PTERYLOGRAPHY AND NATURAL AND EXPERIMENTALLY INDUCED MOLT IN CLARK'S NUTCRACKER

By L. RICHARD MEWALDT

One of the more demanding processes in the lives of birds in the higher latitudes is the annual molt. When data on the molt from 439 Clark's Nutcrackers (*Nucifraga columbiana*) became available, it was apparent that its timing and duration were somewhat unusual. Early in the study of the nesting cycle (Mewaldt, 1956), it was noted that some birds were in molt at the height of the nesting season. Although some species of birds in equatorial regions are known to be in molt while nesting (Moreau, Wilk, and Rowan, 1947; Miller, 1955), birds in the high latitudes generally do not molt until the nesting season is over.

To reinforce the data from the collected birds, records on the sequence of molt were obtained from 65 nutcrackers kept in captivity for varying lengths of time. These captive birds yielded information which is difficult to obtain from preserved specimens.

I am grateful to the following persons for the loan of specimens under their care: Herbert Friedmann, United States National Museum; George E. Hudson, Charles R. Conner Museum; and Ernst Mayr, then at the American Museum of Natural History. To the following persons I am indebted for help in the collection of specimens in the field: Fletcher E. Newby, Ludvig G. Browman, Thomas D. Burleigh, Clinton Conaway, Rexford Daubenmire, Frances Lee Mewaldt, and George C. Ruhle. I am especially grateful to Philip L. Wright, Montana State University, and Donald S. Farner, State College of Washington, who gave freely of their encouragement, good counsel, and material assistance. This investigation was supported in part by a Louis Agassiz Fuertes Research Grant of the Wilson Ornithological Society, by the Departments of Zoology, Montana State University and the State College of Washington, and by funds provided for biological and medical research by the State of Washington Initiative Measure No. 171.

MATERIAL AND METHODS

From October, 1946, to October, 1951, 439 Clark's Nutcrackers were collected. Of these, 428 were collected in western Montana, seven in eastern Washington, two in northern Idaho, and two in Oregon. Although most collections were made in the winter and spring months, some specimens were taken in every month of the year.

The fresh skins were removed and treated on the inside with sodium chloride. Skins of the first 200 (Nc 1 to Nc 200) were washed in detergent and prepared as conventional study skins. The remaining skins were washed in detergent, slit open, and dried flat to facilitate examination of the feather tracts on the inside of the skin. A few specimens were preserved in 70 per cent alcohol for study of their pterylography.

From December, 1948, through December, 1951, from two to 45 nutcrackers were maintained in captivity at Pullman, Washington. In all, 51 were trapped in northwestern Idaho and 14 in the Cascade Mountains of southern Oregon. Individual records of weight and molt were kept until the last six were sacrificed in December, 1951.

Except as noted, the nutcrackers were maintained in cages 12 feet long, 8 feet wide, and 6 feet high. The top and sides were covered with half-inch hardware cloth. At one upper corner, three 4×4 foot panels converged to form a shelter, under which were placed perches and a feed shelf. A 4×4 foot compartment, 6 feet high, in the opposite corner from the shelter served as a safety entrance and a catching chamber. Perches were placed in several positions about each cage. No more than 12 nutcrackers were placed in each cage. Two birds which escaped, after having been held captive for more

than a year, proved that they were still strong fliers by making their escape by sustained flight away from the aviary. Cages for experimental birds were located on the roof (sixth level) of Science Hall. These cages were protected from direct wind blast and city lights by a screen made of one-fourth inch corrugated cement asbestos board seven feet high. Control birds were kept in cages of the same construction at ground level about 400 yards from Science Hall.

The basic diet, kept constantly available, consisted of Larro Egg Mash Pellets, a commercial poultry feed containing about 20 per cent protein. A weekly supplement of about 15 grams of fresh pork liver per bird was provided. Especially in the winter months, the carcasses of mice and other mammals were quickly eaten when available. Fresh water was provided daily except that snow, when present, was taken by the nutcrackers in preference to water. Raw piñon seeds (from *Pinus edulis*) obtained from New Mexico were eagerly taken whenever placed in the cages.

PTERYLOGRAPHY

What few references I have been able to find pertaining to pterylography in the genus *Nucifraga* have been fragmentary. A résumé of the feather tracts of Clark's Nutcracker follows. It was obtained, in the main, from 12 specimens preserved in alcohol. The terminology used is adapted from Boulton (1927), Pitelka (1945), and Mayaud (1950). Figures 1 and 2 are designed to assist in following this résumé.

Alar tract.—Clark's Nutcracker has 20 remiges. All ten primaries, the proximal designated as number 1, are well developed. The shortest is number 10 and the longest either number 5 or 6. The small tenth (proximal) secondary is usually distinguishable from nearby coverts by its slightly duller coloration and by its extension somewhat posterior and proximal to overlying coverts. Although there are ten greater primary coverts, only nine middle primary coverts were found, the first (proximal) being absent. No lesser primary coverts could be distinguished. The carpal remex (Mayaud, 1950) was found at the base of the first primary, approximately where the first primary covert would be expected. It is intermediate in size between the second middle primary covert and the first middle secondary covert. The carpal covert is inserted between the bases of the first primary and the first secondary. Ten greater secondary coverts are inserted at the base of and slightly proximal to each corresponding secondary. Nine middle secondary coverts have their insertions alternating with the greater secondary coverts. No lesser secondary coverts were distinguished. Another covert-like feather described by Pitelka (1945:232) for a race of the Scrub Jay (*Aphelocoma coerulescens insularis*) as a small covert lying "posterior and medial to the innermost of the three feathers of the alula . . . ," seems in the nutcracker to be definitely associated with the alula. The alula supports three principal feathers, the one covert just mentioned, which is probably a degenerate fourth alular feather, and a number of small coverts which are continuous with the numerous marginal coverts. The marginal coverts extend from the leading edge of the wing toward the bases of the primary and secondary coverts. The carpometacarpal coverts extend distally from the alula to the base of the tenth primary along the leading edge of the manus.

There are ten lower greater primary coverts and ten lower lesser primary coverts. The homology of the first lower lesser primary covert is in doubt. It may be the displaced first lower lesser secondary covert (Pitelka, 1945), or the lower carpal remex covert (Boulton, 1927). In Clark's Nutcracker, just proximal to the first lower lesser primary covert is seen a substantial down-like feather. There are no lower middle primary coverts. A careful search reveals what may be six or seven much reduced lower greater secondary coverts proximal to each of the six or seven secondaries. There are what appear to be nine lower middle secondary coverts, the first inserted between the first primary and the first secondary, below the first lower lesser primary covert. There are apparently ten lower lesser secondary coverts. However, either of the last two mentioned coverts may actually be a part of the series of lower middle secondary coverts, forming the tenth feather of that series. The long and fine lower marginal coverts only sparsely cover the lower wing area proximal to the metacarpal region. The ten or 12 tertiaries extend in a single row along the trailing edge of the wing posterior to the humerus and, along with scattered down feathers, complete the wing cover.

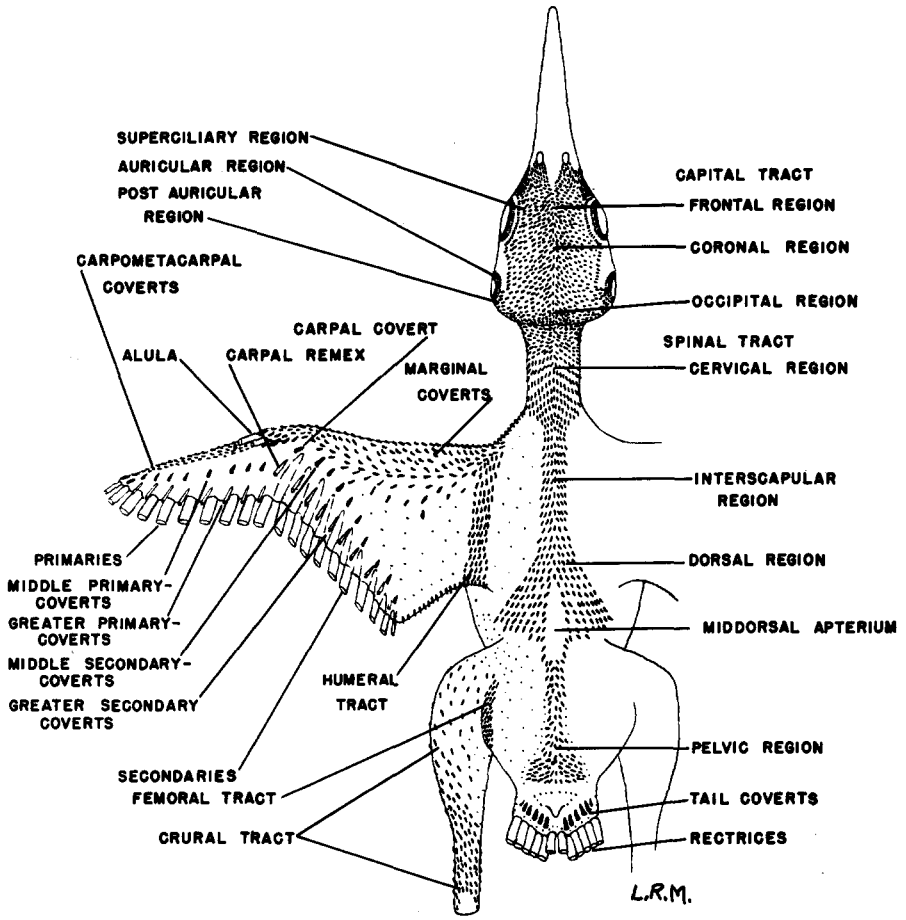

Fig. 1. Pterylography of Clark's Nutcracker, dorsal view.

