THE WING MOLT OF THE BOB-WHITE

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CONSIDERABLE interest has recently developed in the determination of age in juvenile gallinaceous birds by the measurement of the length of the growing replacement-primaries during the postjuvenal molt. Knowing the age at the time of collection or observation, then events in the nesting phenology can be dated (Thompson and Taber, 1948; Thompson and Kabat, 1949). Such facts provide a basis for comparing nesting seasons between years and between areas, they facilitate productivity analysis, and they may reveal relationships with other characteristics of the population (such as density and sex and age ratios) and with other environmental conditions.

Since the accuracy of the wing-molt technique of aging depends on the uniformity of the postjuvenal wing molt, there would seem to be a need for further analysis of this uniformity in wild birds. This paper attempts to present such an analysis and a discussion of the irregularities that may be encountered for the juvenile Bob-white (*Colinus virginianus*), and, further, it supplies a discussion of the parallel molt of primaries occurring in the adult during the postnuptial molt.

Normally the juvenile Bob-white commences the postjuvenal primary molt at 28 days of age (Petrides and Nestler, 1943). At this time the juvenal primaries have all developed except the outer 2, IX and X, which are still growing. The process of shedding and replacing these juvenal primaries progresses from the innermost primary (I) distally through primary VIII which completes its growth at 150 days of age. Juvenal primaries IX and X, which have completed their growth at 63 and 65 days of age, respectively, are retained until the postnuptial molt of the following year. This retention was first described by Dwight (1900). The constancy of the rate of this wing molt, according to Petrides and Nestler (1943), who have given the above description, provides the most accurate method available at present for determination of the age of juvenile Bob-whites up to 150 days of age. Their table (p. 779) gives the lengths of the various developing primaries for each day of age from 24 to 150 days.

Little has been written about the molt of quail that are over one year old. Bent (1932) implies that a primary molt occurs in adults by referring to the postnuptial molt as "complete". He also refers to the time of the molt in the statement: "The first postnuptial molt, the following summer and fall, chiefly in September, is complete and produces the adult winter plumage. Adults then continue to have similar molts each year, a very limited head molt in the spring and a complete postnuptial molt from August to October" (p. 17).

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Materials and Methods

Bob-white have been collected periodically in Wisconsin since 1943 with mass collections being made in the autumns of 1947 and 1948. Some additional material was obtained by soliciting quail hunters for wings from shot birds. All materials thus assembled were obtained during the period October 1 to December 10 of each year. Winter trapping of quail provided supplementary material which is described later in the paper. An examination was also made of 97 wings selected from a group furnished by the Missouri Cooperative Wildlife Research Unit.

In the course of the Wisconsin collections, data were recorded on covey size and location, and weight, sex, and age data were taken on individual birds. On each wing the length of each of the developing primaries was measured in millimeters from the point of insertion of the primary in the manus out along the vane of the feather to the tip. This was considered to be a more accurate and more easily replicable method of measurement than that used by Petrides and Nestler (1943) who made their measurements from the leading edge of the wing. To equate our measurements with theirs a correction of 12 mm. was added to ours to compensate for the width of the manus. Thus a measurement of 52 mm. from the point of insertion to the tip of the feather corresponds to a length of 64 mm. when measured from the leading edge (cf. primary II, Fig. 1).

Uniformity of the Postjuvenal Primary Molt

Petrides and Nestler (1943), in deriving their table showing ages corresponding to various lengths of developing primaries, made daily measurements on a pair of quail raised in captivity. These were supplemented and modified by periodic measurements on 7 groups of birds which were raised in captivity and whose ages were known. These 7 groups each contained 10 to 35 birds, whose age at the time of measurement varied from 45 to 128 days. One to 3 developing primaries were measured on each individual. (Thus in Fig. 1 two postjuvenal, or first winter, primaries are in a developmental state, II and III. Primary I has completed its growth.) The mean lengths of the various developing primaries for each of the 7 groups thus provided check points for the table and enabled modification of the daily measurements on the pair to be made.

