THE INFLUENCE OF DAYLENGTH ON REPRODUCTIVE TIMING IN THE RED CROSSBILL

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Early studies of reproductive timing in birds led to generalizations overemphasizing the importance of daylength as a regulating factor. Daylength is certainly important in stimulating gonadal development in many insectivorous passerines of temperate latitudes, but other factors, such as rainfall or its consequences, appear to control time of breeding in some birds of desert and tropical regions (Keast and Marshall, 1954; Miller, 1959, 1961; Immelmann, 1963; Oksche *et al.*, 1963). Moreover, the unpredictable occurrence of reproduction in the Red Crossbill (*Loxia curvirostra*) suggests the influence of nonphotoperiodic factors on this largely boreal species. The Red Crossbill probably has the most erratic breeding schedule of any North American bird. At various localities in its range, it has been found over a period of time breeding in every month of the year. The nomadic tendencies of this species make the situation even more unusual. A locality inhabited by breeding birds in one year may not be used for several years thereafter. These irregularities in timing and location of breeding suggest that reproduction in this species is not primarily dependent on daylength. The extent of this dependence is analyzed in this paper.

MATERIALS AND METHODS

The Red Crossbills used in this study were trapped at the Huron Mountain Club, Marquette County, Michigan, in September and October, 1960, and immediately transported to Ann Arbor, Michigan, for study. They are referable to the subspecies *L. c. sitkensis*. Males used in the photoperiod experiments were housed indoors in cages measuring $2 \times 3 \times 4$ feet. They were fed piñon nuts and sunflower, thistle, and canary seeds. Water, grit, and cuttlebone were continuously available. A vitamin supplement (ABDEC) was added to the drinking water one day each week.

Size of gonads was determined by laparotomy of each experimental bird at the start of the experiment on December 10, 1960, and at monthly intervals thereafter until late April, 1961. Observations were also made during this period to determine whether or not other indications of breeding activity, such as change in weight, molt, song, and development of a cloacal protuberance, were present. A final laparotomy was performed on December 28, 1961, and the experiment was terminated on January 15, 1962, when nine birds were sacrificed for histological examination of the gonads.

Four experimental groups of eight birds each were established. In each group, five birds were laparotomized monthly while three were kept as controls to check on possible effects of this surgery. No differences were detected between the laparotomized birds and the controls in amount of song, timing of molt, or other overt evidence of sexual activity. Each group was maintained throughout the experiment in a single cage on a daily light–dark schedule as follows: group 1, 16 hours of light, 8 hours of dark; group 2, 12 hours of light, 12 hours of dark; group 3, 8 hours of light, 16 hours of dark; group 4, natural photoperiod for latitude 42° N, the approximate latitude of Ann Arbor (window light augmented by fluorescent light in the daytime). Illumination was provided for all experimental groups by "daylight" fluorescent lights at levels exceeding 50 foot-candles.

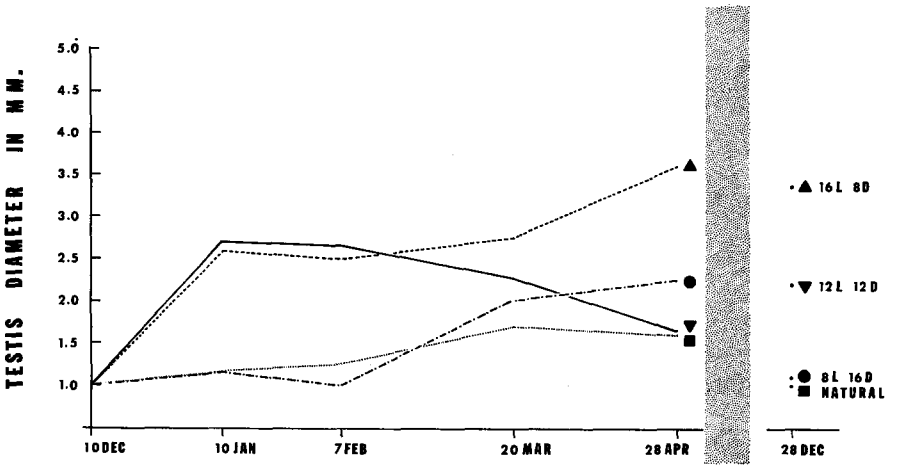

Fig. 1. Changes in mean testis diameter for four groups of Red Crossbills exposed to different photoperiods. Light regime indicated for each group by symbol at right.