Caudal tract.—There are 12 fully developed rectrices. The center pair (1–1) have been displaced dorsally. There are either ten or 12 upper tail coverts. The outermost pair (6–6) is always small if present. This outermost pair was present on nine out of 12 specimens of nutcrackers preserved in alcohol, although it was very much reduced on three of these nine. Twelve down feathers form an incomplete ring anterior to the uropygial gland. There are two principal rows of lower tail coverts of ten each, plus another 14 or 15 smaller feathers on each side enclosing an apterium between the anterior row of under tail coverts and the anal circlet. The anal circlet appears to be composed of four or five rings of feathers almost completely encircling the cloacal aperture.

Capital tract.—The dorsal and lateral surfaces of the head are densely feathered except for two pairs of lateral apteria. The down-filled temporal apterium extends from the corner of the mouth (gape), between the eye and ear, to a point just dorsal to the posterior margin of the ear. The post-auricular apterium is essentially continuous with the lateral neck apterium. The eye is surrounded by two complete circles, and the ear is surrounded by three complete circles of small feathers.

Spinal tract.—The spinal tract is alternately six and seven feathers broad (see fig. 1) in the interscapular region and two or three times as broad in the dorsal and cervical regions. An elongated middorsal apterium, which parallels the long axis of the body, may be found in the posterior portion of the dorsal region of the spinal tract of fresh and spirit specimens. The spinal tract becomes wider in the cervical region and at its terminus in the pelvic region.

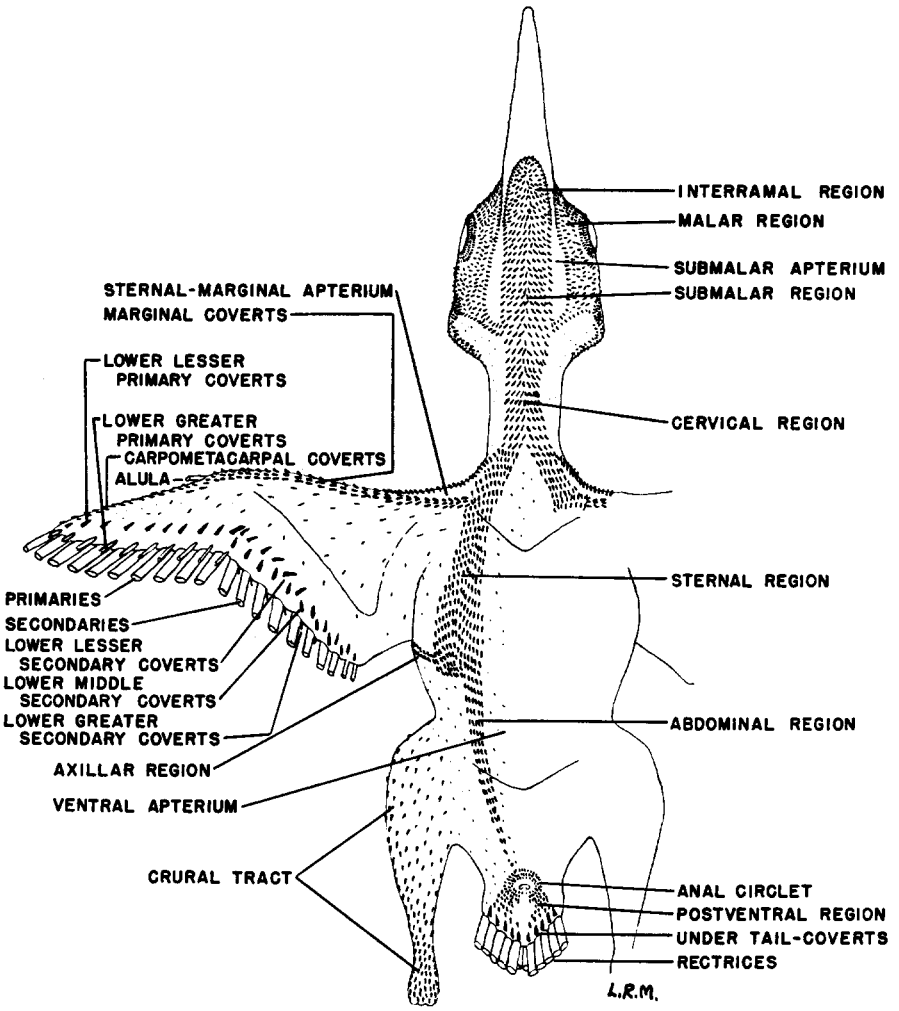

Fig. 2. Pterylography of Clark's Nutcracker, ventral view.

Humeral tract.—From the junction of the leading edge of the wing with the body, the humeral tract extends over the dorsal surface of the base of the wing to the medial tertiaries of the alar tract.

Femoral tract.—Four to five feathers broad, the femoral tract crosses the dorsal surface of the thigh, with the proximal portion directed toward the caudal tract.

Crural tract.—The feather covering of the hock varies from sparse on the proximal portions, to relatively dense just above its junction with the shank.

Ventral tract.—The submalar apteria which separate the interramal region from the malar regions are distinct but contain considerable down. There is an acute triangular apterium butting on the ventral tract and extending between the dorsal and ventral marginal coverts along the leading edge of the wing. The axillar region extends from the base of the sternal region of the ventral tract to the ventral border of the axilla.

Apteria.—The apteria contain some down feathers which tend to obscure some of the feather-free areas on certain parts of the bird. The abdominal apterium of breeding birds becomes free of down feathers when the incubation patch is formed in females and males (Mewaldt, 1952) during active nesting seasons.

DISCUSSION OF PTERYLOGRAPHY

In most instances, differences in feather distributional pattern were not detected upon comparison with the accounts published by investigators concerned with pterylography in Corvidae. However, two variations were evident and seem of sufficient importance for discussion. Comparisons were made among specimens of 13 genera, as follows: five *Aphelocoma coerulescens coerulescens,* one *Aphelocoma coerulescens californica,* one *Calocitta formosa,* one *Cissilopha beecheyi,* two *Corvus brachyrhynchos,* one *Corvus corax,* one *Gymnorhinus cyanocephala,* four *Cyanocitta stelleri,* one *Cyanocorax chrysops,* one *Cyanocorax yncas,* one *Garrulus* sp.?, one *Kitta chinensis chinensis,* 12 *Nucifraga columbiana,* two *Perisoreus canadensis,* five *Pica pica hudsonia,* and one *Psilorhinus morio.*

The middorsal apterium.—Pitelka (1945) reported the absence of the fissure-like space, here designated as the middorsal apterium, in the dorsal region of the spinal tract in *Aphelocoma* and *Cyanocitta,* while confirming its presence in *Corvus.* In the material available to me, I have found the middorsal apterium discernible in representatives of all genera except *Aphelocoma, Cissilopha, Cyanocitta, Perisoreus,* and in *Cyanocorax yncas. Cyanocorax chrysops,* presumed to be closely related to the genus *Aphelocoma* (Pitelka, 1945), was found to have the middorsal apterium present in agreement with Nitzsch (*fide* Sclater, 1867). However, *Kitta chinensis,* included by Nitzsch in the Paradisaeidae and figured without the middorsal apterium, was found to have this apterium distinctly present on the one specimen (USNM 19579) examined. It is perhaps significant to note that Stonor (1942) reported the absence of the apterium in *Callaeas cinerea,* the Blue-wattled Crow of New Zealand, which is not generally included in the Corvidae.