Errors in age determination were evaluated from the groups by comparing the lengths of primaries on all the individuals with the modified measurements on the pair of birds. Thus a bird in the 70-day group may have had a sixth primary replacement whose length was 24 mm., rather than the 41 mm. length which is the average length of the sixth primary in the 70-day group. Since 24 mm. correspond to a length characteristic of birds 66 days old, according to the modified measurements on the pair of birds, the error in age determination would be 4 days if age determination were based on the length of the sixth

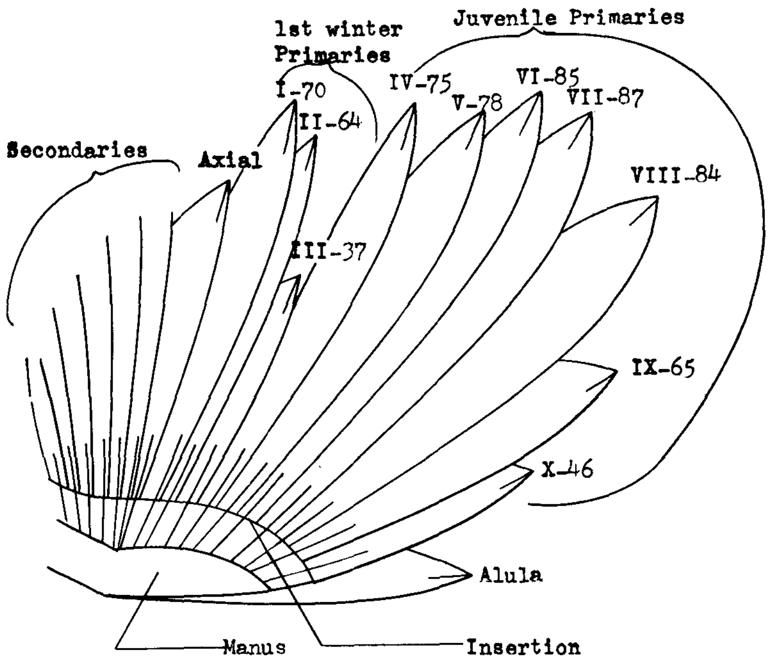

FIG. 1. Postjuvenal primary molt in the Bob-white. Juvenal primaries I, II, and III have been replaced by first-winter primaries. The length of II indicates the quail to be 51 days of age, while the length of III indicates 48 days of age. Numbers are the lengths of the primaries in millimeters found on an actual wing.

primary. The largest error which they found by this method was 13 days, though in some of the groups the maximum individual error was as little as 4 days. The older birds tended to have a larger range of variation between the indicated and the known age than did the younger birds.

These errors led Petrides and Nestler to believe that this method of age determination was limited in its accuracy. Unfortunately they did not give standard deviations of the errors which they found, but these would be considerably smaller than the maximum errors reported.

Inasmuch as the birds used by Petrides and Nestler were 5 or more generations removed from the wild and were reared under uniform conditions in captivity, the essential uniformity which they exhibited would not necessarily be characteristic of wild birds. Hence, it was felt necessary to evaluate the uniformity of the postjuvenal primary molt as it occurs in wild birds. Because it is difficult to obtain wild birds of known age in large numbers, other approaches must be used for this evaluation. Two alternative methods were employed by us, one based on variation of indicated ages in the same individual, and the other on variation of indicated age within family groups. These do not in a strict sense define the true error in age determination; however, they do provide a valuable delimitation of the uniformity of the primary molt.

The method based on the variation of indicated ages in the same individual can be applied because the age indicated by one growing primary does not necessarily agree with the age estimate from another growing primary on the same wing which is in a developmental state at the same time. This is due to a deviation of the length of one or more of the developing primaries from the lengths listed as characteristic for each day of age by Petrides and Nestler. For each individual wing examined for this study the ages of the quail indicated by each of the growing primaries present were determined from Petrides and Nestler's table. Only birds under approximately 124 days of age were examined, since all primaries except VIII have completed their growth by this age, and hence 2 primaries simultaneously in development cannot be found for comparison of indicated ages.

The difference in the 2 or more age readings for each wing is termed "discrepancy" (Fig. 2), and it is obtained by subtracting algebraically the age indicated by the more distal primary replacement from the age indicated by the more proximal developing primary. An example of this is shown in Figure 1. Here the first-winter primary III has reached a length of 37 mm. The indicated age from this more distal developing primary is 48 days. Primary II, on the other hand, indicates the age to be 51 days, as it is 64 mm. long. Hence the algebraic difference or "discrepancy" is (+) 3 days. It is felt that "discrepancy" is a better term than "error" for the present use inasmuch as the true age is unknown and hence cannot be used as a reference point. The true age in most cases will lie between the 2 indicated ages, especially if the discrepancy is large. Hence the discrepancies are larger than the actual error that would be incurred in aging birds.

