PLUMAGE DEVELOPMENT AND MOLTS OF CALIFORNIA QUAIL

By RALPH J. RAITT, JR.

In recent years much attention has been focused on the timing of plumage development in young galliforms. The Bobwhite (*Colinus virginianus*) has been the subject of several recent studies on molts; particularly valuable are those of Petrides and Nestler (1943 and 1952) and Thompson and Kabat (1950). These studies, and others on the Bobwhite, the Scaled Quail, *Callipepla squamata* (Wallmo, 1956), the Ring-necked Pheasant, *Phasianus colchicus* (Buss, 1946; Thompson and Taber, 1948; Westerskov, 1957), and the Hungarian Partridge, *Perdix perdix* (McCabe and Hawkins, 1946; Thompson and Taber, *op. cit.*), were conducted with the aim of establishing criteria for accurate age determination based upon the stage of plumage development of young birds. Similar detailed studies had not been published for the California Quail (*Lophortyx californicus*) at the time of this study. However, following the completion of the present investigation, Williams (1959) described in detail the growth of first winter primaries of California Quail of known age in New Zealand. The present report partly duplicates that of Williams, but differences in the results obtained necessitate the presentation and analysis of data obtained in my study.

Genelly (1955:280–281) constructed graphs of replacement rates of primary flight feathers in young California Quail based on repeated captures of wild young birds and on captive young of known ages. The resulting curves agree closely with a similar curve based on the data of Petrides and Nestler (*op. cit.*) on age determination of young Bobwhites. The curves given by Genelly are adequate for the aging of most young in the field. However, in view of the paucity of information on plumage development of young of this species, it was felt that a more detailed study of the wing molts and body plumage would be desirable. Accordingly, several groups of young of known age were purchased from a dealer in Berkeley, California, in the summer of 1957, raised in cages, and their plumage development followed. Preserved specimens and dried wings of young of known age and museum study skins of wild young quail provided supplemental data.

The postnuptial molt of the adult birds is of interest as an important part of the annual cycle. Data as to the timing of this molt were obtained by the examination of live birds trapped in the course of a population study.

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METHODS

A total of 23 young quail were purchased in four lots. All but five were about one week old when they were obtained. The other five were taken directly from the incubator as they hatched. All birds in the latter group died before they were ten days old. Because of escape or death only eleven birds were raised to the age of completion or near completion of the postjuvenal molt. Although the birds from which most of the data were derived were not obtained until they were a week old, the dealer kept records on the hatching dates of the various groups and there is not likely to have been an error in the ages as given by him. The young birds were kept in a large cardboard carton with a red light bulb for warmth until they were about a month old, when they were transferred to wire cages. From one to four birds were kept in a cage. They were fed a start-

ing mash mixed with cracked corn, spread in a layer on the bottom of the cage; water was amply provided.

During the first few weeks the birds were checked daily. Subsequently, they were checked less often as plumage changes became slower. In the last month of plumage development they were examined only once every four or five days. On each examination the lengths of selected growing remiges and rectrices were measured, and changes in the several other tracts were recorded.

All wild quail trapped during the late summer and autumn were checked for signs of molt and the length and number of each growing flight feather was recorded. A total of 161 captures during four molting seasons provided the data on the postnuptial molt.

NATAL DOWN

The young quail is hatched with a full covering of down. This downy plumage gives the young bird its characteristic concealing coloration of longitudinal, dark brown stripes on a background of buff. Replacement of the natal plumage begins early, for at hatching the tiny wings show slender, short pinfeathers of the first seven primaries of the juvenal plumage. The natal down behind the eye persists until the bird is about seven weeks old.

JUVENAL PLUMAGE

The juvenal plumage begins to emerge before hatching and is not fully developed until the age of about ten weeks. Figure 1 summarizes the development of juvenal and first winter remiges and rectrices. The period of growth of the primaries spans the entire period of development of the juvenal plumage. This tract is regular in its development and shows little individual variation. For these reasons and because primaries are easy to identify individually and to measure, their development has been emphasized in establishing criteria for age determination in the California Quail, as has been the case in developmental studies of other young galliforms.

In the discussion of remiges in this paper the innermost primary is designated number 1 and the outermost number 10. The outermost secondary is number 1 and the innermost is number 15.