How important the presence or absence of the middorsal apterium may be in a phylogenetic consideration is questionable. It is worth noting that the representatives of *Aphelocoma, Cissilopha,* and *Cyanocitta* examined, all included as subgenera in the genus *Cyanocitta* by Amadon (1944), were found to be without a middorsal apterium. However, a middorsal apterium was present in the representatives of three genera examined (*Psilorhinus, Calocitta,* and *Cyanocorax chrysops*) which were shown by Amadon (1944:17), in a proposed phylogenetic tree, to have arisen from a *Cyanocitta*-like ancestor. Also *Perisoreus* (*Cractes* of Amadon), which lacks the apterium, was believed to have arisen from a stock in common with *Garrulus,* a representative of which was found to possess the middorsal apterium.

The upper tail coverts.—Boulton (1927) and Pitelka (1945) showed only five pairs of upper tail coverts and they presumed the most recently degenerate pair to be 1–1, represented by two down feathers near the bases of rectrices 1–1. Some species of the Corvidae which were examined had distinct, although reduced, upper tail coverts 6–6. Not all specimens of these species were found to have coverts 6–6, for example, *Nucifraga columbiana.* Some genera, including *Aphelocoma,* showed no trace of coverts 6–6. However, the presence of coverts 6–6 in some specimens, and a down feather remnant in others, suggests that, at least in the Corvidae, upper tail coverts 6–6 may be the most recently degenerating coverts, rather than coverts 1–1.

MOLT

The plumages of Clark's Nutcracker may be summarized as follows: (1) the juvenal plumage, acquired by the postnatal molt, is the first covering of feathers and is the plumage designation until the completion of the postjuvenal molt; (2) the first-year plumage, acquired by the postjuvenal molt, is the plumage designation until, during their first postnuptial molt, first-year birds are no longer distinguishable from adults;

(3) the adult plumage, acquired by the first postnuptial molt, is renewed each year by subsequent postnuptial molts.

Molt as here used is the orderly dropping of feathers and their replacement in a sequence characteristic of the species concerned. It does not include the accidental dropping of feathers and their subsequent replacement. The period of a molt extends from the time that the first feathers are dropped until the last feathers dropped in that molt are fully replaced and hardened.

Nutcrackers in the postnatal molt are the youngest birds considered. They are classified as juveniles (in juvenal plumage) until the partial postjuvenal molt is completed. First-year birds (in first-year plumage) can be identified as such by the incompleteness of the postjuvenal molt. Birds in first-year plumage can usually be distinguished until about July of their second year (when they are 13 to 16 months of age) when their first postnuptial molt is so advanced that they are indistinguishable from adults on the basis of plumage characters. Males and females within each age group are treated together, for no significant differences in the time or in the sequence of molt were detected. A discussion of plumage as it is related to age and sex may be found in the section on age and sex heteromorphism.

Postnatal molt.—It is by means of the postnatal molt that the young bird acquires its first feather covering. Although the young nutcracker is fairly well covered with feathers when it leaves the nest at about 20 days of age (Mewaldt, 1956), feather growth continues for at least two or three weeks.

Birds at the time they leave the nest have gray eyes, gray feet, and the inside surfaces of their bill and mouth vary from pale salmon-red to white. Feathers are growing in every tract except the capital tract. Usually primaries 1 to 9 are soft and still growing, whereas primary 10 and the ten secondaries are fully grown and are hard. The upper wing coverts are usually hard, with the exception of the marginal coverts, many of which are incompletely grown. The lower wing coverts are more than half grown. Pitelka (1945) found young *Aphelocoma coerulescens* lacking lower wing coverts as late as the time of departure from the nest. Feathers in the central portions of most feather tracts on the body are fully grown, but those along the edges of the spinal and ventral tracts, and the posterior portions of the humeral and femoral tracts, are soft and only partially grown.

The last traces of the postnatal molt appear in the lateral portions of the dorsal region of the spinal tract; however, feathers apparently do not completely fill the lateral angles to their apices until near the end of the postjuvenal molt.

During the postnatal molt, the eyes change gradually in color from gray to brown and the feet from gray to black. Black areas appear in the white inside surfaces of the bill and mouth and gradually increase in size until well into the postjuvenal molt when the inside of the bill and mouth of most specimens is black.

Postjuvenal molt.—Evidence from the few specimens collected in sufficiently early stages of the postjuvenal molt suggests a sequence of body molt similar to the body molt in the postnuptial molt of first-year and adult birds. The partial postjuvenal molt involves all body feathers, but in the alar and caudal tracts it is restricted to certain of the smaller feathers.

The primaries and their coverts, the carpometacarpal coverts, the alula and its coverts, the carpal remex and its covert, and the secondaries are not molted. The greater secondary coverts are not molted with the occasional exception of numbers 8 and 9. Middle secondary coverts 6, 7, and 8 are usually (but not always) molted, and occasionally numbers 4, 5, and 9 are molted in addition. Pitelka (1945) found in *Aphelocoma coerulescens* that most greater secondary coverts and all middle secondary coverts were

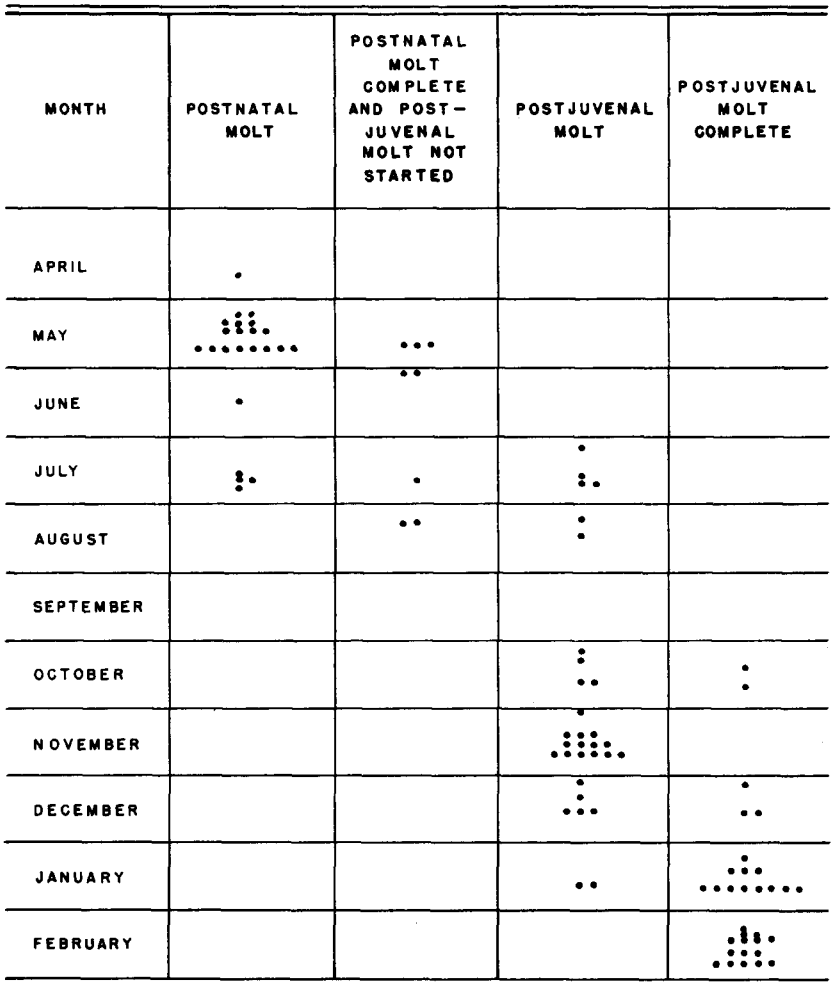

Fig. 3. Occurrence of molt by months in juvenal and first-year Clark's Nutcrackers.

replaced. He also determined in two races of *Aphelocoma coerulescens* that secondaries 7 to 10 were all, or in part, replaced in 12 of 41 first-year specimens. Mayaud (1948) found in *Garrulus glandarius* that the three proximal secondaries and six proximal greater secondary coverts are replaced as well as all of the middle secondary coverts. Usually all of the marginal feathers on the dorsal surface of the wing of *Nucifraga columbiana* are renewed.

The rectrices are not replaced in the postjuvenal molt. The upper tail coverts are usually molted, but occasionally the middle pair remains until the first postnuptial molt. At least some of the lower tail coverts are replaced.

The postjuvenal molt of the *Nucifraga columbiana* collected in western Montana differs only in detail from that reported for *Aphelocoma coerulescens* (Pitelka, 1945) and from that reported for *Corvus brachyrhynchos* (Emlen, 1936), *Corvus frugilegus frugilegus* (Witherby, 1913), *Cyanocitta cristata* (Arnold, MS), and several other corvids (Dwight, 1900).

In *Aphelocoma coerulescens,* Pitelka (1945) found that the last juvenal feathers to be dropped in the postjuvenal molt are those of the lateral neck region. In *Nucifraga columbiana,* however, it appears that the last trace of postjuvenal molt occurs in the lateral angles of the dorsal region of the spinal tract.