The discrepancies arising from each pair of measurements were assigned to an "age class" on the basis of the age indicated by the more distal replacement. The magnitude of these discrepancies in days and the frequency with which they were found in the various age classes are given in Figure 2. An examination of the standard deviations accompanying each age class indicates that up to 75 days of age these discrepancies are small with only 1 case out of 121 showing a discrepancy as great as 6 days. Beyond 75 days of age the discrepancies increase in magnitude, with 14 days being the maximum discrepancy

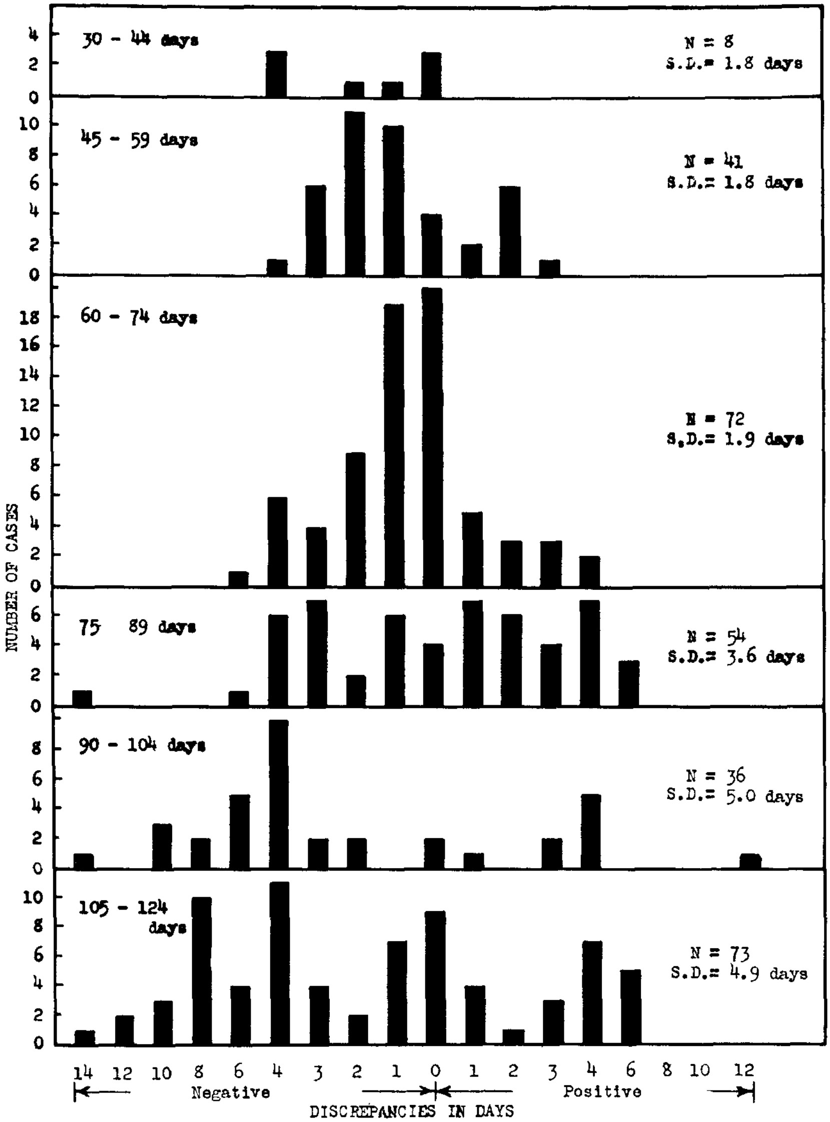

FIG. 2. Distribution of frequencies of discrepancies in age indication on individual wings of quail in various age classes. N = no. of specimens; S.D. = standard deviation.

in any age class. For the entire group of 284 pairs of age estimations here analyzed the number and magnitude of the discrepancies are as follows:

Discrepancies				Negative							Positive							
in days....	14	12	10	8	6	4	3	2	1	0	1	2	3	4	6	8	10	12
No. of cases.	3	2	6	12	11	37	23	27	43	42	19	16	13	21	8	0	0	1

The standard deviation for the entire group is 3.8 days. However, as indicated above the younger birds show lesser discrepancies, and in practice the age estimate is the average of the estimate from the 2 or more developing primaries. Thus a bird with a discrepancy of 14 days would be assigned an age that is only 7 days from either extreme. For example, if primary VIII indicated 116 days of age and primary VII, 102 days of age, the final age assigned would be 109 days. Even in this case of an extreme discrepancy the final age estimate is almost certain to be within 7 days of the true age. When interpreting the meaning of the standard deviations of the discrepancies, the observer should thus keep in mind the fact that the error in age determination will only seldom be over one-half of the value of large discrepancies. On the other hand, when the discrepancy is small, the error would tend to be more than one-half the discrepancy.