RESULTS

Results of the experiment are shown in figures 1 and 2. Testis diameter for all birds initially averaged 1.0 mm. Individuals on 16 hours of light and 8 hours of dark reached an average testis size of 2.6 mm. within 30 days; this increased slowly to 3.6 mm. by April 28, almost five months after the experiment began. The birds on 12 hours of light and 12 hours of dark had testes averaging about 2.7 mm. in diameter after 30 days; subsequently, a slow regression occurred and the average diameter on April 28 was only 1.6 mm. No increase in mean testis size occurred in the group on 8 hours of light and 16 hours of dark through the first two months. However, a slight enlargement then began, so that the diameter averaged 2.3 mm. in April. The birds on natural photoperiod showed a pattern similar to that noted for the group on 8 hours of light and 16 hours of dark, with even smaller gonads (mean, 1.6 mm.) at the end of April.

Figure 1 represents mean testis diameter for the four groups, and therefore does not show the extent of individual variation, which was considerable. The testes of five birds on natural photoperiod ranged from 1.0 to 1.2 mm. on January 10 and from 1.0 to 3.0 mm. on April 28; those of five birds on 8 hours of light and 16 hours of dark ranged from only 1.0 to 1.3 mm. on January 10 but on April 28 they ranged from 1.0 to 4.5 mm.; those of five birds on 12 hours of light and 12 hours of dark ranged from 1.5 to 5.0 on January 10 and from 1.0 to 3.0 on April 28; birds on 16 hours of light and 8 hours of dark had testes that ranged from 2.0 to 4.0 mm. on January 10 and from 1.0 to 6.0 mm. on April 28.

We were able to sample wild populations of crossbills to check gonadal condition at intervals through our photoperiod experiment. We examined over 20 birds; most were taken in February in Marquette and Chippewa counties in the Upper Peninsula. Some were taken in March, April, and late May from Washtenaw County in the Lower Peninsula. No gonadal activity was detected—testes were about 1 mm. in diameter and ovaries less than 4 mm. in length.

The stages of testicular development (see Bartholomew, 1949) for the nine birds

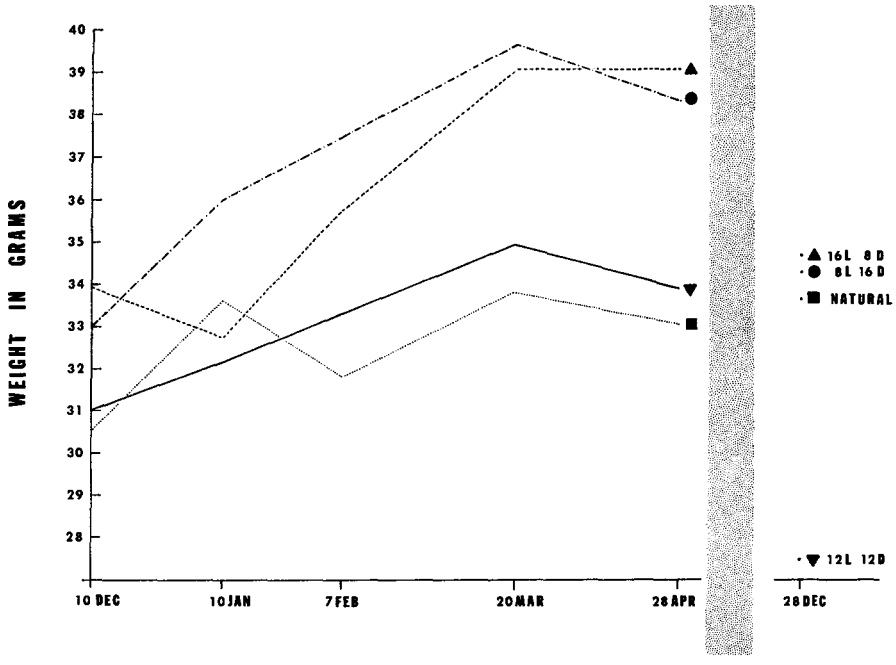

Fig. 2. Changes in mean body weight for four groups of Red Crossbills exposed to different photoperiods. Light regime indicated for each group by symbol at right.

sacrificed for histological study on January 15, 1962, were as follows: 16 hours of light, 8 hours of dark—one bird, stage II, testis diameter 1.0 mm.; two birds, stage IV to V, testis diameter 3.5 and 4.5; 12 hours of light, 12 hours of dark—two birds, stage II, testis diameter 2.0 mm. and 1.5 mm.; 8 hours of light, 16 hours of dark—two birds, stage II, testis diameter 1.0 and 1.5 mm.; natural daylength—two birds, stage II, testis diameter 1.0 and 1.0 mm. These birds were sacrificed after 13 months of continuous exposure to their particular light regime. The picture is complicated by the fact that some birds had molted early and some later in this period. It cannot be assumed that testicular activity remained constant in any of these birds throughout the experiment. One point evident from the above data is that spermatozoa are produced at testis sizes far below maximum for the species. However, this does not necessarily mean that birds with partly developed gonads are reproductively competent.