Figure 3 summarizes the condition of molt of juvenal and first-year nutcrackers collected during their first twelve months. It is perhaps significant to note that four juveniles in postnatal molt were collected in the second half of July. Actually two of these four had left their nests only three or four days earlier, for their rectrices and most of their primaries were incompletely grown.

Postnuptial molt.—Adult and first-year Clark's Nutcrackers undergo one complete molt, the postnuptial molt, each year starting usually in March or April. This one complete molt is characteristic of adult Corvidae (Sclater, 1867; Dwight, 1900). Pitelka (1945:246) found in *Aphelocoma coerulescens* that this "first complete molt of birds one year of age is initiated, sometimes, before that of older individuals of a given population and usually within the first half of the molt period of the population." That a similar situation occurs in Clark's Nutcracker may be seen in table 1. All first-year birds collected after March 9 were in molt, whereas some adults had not begun to molt when collected in April and May. The first adult molt was found on a specimen collected on March 17.

Table 1

Occurrence by Months of Postnuptial Molt in Adult and First-year Clark's Nutcrackers Collected from February 1 to June 30

	Adults			First-year birds		
		Per cent with			Per cent with	
Month	Number	No molt	Molt	Number	No molt	Molt
Feb.	31	100	.....	15	100	.....
Mar.	25	92	8	36	42	58
April	44	27	73	53	.....	100
May	24	12	88	11	.....	100
June	8	.....	100	3	.....	100

Beginning in July, first-year nutcrackers in their first postnuptial molt could not be distinguished from adults in postnuptial molt. The sequence of molt appears to be the same in both first-year birds and adults, even though first-year birds commence molting sooner than adults.

The sequence of loss of the principal feathers of the caudal and especially of the alar tracts in the postnuptial molt is relatively constant. This is true not only within a species but probably throughout the order Passeriformes (Dwight, 1900; Jones, 1930; and Mayaud, 1950). Variations which occur are largly due to differences in overall molting time rather than to differences in order within each feather tract.

The postnuptial molt in Clark's Nutcracker begins with the dropping of primary 1. The molt on the two wings is usually well synchronized. The remainder of the primaries are dropped in order, one at a time, before the next proximal primary is fully grown. Shortly after new primary 5 has begun to grow, secondary 8 is dropped. Within a few days secondaries 9, 2, and 7, usually in that order, are dropped and replaced. Secondaries 3 and 10 are replaced while new primary 8 is growing. Growth of new secondary 4 usually overlaps growth of new primary 9. The three principal feathers of the alula and secondary 5 are usually replaced while new primary 10 is growing. The last remex to be dropped and to be renewed is secondary 6. The rectrices are dropped one pair at a time from the center pair outward, beginning with 1–1 while primaries 4 and 5 are grow-

ing; followed by 2–2 during the growth of primary 6; 3–3 during the growth of primary 7; 4–4 during the growth of primary 8; 5–5 during the growth of primary 9; and 6–6 during the growth of primary 10.

This sequence follows closely that reported for *Aphelocoma coerulescens* (Pitelka, 1945) except that secondary molt begins slightly earlier (with primary 4) and the feathers of the alula are dropped considerably sooner (with primary 6 or 7) in *Aphelocoma coerulescens*. Differences in the time relationships between feather tracts are not apparent when comparison is made between molt in Clark's Nutcracker and molt in the Rook, *Corvus frugilegus frugilegus* (Witherby, 1913). Witherby found that the Rook's secondaries begin to molt when half (five) of the primaries have molted, and that when the tenth primary is growing, the alula is in molt. It should be noted that secondary 7 in *Nucifraga columbiana* is molted earlier than in either *Corvus frugilegus frugilegus* (Witherby, *op. cit.*) or *Garrulus glandarius* (Mayaud, 1948). Except that the Canary (*Serinus canarius*) has but nine primaries and nine secondaries, the order of molt of the flight feathers of an adult male, reported by Vaugien (1948), agrees more exactly with the order in *Nucifraga columbiana* than do the published accounts for other species of Corvidae.

The duration of the postnuptial molt is extremely variable, lasting from a few weeks in some passerine birds to several months in some species in the order Falconiformes (Mayaud, 1950). Most passerine birds complete their postnuptial molt within two months after its inception. Presumably because some species nest late in the summer (July and August) in the north temperate zone, they are found in molt into November (Dwight, 1900).

As more precise information is accumulated regarding the molt in the Corvidae, we find that, as a group, the duration of their postnuptial molt is apparently considerably longer than for most other passeriform birds. Witherby (1913) found that the primary molt of *Corvus frugilegus frugilegus* extended over four or five months, from early May to September in Great Britain. Whereas the postnuptial molt occupies about three months in certain races of the genus *Aphelocoma,* this complete molt in at least one race, *Aphelocoma ultramarina arizonae,* lasts from more than four months to almost six months (Pitelka, 1945). Arnold (MS) found specimens of *Cyanocitta cristata bromia* from New York in molt from June into October, or for from four to five months. Mayaud (1948) found specimens of *Garrulus glandarius* from western France in molt from the beginning of July until the end of September.

The postnuptial molt of Clark's Nutcrackers collected in western Montana extends over a substantially longer period than do the molts of at least some other species of Corvidae. All first-year and adult nutcrackers collected between May 15 and September 18, a four month period, were in the postnuptial molt. Of 243 collected between March 31 and December 1, 93 per cent were in molt. This suggests that the duration of the postnuptial molt for most individual nutcrackers lasts eight or nine months. Although the molt for about the last two months of the period is largely restricted to the lateral portions of the spinal tract, its high frequency of occurrence and constancy of location are deemed sufficient to justify its inclusion within the postnuptial molt. In the populations sampled, some trace of postnuptial molt was detected in every month except February. Miller (1928) noted growing feathers on the throat of *Lanius ludovicianus* for one or two months after what he considered the termination of the regular postnuptial molt.

All first-year and adult nutcrackers collected between May 15 and September 5, a three and one-half month period, were molting flight feathers. Between March 31 and September 1, 91 per cent of 174 nutcrackers collected showed molt of flight feathers,

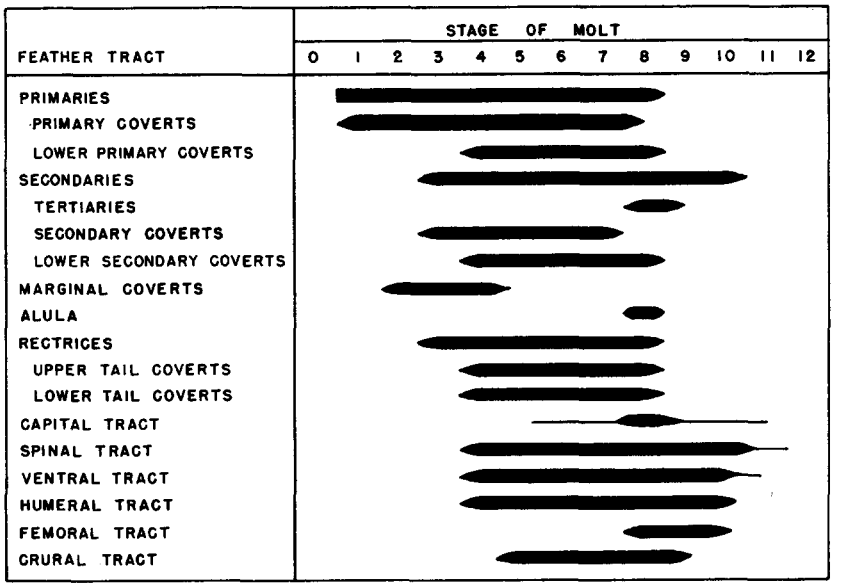

Fig. 4. Sequence of molt by selected groups of feathers as related to thirteen arbitrary stages in the postnuptial molt of Clark's Nutcracker.

indicating that individual nutcrackers take four and one-half or five months to completely replace their remiges and rectrices.

Individual case histories show that 35 captive nutcrackers on normal photoperiods took from six to more than eight months to complete molt of the flight feathers. It is highly probable that the molt of the flight feathers of these captive birds was extended into October and November as a result of their captivity. Similar prolongation of molt was noted by Pitelka (1945) for captive *Aphelocoma coerulescens*.

A series of arbitrary molt stages similar to those used by Pitelka (*op. cit.*) for *Aphelocoma coerulescens* has been outlined so that the progress of the postnuptial molt may be considered with respect to time. Figure 4 displays graphically the portions of the plumage that are in molt simultaneously. There is individual variation, but on the whole the pattern appears relatively constant. Molt of captive control nutcrackers followed the same pattern.