Thus the finding of a small discrepancy does not necessarily indicate greater precision in age determination than does the occurrence of a large discrepancy. The logic of this becomes apparent when it is considered that a small discrepancy is likely to arise through the occurrence of 2 measurements that err in the same direction from the average lengths for the true age, while large discrepancies would be more likely to arise from measurements that err in opposite directions from the average lengths for the true age. Thus an exact value cannot be arrived at, by this means of analysis, for the error in age determination. But it seems justifiable to consider the standard deviation of "errors" would be one-half of the standard deviation of "discrepancies" (3.9) or 2.0 days.

The second method used by us in testing the uniformity of the postjuvenal primary molt was to compare the indicated ages of all juveniles collected from the same covey of quail, and to note the discrepancies between the indicated ages of these juveniles. In general the indicated ages of individual juveniles in a covey fall naturally into one or more groups of ages, because there are 1 or more different-aged broods composing the covey. Thus in a small covey, which may consist of only 1 brood, the indicated ages will usually fall into a single group, whereas in a larger covey, which may consist of 2 or more broods, 2 or more natural groupings of ages may be discernible.

In all the collections and materials gathered for this study 78 of these groupings were apparent, and the total number of birds included in these groupings was 233. Material had to be discarded in some cases where overlapping of indicated ages was possible, as in a covey composed of 2 broods of closely similar age. In such cases it was impossible to assign the intermediate ages to the proper group. It is possible that among some of the groups used in the compilation the extreme discrepancies have been eliminated, since the presence of only one extreme in a group leads to a suspicion that it is a sole representative of a different-aged brood, and hence it was not included. These facts lead to an artificial bias in the data which would tend to reduce the magnitude of the discrepancies. This may be partially compensated for by some of the groupings

