at 0.01 (= 0.05/5 comparisons; see Results). The corresponding level used for the proportion of juveniles equaled 0.0045 (0.05/11 comparisons; see Results). To identify seasonal

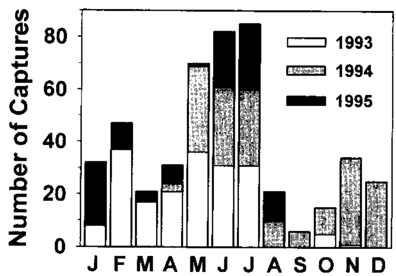

FIGURE 1. Monthly distribution of captures of White-winged Crossbills from a single site in Fairbanks, Alaska (64°50′N, 147°50′W) during 1993–1995.

changes in adult male BM and CP width, mean monthly values of these parameters were compared using one way analyses of variance (ANOVA) followed by Student-Newman-Keuls multiple pair-wise comparison tests. In this case, statistical significance level was set at 0.05.

RESULTS

Capture distribution.–Totals of 187, 179, and 103 White-winged Crossbills were caught in 1993, 1994, and 1995, respectively (Fig. 1). Though the numbers of crossbills caught in 1993 and 1994 were similar, there were large differences between these two years with respect to monthly capture numbers. For example, 37 crossbills were caught in February 1993, but none were caught during the same month in 1994. Conversely, 1 and 33 birds were caught in November 1993 and 1994, respectively. The total number of crossbills caught during a given month (years combined) also fluctuated greatly, ranging from 6 (September) to 85 (July).

Yearly and seasonal differences in capture numbers probably resulted partly from the fact that mist-netting efforts were not standardized, and the decoy males sang more vigorously during winter, spring, and early summer than fall, which possibly altered their attractiveness. Only eight White-winged Crossbills were found in the Fairbanks area during the December 1993 Christmas Bird Count of the National Audubon Society (National Audubon Society Field Notes 1994). In contrast, 830 birds (an unusually high number) were tallied during the December 1994 Count (National Audubon Society Field Notes 1995). This difference did not result from a less rigorous censusing effort in 1993 than in 1994, since the 1993 Count actually involved more party-hours than the 1994 Count. It is, therefore, likely that temporal differences in capture numbers also reflected changes in local abundance of the species.

Proportion of juveniles.—No juvenile bird was caught prior to April or after September (Fig. 2). Monthly changes in the percentage of juveniles caught followed a unimodal distribution, increasing significantly between April and May and again between June and July. The largest proportion of juveniles in the sampled population occurred in August, when 71% of the birds caught belonged to this age class.

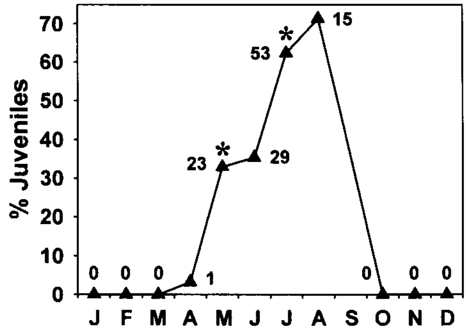

FIGURE 2. Seasonal changes in the proportion of juvenile birds of the sampled population. Figures next to the symbols refer to the total number of juveniles caught during the corresponding month. * = $P < 0.0045$, comparison with previous month (χ^2-test or two-tailed Fisher exact probability test).

Proportion of females with a brood patch.—The percentages of females captured with a brood patch varied between January and July (Fig. 3). The first females with a brood patch (all stage 1) were caught in February. Percentage of females with a brood patch significantly increased between March/April and May, but not thereafter. In the majority of cases, brood patches were either at stage 1 (early development) or 3 (regression), and only four females (May: n = 1; June: n = 1; July: n = 2) had a fully developed, highly vascularized brood patch (stage 2).

Male cloacal protuberance width and body mass.—CP size and BM underwent highly significant seasonal changes (ANOVA: CP size: $F_{8,118}$ = 4.7; BM: $F_{8,137}$ = 4.8; *P*s < 0.001; Fig. 4). These changes were gradual, so that no comparison between measurements obtained for consecutive months was statistically significant. CP size increased significantly between January (and February) and July, then decreased significantly between

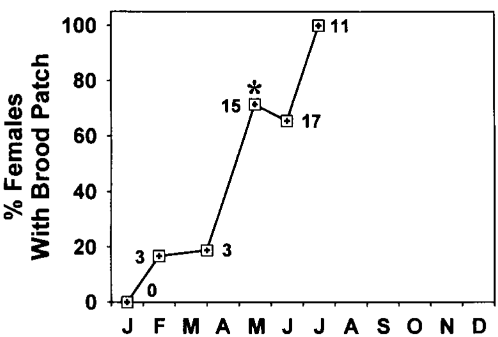

FIGURE 3. Seasonal changes in the proportion of sampled adult females with a brood patch. Figures next to the symbols refer to the total number of females with a brood patch that were caught during the corresponding period. * = $P < 0.01$, comparison with previous period (χ^2-test).