The skin of each adult and first-year nutcracker was assigned to one of 13 groups according to its condition of molt as follows:

Stage 0 Postnuptial molt not yet begun.
Stage 1 Primaries 1 and/or 2 missing or growing, 3 to 10 old.
Stage 2 Primaries 1 and 2 grown, 3 growing, and 4 to 10 old.
Stage 3 Primaries 1 to 3 grown, 4 and 5 growing, and 6 to 10 old.
Stage 4 Primaries 1 to 4 grown, 5 and 6 growing, and 7 to 10 old.
Stage 5 Primaries 1 to 6 grown, 7 growing, and 8 to 10 old.
Stage 6 Primaries 1 to 7 grown, 8 growing, and 9 to 10 old.
Stage 7 Primaries 1 to 8 grown, 9 growing, and 10 old.
Stage 8 Primaries 1 to 9 grown, and 10 growing; secondaries 1 to 3 and 7 to 10 grown, 4 and 5 growing, and 6 old.
Stage 9 Primaries 1 to 10 grown; secondaries 1 to 4 and 7 to 10 grown, 5 growing, and 6 old.
Stage 10 Secondaries 1 to 5 and 7 to 10 grown, and 6 growing.

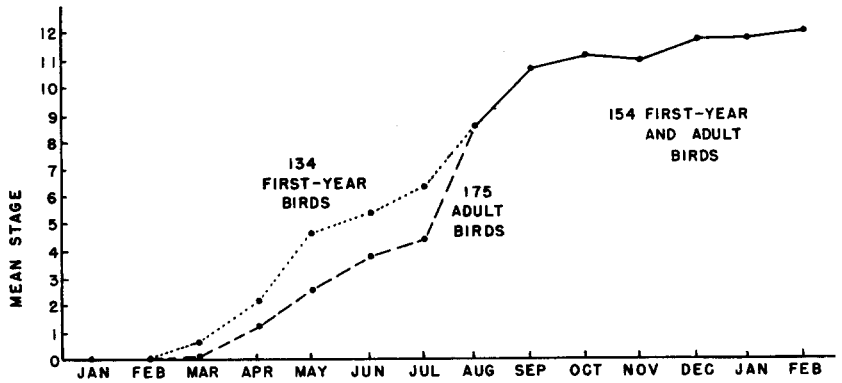

Fig. 5. Progress of postnuptial molt in Clark's Nutcracker as shown by mean stage reached in the month of collection.

Stage 11 Secondaries 1 to 10 grown. Feathers of spinal tract growing.

Stage 12 Postnuptial molt completed.

A single specimen may be assigned to either stage 0 or stage 12 for purposes of postnuptial molt analysis. In the consideration of molt data gathered from live birds, only 12 stages (0 to 11) are employed where stage 11 is assigned to birds which have completed the molt of flight feathers.

We have already seen (table 1) that first-year birds begin the postnuptial molt earlier than adults. First-year birds continued to be in a more advanced stage of molt than adults as long as the two age groups could be distinguished (fig. 5).

Inasmuch as first-year nutcrackers were not found to breed (Mewaldt, 1952), these data suggest that the breeding activity of the adults may have a delaying influence upon the start of molt. That this influence is not directly attributable to the gonads is highly probable (Lesher and Kendeigh, 1941; and Damsté, 1947). It should be noted that castrates of several species of birds have been found to molt (Keck, 1934; Witschi, 1935; and Domm, 1939). Except for a treatment of the influence of increased photoperiod upon molt, the physiological mechanism controlling molt is beyond the scope of this investigation. Some quantitative data, however, obtained from wild Clark's Nutcrackers, should prove suggestive in an interpretation of the relationship between the reproductive cycle and the postnuptial molt. These data are:

Nc 73, an incubating female with an incubation patch, was collected in the early afternoon of April 23, 1947, on Mitouer Ridge near Missoula, Montana. This female and her mate, Nc 72, started building a nest on April 15 and were observed still carrying material on April 17. The ovary, which weighed 436 milligrams, contained three freshly ovulated follicles. No other follicles were large enough to indicate further laying. The nest could not be reached for verification by egg count. The empty oviduct weighed 5050 milligrams. The postnuptial molt was in progress: right primary 1 was three centimeters long, right primary 2 was missing, and left primary 1 was missing.

Nc 72, a male with incubation patch, was collected an instant before his mate, Nc 73, on April 23, 1947. The combined weights of the testes, which were producing mature sperm, totaled 1188 milligrams. The postnuptial molt was in progress; primaries 1 and 2 of both wings were new and nearly fully grown, and primary 3 of both wings was four centimeters long.

Nc 76, a banded female whose incubation patch was nearly gone, was collected on the morning of April 29, 1947, on Mitouer Ridge near Missoula, Montana. Her two surviving young had probably left the nest on the preceding day. This bird and her mate started nest building on March 11; eggs were deposited on March 19, 20, 21; three young hatched on April 7 and 8; and the two surviving young left the nest when about 20 days of age, probably on April 28. The ovary weighed 43 milligrams,

and the oviduct weighed 243 milligrams. On the day of collection, postnuptial molt was in progress; primaries 1 to 3 were new and fully grown on both wings, and primary 4 was missing from both wings.

Nc 222, a female with a heavy incubation patch, was collected on April 13, 1948, near Big Creek, in the Bitterroot Mountains, Ravalli County, Montana. Her nest contained three eggs which had been incubated about 11 days. The ovary weighed 93 milligrams and the oviduct 594 milligrams. No molt was in progress.

Nc 223, a male with a heavy incubation patch, was collected a few seconds after Nc 222 as it left the nest mentioned in the preceding paragraph. The combined weight of the two regressing testes was 518 milligrams. The postnuptial molt was in progress; primaries 1 and 2 of both wings were new and fully grown, new primary 3 of both wings was nine centimeters long, primary 4 of both wings was missing.

From these data two suggestions concerning the postnuptial molt may be made. First, the postnuptial molt in the adult Clark's Nutcracker may begin before the eggs are laid. Wright and Wright (1944) found, however, that male *Agelaius phoeniceus* began postnuptial molt when the testes had regressed to about 20 milligrams in combined weight from a maximum of about 900 milligrams. In the tropics, Moreau, Wilk, and Rowan (1947) found that one of three species of birds studied, a coly (*Colius striatus mombassicus*), is in continuous molt through the nesting season. The other two, *Pycnonotus xanthopygos micrus* and *Phyllastrephus flavostriatus tenuirostris,* have a more concentrated molt which starts while there are still active spermatozoa in the testes. Miller (1955:503) reports in regard to birds in Colombia, South America, that molt "in many tropical species may take place when birds are in full breeding condition." The second suggestion concerning postnuptial molt is that males begin their postnuptial molt sooner than their mates. Olsen and Marsden (1951) found that male domestic white turkeys were induced to molt by exposure to long artificial days in winter whereas females showed no such response.

EXPERIMENTAL ALTERATION OF MOLT

Several species of finches, which normally undergo a prenuptial molt, have been induced to undergo a prenuptial-like molt by exposing them to increased photoperiods in autumn (Lesher and Kendeigh, 1941; Miller, 1948 and 1954; and Farner and Mewaldt, 1955). These finches, and several species which do not undergo a prenuptial molt, have responded to extended long photoperiods by undergoing a postnuptial-like molt (Walton, 1937; Burger, 1941; Vaugien, 1948; Wolfson, 1952; and Miller, 1954). A postnuptial-like molt has been induced in many species in spring or early summer by reducing the length of the daily photoperiod (Miyazaki, 1934; Burger, 1941; and Damsté, 1947).

EXPERIMENTAL MODIFICATION OF MOLT IN CLARK'S NUTCRACKER

Experiment 1.—A well ventilated, windowless room was used in which a constant photoperiod was provided. This room, which was about 13 feet long, 7 feet wide, and 8 feet high, was lighted by three 200-watt frosted incandescent electric lamps. Illumination for the final 15 minutes of each daily light period was provided by a seven and one-half watt lamp which enabled the birds to go to roost. Light readings, taken with a Weston Foot-Candle Meter (Model 614), varied from ten foot-candles on the darkest part of the floor to about 150 foot-candles on the higher perches. The nutcrackers received an average of from 40 to 60 foot-candles of light. The temperature of the air in this unheated room was about 0°C. when the roof aviary temperature was about —18° C., about 9°C. when the roof aviary temperature was 0°C., and about 26°C. when the roof aviary temperature was 21°C. The birds kept in this room received the same diet as those in the outdoor aviaries.

Ten nutcrackers were placed in this room on October 8, 1950, on an initial 12-hour

photoperiod, which approximated length of day on that date, including civil twilight. Seven and one-half minute decrements, alternating morning and evening, were applied until November 5, 1950, when an 8 ½-hour photoperiod was attained. These birds remained on this reduced light ration until November 27, 1951, when the three remaining nutcrackers were moved to the roof aviary. These three birds started molting at the usual time near the end of March. They completed their molt of flight feathers nearly three months earlier than controls (see fig. 6). They also completed their molt more rapidly than they had the previous year when they underwent all but the initial stages of their first complete molt in outdoor cages where they received natural light.