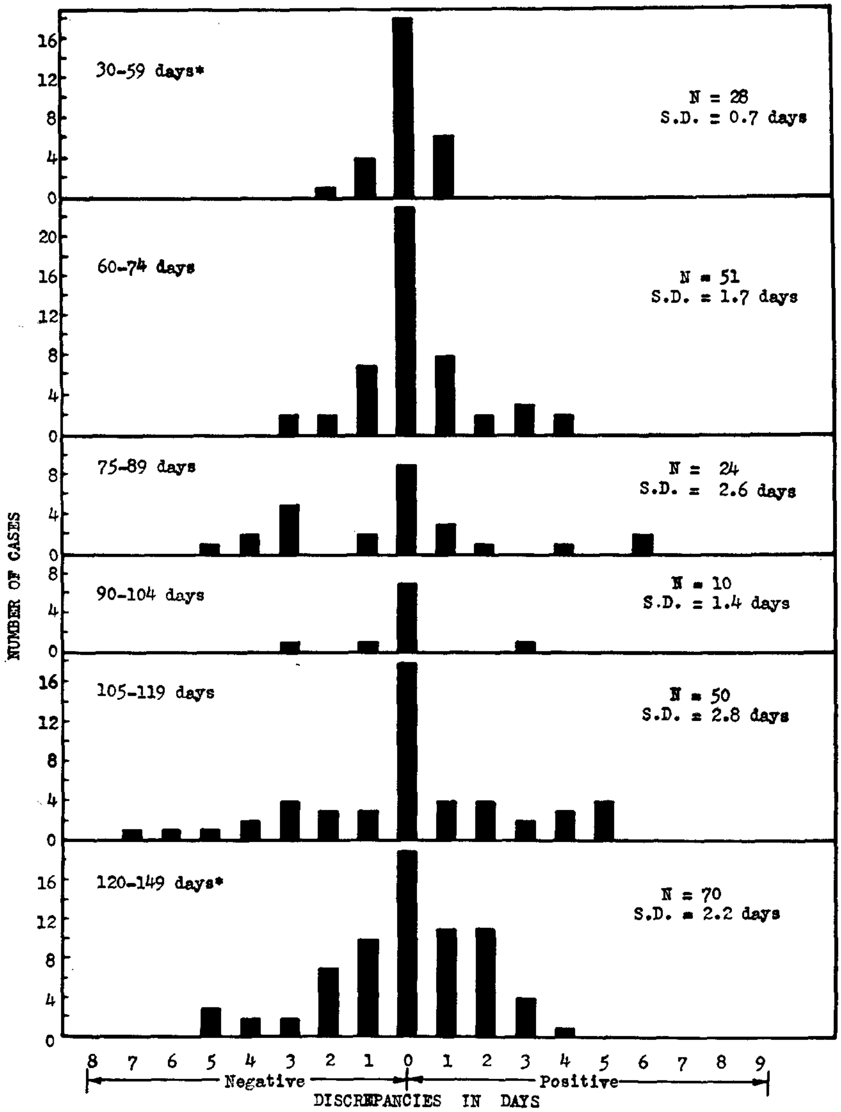

FIG. 3. Distribution of frequencies of discrepancies in age indication between juveniles collected from family groups of various age classes. N = no. of specimens; S.D. = standard deviation. * Note that these 2 age classes have twice the span of the others.

unknowingly including more than one true age of young leading to discrepancies of greater magnitude than actually exist.

Usually only the outermost developing primary was considered in deriving the indicated age of the individual from the table of Petrides and Nestler, though in some cases the average age as indicated by more than one developing primary was used. In compiling the data the mean indicated age was calculated for each of the groups. The departure of the individual indicated ages of birds within each group from this mean were tabulated, and these are termed "discrepancies" as in the previous method. It should be noted that this method differs from the previous in that discrepancies are taken from a midpoint rather than between extremes. Hence the value of the discrepancies are considerably smaller than in the other method. Each group of birds was then assigned to an "age class" according to the mean indicated age of the group, and frequency distributions of the individual discrepancies which were found are given in Figure 3. Again the younger age classes tend to have a smaller standard deviation. The combined data of all age classes embodying 233 birds is as follows:

	Negative								Positive					
Discrepancies in days	7	6	5	4	3	2	1	0	1	2	3	4	5	6
No. of cases	1	1	5	6	14	13	27	93	32	18	10	7	4	2

The standard deviation of this distribution is 2.1 days, and this corresponds very closely with the standard deviation of "errors" (2.0 days) derived by the first method of analysis. Both imply that the maximum error in age determination using the postjuvenal primary molt is probably about 4 days at the 95% level of confidence.

These treatments indicate a relatively high uniformity of the postjuvenal primary molt in the wild Bob-white, and this uniformity is as great or greater than that reported by Petrides and Nestler (1943) for captive birds. Thompson and Kabat (1949) used one-week intervals in plotting hatching dates of Bob-white, and this degree of refinement in age estimation seems well justified by the above considerations.

Irregularities in the Postjuvenal Molt

While the juvenile Bob-white normally molts through primary VIII in the postjuvenal molt, a number of cases have been found where this was not true. During the course of winter trapping of quail, 32 birds were given a special examination in March of 1948. Of the juvenile birds 9 were found to have had an arrested molt. Replacement of only 7 of the juvenal primaries had occurred. The retention of the outer 3 juvenal primaries was evident from the distinctly brownish coloration of these which is a result of fading of the original pearly gray color. The replacement, that is, the first-winter, primaries are relatively unfaded at this time, and under moderately good daylight illumination the contrast with the unreplaced juvenal primaries, which are more faded, is readily apparent. Recognition of the more pointed nature of juvenal primaries (Stoddard, 1931), is not sufficiently reliable for positively detecting the presence of juvenal primaries.

A different line of evidence for an arrested molt was obtained on 15 juveniles trapped alive in early December of 1947. The seventh replacement primaries on these birds were 74 to 98 mm. in length, and the eighth juvenal primaries had not been dropped and were not loose.

According to the table of Petrides and Nestler (1943) the eighth primary should have been dropped when primary VII was 72 mm. long. Confirmation of the arrested condition was later obtained on 5 of these 15 juveniles by retrapping in February. On these 5 birds primary VIII had not been replaced, and the length of primary VII in early December on these 5 had been 74 to 98 mm. This strongly suggests that the other 10 birds which were not retrapped also had an arrested molt, since the lengths of their seventh primaries in early December were of the same order as those on which the arrested molt was confirmed.