Weights of the experimental birds seemed independent of photoperiod (fig. 2). Most birds gained weight during the experiment and the mean rose from 32.1 gm. at the start to 35.8 gm. at the end of April. The birds heaviest at the start were also heaviest at the end.

The crossbills used in this study were in late stages of postjuvenal or postnuptial molt when trapped in September, 1960. We estimate that this molt had begun in July or August. It was completed by early October. Surprisingly, most of the birds on experimental photoperiods molted at about the same time, in November and December, 1961. The group on 8 hours of light, 16 hours of dark and the group on 16 hours of light, 8 hours of dark molted a little later than the others, but there was

great overlap. Despite the widely different photoperiods, the interval between the last molt in the wild and the next "annual" molt in captivity was about 15 months for most of the birds. However, one bird on 12 hours of light and 12 hours of dark and another on 8 hours of light and 16 hours of dark molted through April and May, 1961.

DISCUSSION

The clear difference in rate of gonadal enlargement in the first 30 days (no change in group on natural daylength and 8 hours of light, 16 hours of dark; enlargement to over 2.5 mm. in the group on 16 hours of light, 8 hours of dark and in the group on 12 hours of light and 12 hours of dark) indicates that photoperiod has some effect. However, none of the birds went on to complete enlargement of the gonads (about 7 to 8 mm. in diameter in wild-taken breeding birds). Furthermore, the differences between the groups diminished as the experiment progressed, due to a gradual gonadal enlargement in the two groups on short days. We suspect that this species can undergo initial development of the gonads to a state of partial readiness on any naturally occurring photoperiod, although this condition may be reached more quickly under the influence of long days. Daylength alone then is inadequate to stimulate completion of reproductive development. In these respects, the response of Red Crossbills to photoperiod is quite unlike that of juncos and of sparrows of the genus *Zonotrichia* (Wolfson, 1959; Farner, 1959).

Demonstration of the secondary role of daylength in breeding of crossbills makes it reasonable to ask what are the proximate environmental factors controlling breeding times of wild populations? The most likely and most obvious is food itself. Food is the ultimate factor in the vast majority of birds, since breeding appears ordinarily timed to conditions optimal for production and survival of young. With seasonally fluctuating food supplies, most birds are keyed to respond to environmental factors that will bring about breeding at the most favorable time. This means that food as an ultimate factor cannot be used as a proximate stimulus if a wasteful time lag during gonadal maturation and other events leading to hatching of eggs is to be avoided—hence the widespread reliance on daylength, rainfall, green vegetation, and other environmental factors as proximate stimuli.

Crossbills are faced with special problems in nature, and they have some special advantages. Their primary food, conifer seeds, is produced in abundance only infrequently and at irregular intervals at any locality. When the conifers do produce a good seed crop, however, the seeds are protected by the cones long enough to permit crossbills to come into breeding condition and still exploit the food before it becomes available to most other animals. Red Crossbills need no insect food, even for the newly hatched young. This has been inferred from their nesting during winter in the wild and confirmed by repeated successful nestings in our laboratory. The nomadic nature of these birds, their indifference to cold, and their gregarious nature, even when breeding, afford additional advantages for effective utilization of conifer seeds (Dawson and Tordoff, 1964). In fact, we are impressed by the parallel between the situations facing nomadic desert finches of Australia (Serventy and Marshall, 1957; Immelmann, 1963; see also Oksche *et al.*, 1963) and crossbills. In each case, the birds move in flocks through vast areas of fairly uniform and generally unproductive habitat, until their wanderings, or the passing of time, bring them to an area suitable for breeding. With the desert birds, rainfall or its immediate consequences serves as the proximate stimulus, and hatching of young is well synchro-

nized with maturation of seeds and build-up of insect populations following the rain. In crossbills, on the other hand, food probably is both the proximate and ultimate factor producing breeding.