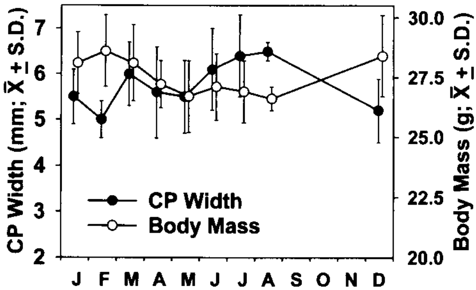

FIGURE 4. Seasonal changes (years combined) in adult male White-winged Crossbill mean cloacal protuberance (CP) width and body mass.

June (and July) and December. In contrast, BM decreased significantly between February and May, June, and July, then increased significantly between July and December. Thus, the patterns of seasonal changes in CP sizes and BM were opposite, indicating that CP sizes did not vary simply as a result of BM alterations.

Adult molt.—Throughout the duration of the study, the only three birds captured undergoing contour feather molt were adult males (February, March, October). No adult males were molting flight feathers, but two females molting these feathers were captured (August and September). Previous studies found pre-basic molt in White-winged Crossbills to take place mostly during the fall and early winter (Benkman 1992, Pyle et al. 1987), and in this study, relatively few adult birds were caught during this period (August to November: males: n = 5; females: n = 4).

DISCUSSION

I used three independent criteria (proportion of juveniles in the sampled population; proportion of females with a brood patch; seasonal changes in adult male CP size) to assess the timing of reproductive development and breeding of interior Alaska White-winged Crossbills. The results indicate that (1) no juvenile bird was caught September–March, (2) females with brood patches were not caught in substantial frequency until May, and (3) the reproductive systems of adult males, as assessed by CP size, were most active during the summer months. Taken together, these observations suggest that the breeding season of White-winged Crossbills nesting in interior Alaska is confined to spring and summer and does not extend into fall and winter. This conclusion contrasts with studies done at lower latitudes and indicating that White-winged Crossbills are opportunistic breeders that can nest at any time of the year if food supply is sufficient (Benkman 1990, Bent 1968).

One interpretation of the lack of fall and winter breeding in the study area is that during these seasons, reproductive system activity is inhibited by proximate environmental factors such as low temperatures and/or short photoperiod. In Fairbanks, the average low temperature in January is approximately −30 C, and the winter-solstice photoperiod is 3.75 h. In other species, gonadal recrudescence rates are reduced at low temperatures (Jones 1986, Silverin and Viebke 1994, Storey and Nicholls 1982), and sufficiently long photoperiods are essential for gonadal development in a related species, the Red Crossbill (Hahn 1995). No experimental study has examined the influence of temperature or photoperiod on White-winged Crossbill reproduction, but results obtained in other species suggest that these factors may directly modulate reproductive physiology in these birds as well.

Alternately, short photoperiod and low temperatures during fall and winter may prevent breeding indirectly, by imposing a limitation on maximum daily energy intake and by increasing energy expenditure beyond a level compatible with reproduction, respectively. There is no evidence that White-winged Crossbills feed in the dark. Data were collected during one winter (1994–1995) when conifer seeds were locally abundant and numerous individuals were present in the study area (personal observations: National Audubon Society Field Notes 1995), suggesting that breeding was not prevented by a lack of food resources. At lower latitudes, availability of an adequate food supply is critical for White-winged Crossbills to initiate breeding (Benkman 1990). Although neither food intake rates nor changes in these rates as a function of ambient conditions were measured, one interpretation of the present data is that breeding did not occur in fall and winter because short photoperiod limited the daily amount of time available for foraging and for nutrient acquisition. As a result, birds could acquire enough energy for self-maintenance, but not for allocation to energy-consuming activities such as egg-laying and food-provisioning to the young. The potentially limiting effect of short photoperiod was probably exacerbated by low ambient temperatures, because the energy expenditure of small birds increases as these temperatures decrease (West 1972).

In conclusion, the present findings do not contradict the idea that crossbills are flexible breeders and potentially are able to initiate breeding during most of the year if adequate food supplies are available. The data, however, suggest that in high latitude populations of crossbills, limitations to this flexibility are imposed by environmental factors. These factors may include low ambient temperatures and/or short photoperiods, and they act to restrict breeding to spring and early summer. Further behavioral and physiological research on high latitude populations of White-winged Crossbills is warranted to confirm the nature and the mechanisms of action of these factors and to determine the energetic cost of self-maintenance versus breeding as a function of ambient conditions.

ACKNOWLEDGMENTS

The author thanks Renee Crain, Cynthia Gulledge, Daniel Gibson, Thomas Pogson, and James Sedinger for comments on an early version of the manuscript.

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Received 7 Nov. 1996; accepted 16 Jan. 1997.