On the other hand an examination of 87 juvenile birds trapped during the winter of 1946–47 revealed only 1 bird which had failed to complete the postjuvenal primary molt. This bird had also stopped with dropping and replacement of the seventh primary. Possibly this difference between the 2 years is explicable by 2 considerations. The first of these is that while inconclusive evidence is at hand for the 1946 hatching season, many birds were hatched late in the season in 1947 compared with other years (Thompson, 1949). The other consideration is that the onset of winter was much earlier in 1947 compared with 1946, and this might have induced premature cessation of molting. The birds on which arrested molt was found in 1947 were about 15 to 18 weeks old when trapped in December and hence had hatched in early August.

As could be surmised on finding cases of arrested molt, cases of extension of the molt beyond its normal limits might also be expected to occur. This has been noted for the postjuvenal primary molt in 2 instances: one bird was taken on Nov. 16, 1947 on which the ninth juvenal primary had been shed and the replacement primary was 62 millimeters in length; the other was taken November 6, 1948 with the ninth replacement primary measuring 52 mm. The eighth postjuvenal primaries were completely developed in these two cases. The identity of these birds as juveniles was established by the presence of buff tips on the greater upper primary coverts (Van Rossem, 1925; A. S. Leopold, 1939), and by the unresorbed bursa of Fabricius. Inasmuch as primary VIII completes its growth at about 150 days of age the first of these birds must have hatched before June 9 and the other before June 19.

The frequency with which these irregularities occur is possibly influenced by a number of factors, but as suggested above, a strongly presumptive one is the date of hatching of the juvenile bird. The hatching period of the Bob-white in Wisconsin covers a long span of time, extending from late May to early October. Since primary VIII is normally shed at 101 days of age, this stage may be reached anytime between early September and mid-January. In the case of birds hatching late the onset of winter may terminate the molt before this stage is reached and result in an arrested molt, whereas early-hatched birds may be induced to continue the molt beyond the normal limit by favorable weather. A. S. Leopold (1943) found hybrid and domestic turkeys to be quite variable in the extent of the molt, though no variation was observed among 5 wild turkeys. While he concluded that heterozygosity of the genotype was responsible for this variation, he cites the review by Salomonsen (1939) which strongly suggests that environmental temperatures, by action through the thyroid on the feather follicle, control both the initiation of the molt and its extent. Genetic and environmental mechanisms are not necessarily at odds, of course, as the one may set the stage for the operation of the other.

The Postnuptial Wing Molt in the Adult

The sequence of the wing molt in the adult is very similar to that of the juvenile Bob-white except that it is complete, the primaries being shed and replaced distally commencing with the innermost primary. Inasmuch as the outer 2 juvenal primaries, IX and X, have been retained by the bird through its first year of life, the first postnuptial molt replaces 8 postjuvenal primaries (I through VIII) and 2 juvenal primaries (IX and X).

In the course of obtaining the collections it seemed apparent that a relationship existed between the stage of the postnuptial molt of the adult birds associated with the juveniles and the molt stage of these juveniles. This correlation is difficult to establish with wild birds because of uncertainties in establishing the adult as the true parent of the juvenile. Mere consort is not proof of parentage, since more than one brood may be present in the covey, and non-breeding adults may also be present. The similarity of the progress of wing molts between adults and juveniles from the same covey arose often enough, however, to lead to further inspection.

A more effective, though less specific, line of approach was adopted to establish this relationship. This entailed a comparison of the wing-molt stages of the adults obtained during the collection period in 1947 with those obtained in 1948. If a correlation exists between the progress of the adult and juvenile wing molt, then the molt stage attained in the adults in 1947 should show a

TABLE 1
Distribution of primary molt stages of adult quail

Year	Sex	Latest primary dropped						
		V	VI	VII	VIII	IX	X	Total
1947	Female	1	1	5		1	2	10
	Male			4	6	7	2	19
	All	1	1	9	6	8	4	29
1948	Female					2	4	6
	Male				2		9	11
	All				2	2	13	17

retardation over those in 1948, since the progress of the wing molt of the juveniles in 1947 lagged greatly behind that of juveniles in 1948.