Experiment 2.—Each large cage in the aviary on the roof of Science Hall was fitted

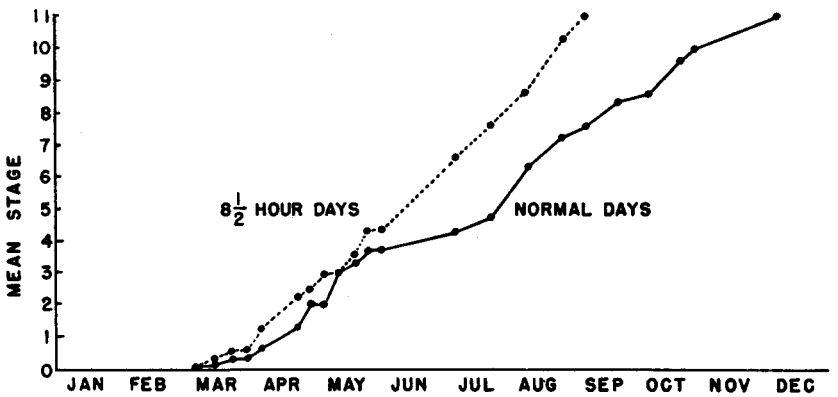

Fig. 6. Progress of molt of flight feathers of captive Clark's Nutcrackers on 8½-hour days and on normal days in 1951.

with four 200-watt frosted incandescent electric lamps. Light intensity readings revealed that the darkest portions of the floor received eight foot-candles and the perches nearest the lamps in excess of 400 foot-candles. The nutcrackers received an average illumination of from 30 to 50 foot-candles from the lamps, plus natural illumination during daylight hours. The lights were regulated by an automatic time switch and were kept burning during daylight hours.

On October 14, when the time from sunrise to sunset at Pullman was approximately 11 hours, supplemental lighting was begun in the morning to produce an initial period of 12 hours. This photoperiod was increased by approximately 7½ minutes each day, alternating morning and evening, until November 15, when a 16-hour photoperiod was attained. The lights in the cages were extinguished 15 minutes before the end of the photoperiod and a 100-watt bulb suspended in the center of the aviary was left lighted for the final 15 minutes to provide artificial twilight for the birds to go to roost. The 16-hour photoperiod was maintained until February 20, 1951, when the period of lighting was reduced by 15-minute daily decrements until March 7, when artificial lighting was discontinued. The first sign of molt occurred on December 19 when one of 20 nutcrackers dropped two primaries. The testes of this male were in the resting stage (testis stage 1) when it was sacrificed on December 27. Primary 1 had grown five centimeters and primary 2, four centimeters.

The sequence of prematurely induced molt did not follow the postnuptial molt pattern in four of the eight cases in which molt appeared. In these four, molt began with secondary 8 and usually involved secondaries 7 and 9, and rectrices 1–1 to 3–3 before

Table 2

Summary of Molt of Flight Feathers Induced by 16-hour Daily Photoperiods During Winter of 1950–51

Date	Number of birds	Number in molt	Stages (and number in each)	Mean stage	Adjusted mean stage*
Dec. 19	20	1	0(19), 1(1)	0.1	0.1
Dec. 27	16	1	0(15), 1(1)	0.1	0.1
Jan. 6	14	3	0(11), 1(3)	0.2	0.2
Jan. 13	14	4	0(10), 1(4)	0.3	0.3
Jan. 20	13	5	0(8), 1(5)	0.4	0.4
Jan. 27	12	5	0(7), 1(3), 2(2)	0.6	0.6
Feb. 3	8	6	0(2), 1(5), 2(1)	0.9	1.2
Feb. 10	8	6	0(2), 1(4), 2(2)	1.0	1.3
Feb. 16	8	6	0(2), 1(3), 2(3)	1.1	1.5
Feb. 25	8	6	0(2), 1(2) 2(2), 3(2)	1.5	2.0
Mar. 4	7	5	0(2), 1(1) 2(1), 3(3)	1.7	2.4
Mar. 11	7	5	0(2), 2(2) 3(2), 4(1)	2.0	2.8
Mar. 17	7	5	0(2), 2(2) 3(2), 4(1)	2.0	2.8
Mar. 24	6	4	0(2), 2(1) 3(2), 4(1)	2.0	3.0
Mar. 30	6	4	0(2), 2(1) 3(1), 4(2)	2.2	3.2
Apr. 7	6	4	0(2), 2(1) 4(2), 5(1)	2.5	3.7

* Excludes two birds which failed to molt although they were held until April.

primary 1 was molted. One of the four started to molt between January 6 and 13 and had new secondaries 7 to 10; it had all new rectrices when sacrificed on April 26. This bird had no further molt of flight feathers. In those cases in which the molt pattern was irregular, molt stages were assigned in accordance with the number of flight feathers dropped so that graphic comparisons could be made with control groups. No molt occurred in two of the nutcrackers retained until April.

Table 2 gives a summary of the molt of the nutcrackers on 16-hour days in the winter of 1950–51, and figure 7 compares these data with the molt of the controls for the same period. None of the birds sampled showed any sign of gonadal recrudescence. It is probable that photoperiods were increased during the gonadal refractory period of the species.

Experiment 3.—On November 27, 1951, the three nutcrackers from experiment one and three which had been a part of the control group since April, 1950, were moved into individual cages in the open air aviary on the roof of Science Hall. These individual cages measured 24 inches long, 14 inches wide, and 18 inches high. The six cages were placed in a frame which gave some protection from rain and snow and which was lighted with incandescent electric lamps. Cage floors received from 50 to 65 foot-candles illumination and perches from 85 to 120 foot-candles. The diet remained unchanged from previous experiments, except that these six birds had piñon seeds constantly available. They had also been receiving these seeds daily during the preceding month.

On November 27, the nutcrackers received an 11-hour photoperiod; on November 28, they received 12 hours of light, and on November 29, they received 14 hours. The

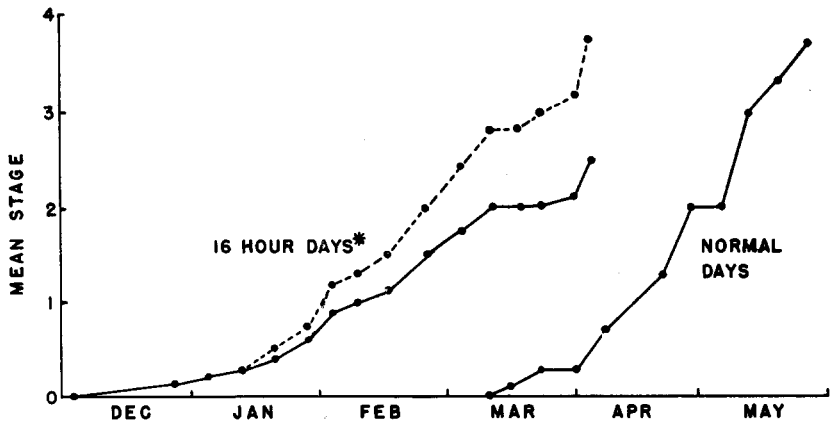

Fig. 7. Progress of molt of flight feathers of captive Clark's Nutcrackers on 16-hour days and on normal days in the winter of 1950–51. (*Two birds which failed to molt are excluded from consideration in the broken line.)

final 15 minutes of the photoperiod again consisted of artificial twilight provided by a 100-watt bulb in the center of the aviary. The 14-hour photoperiod was continued until the six were sacrificed on December 30, 1951.

These six nutcrackers had undergone two previous complete molts in captivity. One of the six had started to molt on December 30 when the six were sacrificed for gonad examination. This bird, a male which had previously been on 8½-hour days, carried a new left primary 1, four centimeters long, and the right primary 1 was missing. Molt must have begun about December 24. The testes of this bird were enlarged and in full breeding condition.

DISCUSSION OF RESULTS

These experiments indicate that Clark's Nutcracker will molt while subjected to daily photoperiods of 8½, 14, or 16 hours. Molt on the 8½-hour photoperiods (experiment 1) started at the normal time, whereas on each of the two longer photoperiods (experiments 2 and 3) molt occurred more than two months ahead of the normal time.

It is perhaps significant that the nutcrackers on the 8½-hour photoperiod molted at the normal time. The time of molt was not changed by having the daily photoperiod reach winter minimum more than a month before the shortest day of the year. The physiological mechanism which timed the start of molt, therefore, was not immediately dependent upon changing photoperiod for its precision. However, Wolfson (1952) reports that some *Junco hyemalis* and *Zonotrichia albicollis*, placed on constant 9- and 12-hour daily photoperiods on December 4, did not molt in the course of an experiment which continued into the following fall. It is unlikely that molting in all groups can be expected to show a similar response to similarly altered photoperiods.