In 1963 and 1964, we provided the crossbills with conditions that allowed them to nest successfully in our outdoor flight cages (which, incidentally, confirms the adequacy of the diet fed the experimental birds studied earlier). Although our birds have produced over 40 young from 12 nestings, from April through August, 1963, and March through June, 1964, circumstances have not permitted us to learn much regarding timing of their breeding. In both years, we judged on the basis of song, courtship feeding, and manipulation of nesting material, that the birds in the community cages were in breeding condition perhaps as early as January. However, they could not start nesting until April and March in these two years because of the earlier unavailability of adequate flight cages for breeding purposes. Within a day or two after suitable isolation was provided, birds that we judged ready to breed were in fact nesting. Additional study of our flock of crossbills should help to determine the time of development of full breeding condition following the postnuptial molt, which in past years has taken place in late summer in the outside cages.

If the onset of reproductive activity in nature is in fact controlled by food supply, it is reasonable to wonder about the factors controlling breeding in the captive birds provided with food *ad libitum*. Since both the quality and the amount of food available to our captive crossbills would allow reproduction at any time, other, secondary factors that are normally permissive to breeding in nature must have been operative in preventing attainment of full reproductive condition by the birds used in the photoperiod experiments. These secondary factors probably are primarily psychological, and may involve response to such things as cage size, availability of nest sites and nesting material, composition of the flock, and so on. The fact that reproductive condition was reached by crossbills in large, outside flight cages but not by the birds in our photoperiod experiments suggests one likely line of investigation into the secondary controlling factors. Whatever their nature, the response of Red Crossbills to manipulation of the photoperiod is quite unlike the positive response so well demonstrated in various emberizine sparrows (Farner, 1959; Wolfson, 1959).

In our captive Red Crossbills, molt has closely followed breeding, or the collapse of the gonads, if breeding was prevented for some reason. A typical series of events occurred in 1964. The birds appeared to be ready to nest as early as January. In late March, six pairs were placed in breeding cages and all nested immediately. By the middle of May, four of these six pairs had completed their nesting and were starting the postnuptial molt. The birds in community cages, with no opportunity to nest, also started to molt in mid-May. Accompanying the onset of molt was a great reduction in song by males, disappearance of incubation patches in the females, and loss of interest in nesting material.

Data on size of gonads in relation to molt is available for some of the experimental birds discussed earlier. One male held on 16 hours of light and 8 hours of dark for 12 months had testes 3.0 mm. in diameter on December 28, 1961, and showed practically no molt. On January 15, 1962, this bird was in very heavy molt and its testes were 1.0 mm. in diameter. Several other males had testes about 1.5 mm. in diameter when laparotomized while in heavy molt. However, one apparent exception is provided by a male held on 12 hours of light and 12 hours of dark from December 10, 1960, to April 28, 1961. This bird was in heavy, symmetrical molt

and had testes 3.0 mm. in diameter on the latter date. It should be noted, however, that this individual's testes were 5.0 mm. at three laparotomies in January, February, and March. In both 1963 and 1964, pairs of crossbills persisted in nesting long after most had quit and gone into molt. In these persistent nesters, no molt was evident until breeding efforts finally ceased.

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SUMMARY

The Red Crossbill (*Loxia curvirostra*) has an erratic breeding schedule which suggests that reproductive timing in this species is not primarily dependent on day-length. To measure this dependence, four groups of male crossbills were exposed experimentally to light–dark schedules as follows: 16 hours of light, 8 hours of dark; 12 hours of light, 12 hours of dark; 8 hours of light, 16 hours of dark; and natural photoperiod. Testis size was determined by laparotomy at monthly intervals for the first four months and again at the termination of the experiment after 12 months. Gonads of birds on 16 hours of light and 8 hours of dark and on 12 hours of light and 12 hours of dark increased from about 1 mm. in diameter to about 2.5 mm. in diameter in the first month, then changed little in size through the next three months. Birds on 8 hours of light and 16 hours of dark and those on natural photoperiod showed no enlargement for two months and then slight gradual enlargement for the next two months. None of the groups approached maximum testis size (about 7 to 8 mm. in diameter) for the species. However, some spermatozoa are produced in birds with only partly developed testes.

The postnuptial molt occurred at about the same time in all of the experimental groups, approximately 15 months after the previous postnuptial molt in the wild.

The failure of any of the experimental birds to complete gonadal development and the ability of even the birds on short photoperiods to undergo partial enlargement of the testes suggest that the Red Crossbill can reach a partial state of readiness on any naturally occurring photoperiod, although this state may be reached more quickly on long days. Final maturation of the gonads is then, presumably, dependent in the wild on availability of suitable food.

In our captive crossbills, molt and breeding have not occurred simultaneously. In fact the most dependable external evidence of gonadal collapse following breeding is the onset of postnuptial molt.

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