The lag in the juveniles was due to the lateness of the hatch in 1947 as compared with 1948. In 1947 the median hatching date fell in the first week in August, whereas in 1948 the median hatching date was in early July (Thompson, 1949). Hence many of the adults were occupied with breeding activities until later in the season in 1947. This might be presumed to delay the onset of the molt in the adults and give rise to a correlation of the progress of the adult molt with that of the juveniles. This has been observed in pheasants (Kabat, Thompson, and Kozlik, in press).

Table 1 shows that such a delay occurred in the molt of the adults in 1947 compared with 1948. Of 29 adults in 1947 the median bird had dropped only 8 primaries, while in 1948 most of the adults in the group of 17 birds were regrowing the tenth primary. The table also suggests that the adult males were somewhat in advance of the females in the molt, although the 1948 data are too scant to show this.

In the discussion on irregularities in the postjuvenal molt it was mentioned that unmolted juvenal primaries are distinguishable from the replacement primaries by their faded color. This fading is far more apparent in adult birds that have not completed their molt, since the old primaries have been exposed to fading for a considerably longer time. The fading produces a cocoa-brown coloration which gives an extreme contrast with the pearly gray color of the new primaries. This characteristic of itself may be used as an indicator of adult condition if the molt has not been completed, for once seen it cannot easily be mistaken.

Three cases have been found in which the postnuptial molt definitely did not go to completion. The first of these was a male trapped in early January of 1947. Primary IX was fully regrown, but the old X was retained. On December 13, 1947 a female was trapped and was retrapped on March 10, 1948. In December the ninth primary was 17 mm. in length but was fully grown in March. The cocoa-colored tenth primary remained. In the final case a male trapped on January 7, 1948 had 9 characteristically new, fully developed primaries and a brown tenth primary. In all these cases both wings displayed the same condition, so that the aberrancy was not due to an accident to a feather follicle. These incompletions parallel the incomplete molts discussed previously for juvenile birds, and probably the same factors that terminate molt in the juveniles are operative in the adults.

While successive postnuptial molts, to our knowledge, are essentially the same, the fact that the first postnuptial molt occurs when the quail is a yearling provides an interesting method of distinguishing yearlings and older birds in the adult category. During the first postnuptial molt, in the yearling, the greater upper primary coverts of the juvenile-type are replaced by ones of the adult-type, and the more pointed outer 2 juvenal primaries (which were retained through the postjuvenal molt) are replaced by the more rounded adult type of primary. The adult type of covert is distinguishable by the lack of the buff or mottled tip and also by its tendency to be flatly rounded rather than pointed. In the case of the adult beyond the yearling class the postnuptial molt results in replacement of adult-type coverts and rounded outer primaries. In other words, 2 types of coverts and primaries are present in yearling birds during the course of the postnuptial molt, whereas in older birds only 1 type is present. Since there are only 9 greater upper primary coverts, and the shedding of these precedes that of the primaries by 1 stage, the last one is dropped about the time the eighth primary is shed. Inasmuch as the outer 2 coverts are often more faded and worn and are less buffy than the other juvenile-type coverts, this criterion of yearling condition is almost impossible to apply after the loss of the seventh covert at about the time of dropping of the sixth primary.

One further remark needs to be made regarding the adult-type greater upper primary covert. Typically, it is readily distinguishable from the juvenile-type covert when comparing adult and juvenile birds in the fall and winter. Without a background of experience, however, there is a possibility of confusing juvenile and adult quail in winter in some cases if the buffness of the tip of the covert is given sole consideration. Out of 22 adult wings given a close examination the coverts of three had a noticeable buffness of tip and seven had a very slight buffness. These might possibly lead an observer to believe that the birds were juveniles. However this tipping of buff on the adult-type covert differs from that on the juvenile type by being of darker hue and by its tendency to be largely marginal rather than "running" down the midrib.

Summary

An analysis of the uniformity of the postjuvenal molt of primaries in wild juvenile Bob-white by 2 independent procedures indicates that the standard deviation of the error of age determination is about 2.0 days. Cases have been found in which the postjuvenal molt of primaries both proceeded beyond the eighth juvenal primary or was arrested with the seventh primary. Adults have also been found with an arrested primary molt. A positive correlation was found between late postnuptial molt in adults and late postjuvenal molt in juveniles. This can probably be ascribed to late completion of breeding activities which delays the onset of the molt in the adults. A method is described for detecting unmolted primaries in both juvenile and adult quail on the basis of the fading of the gray color to brown, and another description enables a distinction to be made between yearling quail and older adults during the postnuptial molt.

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