Changes brought about by caging birds for observation have a greater or lesser effect upon the molt, apparently depending upon how great or how little the environment varies from natural conditions. The molts of captive controls are usually extended in time, while the molts of birds subjected to various experimental procedures may not only be changed in duration but also in time of occurrence, extent, and/or sequence (Miller, 1954). Although light has been demonstrated to have an important effect upon molt in captive birds, the manner in which light exerts this effect is not apparent. Light is employed as a modifying factor in the forced molting of chickens by producers of poul-

try products. Here restriction of movement, reduction of drinking water, and changes in diet are widely employed to induce molt, with an apparent reduction in mortality (Hall, 1946).

Pitelka (1958) suggests that the annual molt in Steller's Jay resident on the Queen Charlotte Islands (latitude 54°N) may be timed to take advantage of peak summer food abundance. He suggests that molting, with its high energy requirements for both adults and immatures, may be as critical, or more critical, in the survival economy of the species than the timing of feeding of nestlings. Consistent with this suggestion is his observation that Steller's Jays on the Queen Charlotte Islands molted earlier in the year and over a shorter period of time (60–80 days) than did Steller's Jays in the San Francisco Bay region of California (latitude 38°N).

In Clark's Nutcracker in central western Montana (latitude 47°N) the molt of flight feathers takes 135 to 150 days. Including the replacement of body feathers, the molt may take as long as 240 days. Superficially these data suggest a somewhat different adaptation in Clark's Nutcracker than Pitelka suggests for Steller's Jay. Molt in the nutcracker is apparently independent of any peak or peaks in food abundance. By being spread over all of the warmer months of the year, molt can progress with little more food than is required for life processes other than molt. We should observe, however, that molt of body feathers becomes heaviest in June, July, and August, when protein foods form a more important part of the diet than during the rest of the year. It may also be observed that replacement of body feathers in the warmer months places less strain on thermoregulatory processes than would such a replacement in the colder months of the year.

In Clark's Nutcracker in central western Montana, breeding is apparently dependent on an adequate supply of seeds from the ponderosa pine (Mewaldt, MS). In 1948, when food was scarce, molt in nonbreeding adults was fully a month later than in 1947 and 1949 when breeding was general. Here we see that, although delayed, molt occurred even when food was not sufficient to stimulate breeding. The reasons for this retardation are not immediately apparent, for first-year birds, which do not breed (Mewaldt, 1952 and MS), molt substantially earlier than adults (fig. 5). That the annual molt can be influenced in its timing by some factor in the reproductive cycle seems likely. However, it is equally apparent that there is no close dependence of molt upon reproduction in Clark's Nutcracker for we have observed that: (1) breeding birds may start postnuptial molt before their eggs are laid; and (2) some, but not all, captive birds, whose gonads failed to respond to increased photoperiods, were forced into an early postnuptial-like molt.

AGE HETEROMORPHISM AND SEXUAL DIMORPHISM

Male and female Clark's Nutcrackers do not appear to have external morphological differences except in size. Although males are on the average larger than females, the smaller males are smaller than the larger females.

In his detailed treatise on American jays of the genus *Aphelocoma,* Pitelka (1951) concluded that no absolute differences in external characteristics occur between the sexes but that, within each race, females are on the average smaller and duller than males.

Dosse (1937) found no correlation between sex and relative skeletal weight in six species of European Corvidae. He reported that the bones of older birds were heavier than those of younger birds (observations based in part on species other than Corvidae) because the water content of the bones declined coincident with an increase in the deposition of salts.

AGE HETEROMORPHISM

Clark's Nutcrackers held in the hand, and to a more limited extent when seen in the field under favorable conditions for observation, can be separated into three classes by plumage characteristics. Most of the characteristics employed are applicable to other species of Corvidae (Emlen, 1936; Pitelka, 1945; Mayaud, 1948) and to a lesser extent to species in some other families of Passeriformes.

A number of external characteristics can be employed to assist in the separation of juvenal, first-year, and adult Clark's Nutcrackers. Usually more than one characteristic is needed to estimate the age of a specimen. The presence or absence of the bursa of Fabricius and, to a more limited extent, the degree of cranial ossification (Miller, 1946; Nero, 1951) are useful, especially during the fall and winter months, to confirm age assignments made on plumage characteristics.

Heteromorphism of external characteristics.—The following external characteristics were found useful for separating juvenal Clark's Nutcrackers from first-year and adult birds. Descriptions of color when capitalized have been taken from Ridgway's (1912) "Color Standards and Color Nomenclature."

1. The gray eyes of the nestling have changed to brown about six weeks after hatching.

2. The gray coloration of the feet, including the tarsus, of the nestling has changed to black about six weeks after hatching.

3. On leaving the nest, the inside surfaces of the bill and mouth are white. Small areas with black pigmentation soon appear. These pigmented areas usually spread until the entire inside surfaces of the bill and mouth become black in the fall months.

4. The feathers in the facial area around the bill of juveniles are of the same color as those of the rest of the head. The feathers of this facial area become white in the postjuvenal molt and are white in all subsequent plumages.

5. The juvenal body feathers are Mouse Gray usually broadly tipped with Pale Ochraceous-Buff, in contrast to the pure Mouse Gray of the body feathers of first-year and adult birds.

6. Juvenal body feathers are typically fluffy, or less compactly formed than the body feathers of first-year and adult birds.

7. Except for occasional accidental feather losses, young birds of a given year do not molt their flight feathers until about one year old. Most first-year and adult nutcrackers have flight feathers in molt in May, June, July, and August, the months when nutcrackers in juvenal plumage are present.

After the postjuvenal molt another set of characteristics is necessary to distinguish first-year birds from adults. Most of these are the result of the incompleteness of the postjuvenal molt. Usually in July of their second year, first-year birds can no longer be distinguished from adults.

1. Pigmentation of the first-year remiges and rectrices is usually weak. These flight feathers tend to become brownish in the fall and winter. Although adult remiges and rectrices show some fading by spring, they are usually substantially darker than those of first-year birds taken at about the same time of year.

2. Juvenal alular feathers, greater primary coverts, greater secondary coverts, and middle secondary coverts retained through the postjuvenal molt tend to be dull and brownish. These stand out in contrast to the renewed marginal coverts and what middle and occasional greater secondary coverts are renewed. The renewed coverts are glossy blue-black.

3. The tips of the rectrices of first-year nutcrackers tend to be rounded, whereas those of adults are usually truncate.

4. Primaries 5 to 9 of first-year birds tend to have their tips more pointed than the same primaries of adults.

5. Remiges and rectrices, especially their terminal portions, of first-year birds usually appear more worn than do those of adults at a given time of the year.

The characteristics enumerated above were employed to place each specimen into an age group before dissection was made. In only two or three instances did inspection

of the internal anatomy force a revision of the age assignment originally based upon the external characteristics.

In addition, differences among the age groups were found in weight, wing length, tail length, length of exposed culmen, and height of the bill at the angle of the gonys.

The bursa of Fabricius.—The occurrence, structure, and ontological history of the bursa of Fabricius in many species of birds, including certain species of Corvidae, have been considered at length by Forbes (1877), Retterer (1885), and Jolly (1915). The practical use of the bursa to ascertain age in upland game birds is discussed by Gower (1939), Linduska (1943), and Kirkpatrick (1944). During the fall hunting season the bursa is present in birds-of-the-year of most upland game species and it is absent from older birds.

In Montana, Wright and Wright (1944) found that the bursa of Fabricius was present in "year-old" Redwinged Blackbirds (*Agelaius phoeniceus*) in January but absent in March. Adults did not have a bursa. Schwartz and Schwartz (1950) found the bursa of Fabricius present in some Barred Doves (*Geopelia striata*) in both juvenal and adult plumages in Hawaii. However, they also found the bursa absent from some Barred Doves in both plumages.

Each nutcracker collected was carefully examined for a bursa of Fabricius. All juveniles were found to have a bursa. Table 3 shows the occurrence of the bursa in 162 juvenal and first-year nutcrackers. The actual numbers of birds having a bursa in the late winter and early spring months was probably somewhat higher. In the late winter of 1946–47 and in the early spring months of 1947, I experienced some difficulty in recognizing the bursa when it was small and surrounded by fatty tissue.

Table 3

Frequency Distribution of Weights of the Bursa of Fabricius of Juvenal and First-year Clark's Nutcrackers by Months After Hatching

			Weight of bursa in milligrams							
Month	Number of birds	Bursa not found	1 to 50	51 to 100	101 to 150	151 to 200	201 to 250	251 to 300	301 to 350	More than 350
Apr.	1	.....	.....	.....	.....	.....	.....	1	.....	.....
May	20	.....	.....	1	3	3	7	4	2	.....
June	3	.....	.....	.....	.....	1	.....	.....	1	1[1]
July	8	.....	.....	.....	1	1	4	2	.....	.....
Aug.	4	.....	.....	.....	1	.....	2	.....	.....	1[2]
Sept.	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
Oct.	6	.....	1	.....	1	3	.....	.....	1	.....
Nov.	14	.....	.....	2	6	4	.....	1	1	.....
Dec.	7	2	1	1	2	1	.....	.....	.....	.....
Jan.	14	1	6	5	2	.....	.....	.....	.....	.....
Feb.	15	4	3	6	2	.....	.....	.....	.....	.....
Mar.	35	20	8	3	3	1	.....	.....	.....	.....
Apr.	18	12	6	.....	.....	.....	.....	.....	.....	.....
May	11	9	2	.....	.....	.....	.....	.....	.....	.....
June	3	3	.....	.....	.....	.....	.....	.....	.....	.....
July	3	2	1	.....	.....	.....	.....	.....	.....	.....
Aug.	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
Sept.	1	.....	1[3]	.....	.....	.....	.....	.....	.....	.....

[1] 403 milligrams.
[2] 588 milligrams.
[3] Male in adult plumage presumed to have been about 18 months old.

The frequency distribution of the weights of alcoholic specimens shown in table 3 suggests that the bursa of Fabricius of Clark's Nutcracker begins to decrease in size in about October of the first year of the bird's life. By the following April, the bursa was found to weigh generally less than 50 milligrams or to be absent. One male (Nc 273) in adult plumage, collected on September 5, 1948, and thought to be about 18 months old, had a distinct bursa which weighed 38 milligrams.

Skin measurements.—The summary of measurements which follows is based upon my series of skins only. Methods of measurement were adapted from Baldwin, Oberholser, and Worley (1931) and may be described as follows:

1. Length of wing: The length of the folded wing was taken with dividers in millimeters from the proximal anterior surface of the first metacarpal portion of the carpometacarpus to the tip of the longest primary with the wing folded. This measurement approximates the length of wing from the bend to the tip of the longest primary with the wing folded, but it can be more accurately duplicated. Measurements were made on the right wing unless it was damaged, in which case the left wing was used.

2. Length of tail: The length of the tail was measured along its dorsal surface, to the nearest tenth of a millimeter, with the inside points of a vernier caliper. One point was placed between the middle rectrices where they emerge from the skin, and the other point was placed at the tip of the longest rectrix.

3. Length of exposed culmen: The proximal limit of the exposed culmen was determined with the inside surface of the thumb-nail. One of the inside points of a vernier caliper was placed against the back of the thumb-nail on the culmen and the other point was adjusted to the tip of the culmen. Readings were made to the nearest tenth of a millimeter. The thickness of the thumb-nail was not added to the reading.

4. Height of the bill at the angle of the gonys: A common pin was inserted through the first free skin in the angle of the gonys. The pin was firmly seated perpendicular to the ventral surface of the gonys. The outside arms of the vernier caliper were employed to take the height anterior to and touching the pin from the angle of the gonys to the top of the culmen. Measurement was taken to the nearest tenth of a millimeter.

Inspection of tables 4 and 5 makes it apparent that size differences do occur in the

Table 4

Measurements in Millimeters of Clark's Nutcrackers by Age and Sex

Measurement	Age and sex	Number	Range	Mean	Standard deviation
Length of wing	Adult males	161	181–202	192	±4.3
	Adult females	90	180–199	186	±4.3
	First-year males	75	178–197	187	±4.2
	First-year females	64	173–193	181	±3.8
Length of tail	Adult males	163	104–124	115	±3.8
	Adult females	87	103–117	111	±3.4
	First-year males	68	103–116	109	±3.1
	First-year females	60	100–112	105	±3.3
Length of exposed culmen	Adult males	184	34.8–47.8	40.1	±1.8
	Adult females	96	34.3–42.8	37.7	±1.9
	First-year males	75	30.3–42.8	37.3	±2.9
	First-year females	65	30.3–39.8	36.0	±2.3
Height of bill	Adult males	180	10.0–12.3	11.0	±0.4
	Adult females	95	9.4–11.4	10.5	±0.4
	First-year males	75	7.8–11.8	10.5	±0.8
	First-year females	71	7.3–11.2	10.2	±0.7

Table 5

A Summary Showing Possible Comparisons of Means of Some External Measurements of Clark's Nutcrackers

Compare means	Is the difference between means in table 4 very significant? (P = 0.003) Length of wing	Length of tail	Length of culmen	Height of bill
Adult males with adult females	Yes	Yes	Yes	Yes
Adult males with first-year males	Yes	Yes	Yes	Yes
Adult males with first-year females	Yes	Yes	Yes	Yes
Adult females with first-year males	No	Yes	No	No
Adult females with first-year females	Yes	Yes	Yes	Yes
First-year males with first-year females	Yes	Yes	Yes	No

age and sex groups of Clark's Nutcracker. Table 5 presents a summary of statistical analyses made to determine whether the means (with their standard deviations) are real, or if they could have arisen by chance. A "yes" in table 5 implies that there is less than 1 chance in 300 that another sample from the same population would not show similar differences in means. Adult males have longer wings, tails, and exposed culmens, and a greater height of bill than any other age and sex group. First-year females are smaller in each of these measurements than the other age and sex groups. Measurements of adult females and first-year males, on the other hand, approach each other very closely. No significant difference was found between the heights of the bills of first-year females and first-year males.

SUMMARY

From October, 1946, to October, 1951, a total of 439 Clark's Nutcrackers (*Nucifraga columbiana*) was collected. Most of these birds were taken in western Montana. An additional 65 were live-trapped and used in an investigation of the effects of altered photoperiods on the molting process.

In its pterylography, Clark's Nutcracker was found to be very similar to *Aphelocoma coerulescens* as described by Pitelka (1945) and to other species of Corvidae as described by other authors. The middorsal apterium was found present in representatives of nine genera of Corvidae examined (including *Nucifraga columbiana*) and absent from representatives of five genera. The outer pair of upper tail coverts (6–6) may be gradually disappearing from some species such as *Nucifraga columbiana* and may be the pair already lost from some other species such as *Aphelocoma coerulescens*.

The postjuvenal and postnuptial molts of Clark's Nutcracker are apparently very similar to the molts reported for other passerine species including *Aphelocoma coerulescens* and *Corvus frugilegus*. First-year Clark's Nutcrackers commence their first postnuptial molt in the first half of March, whereas most adults did not start their postnuptial molt until late March or early April. As long as the two age groups can be distinguished (until July), first-year birds are generally in a more advanced stage of molt than adults. Between March 31 and September 1, 91 per cent of 174 first-year and adult birds collected showed molt of flight feathers, indicating that individual nutcrackers take four and one-half or five months to replace their remiges and rectrices. Between March 31 and December 1, 93 per cent of 243 first-year and adult nutcrackers collected were molting flight feathers or body feathers, suggesting that individual nutcrackers are in molt for eight or nine months. February was the only month in which all specimens collected were free of molt. Postnuptial molt usually begins in this species while the gonads are still in breeding condition and may begin before eggs are deposited in the nest.

In an unheated room three Clark's Nutcrackers which had been receiving 8½ hours of artificial light daily for more than four months began a postnuptial-like molt at the usual time in March. In an outdoor aviary eight nutcrackers were induced to begin a postnuptial-like molt in December and January by exposure in November, December, and January to daily photoperiods of 16 hours. Controls on a normal photoperiod began molting at the usual time in March and April. No gonadal recrudescence was observed to precede or accompany this postnuptial-like molt in controls or experimentals.

A series of plumage differences are enumerated which may be used to distinguish juvenal Clark's Nutcrackers from first-year and adult birds, and to distinguish first-year birds from adults. Most of these differences stem from two observations: (1) juvenal flight feathers are usually less heavily pigmented, and tend to be more pointed than adult flight feathers, (2) flight feathers and many of their coverts are retained through the postjuvenal molt.

All juvenal Clark's Nutcrackers were found to have a bursa of Fabricius. From a maximum of about 300 milligrams the bursa begins to decrease in weight usually by October of the bird's first year. By the following April, the bursa was found to weigh generally less than 50 milligrams, or to be absent.

Adult males were found to have longer wings, tails, and exposed culmens, and a greater height of bill, than adult females, first-year males and first-year females, while first-year females were smaller in each of these measurements than the other age and sex groups. Measurements of adult females and first-year males, on the other hand, approached each other very closely. Although, on the average, males are larger than females, the larger females are larger than the smaller males.

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