The young bird is hatched with juvenal primaries 1 through 7 just erupting through the skin. Of these feathers, numbers 1, 4, and 7 were measured daily on all birds. The method used in all measurements was to place the end of a small ruler at the point of emergence from the follicle and to measure from that point to the tip of the feather. The composite growth curves for these feathers are given in figure 2. All of the points are based on the averages of several birds for each age. The three feathers have similar growth rates, but the proximal ones stop growing sooner. Juvenal primary number 8 does not erupt until the third week after hatching. Numbers 9 and 10 erupt in succession at intervals of about ten days and thirteen days after number 8 emerges.

The first seven greater primary coverts appear at about one week of age followed by the outer two in the third and fourth weeks. Middle coverts emerge in the third week, and the remainder of the upper coverts and all of the under ones erupt later in juvenal plumage development.

At about the same time that primary 10 emerges, number 1 is dropped, marking the beginning of the postjuvenal molt. Subsequently the juvenal primaries through 8 are dropped and replaced by first winter feathers (fig. 1). Juvenal primaries 9 and 10 mature slowly and are not replaced but remain as part of the functional wing through the first winter. Completion of the growth of number 10 in the tenth or eleventh week marks the end of juvenal plumage development.

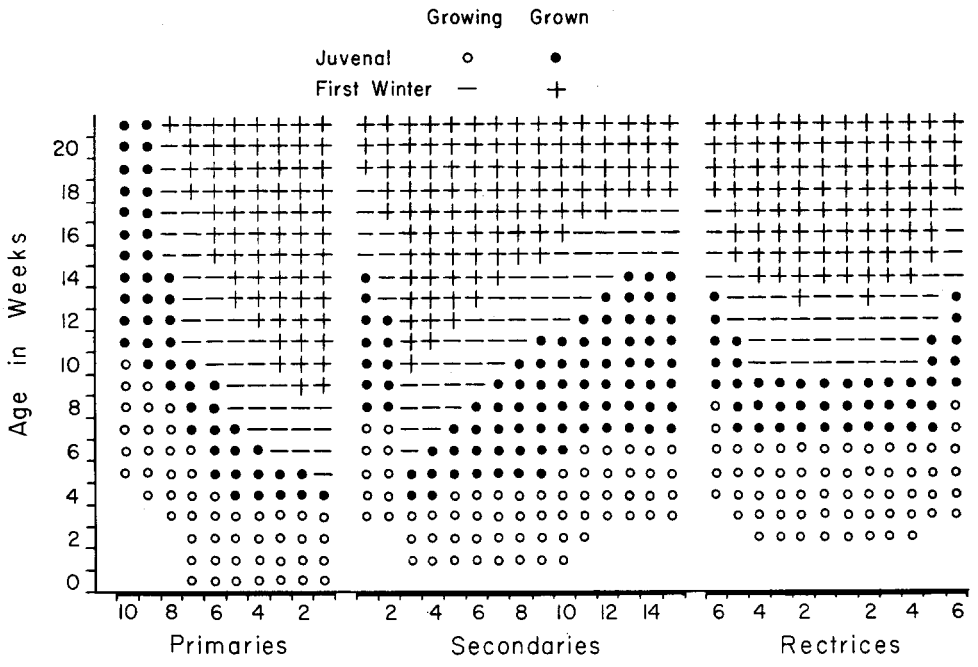

Fig. 1. Summary of postnatal and postjuvenal molts of flight feathers of the California Quail (*Lophortyx californicus*). Method of presentation after Leopold, 1943.

Eight secondaries, numbers 3 through 10, erupt at the age of about one week and the other seven appear in the succeeding three weeks (fig. 1). Both number 1 and number 2, as in the case of the last juvenal primaries to develop, are more like those of the first winter plumage, being plain colored rather than mottled like the other juvenal secondaries. Eight greater secondary coverts erupt at the same time as secondaries 3 through 10, and the other greater secondary coverts erupt at the same time as the corresponding secondaries. Remaining coverts erupt within the following three weeks.

The juvenal alular feathers begin emerging at about ten days of age, the inner one first, then the middle one, and the outer one last, all in close succession. They remain until about the end of the sixth week when they begin to be replaced.

The juvenal rectrices begin to erupt early, the central four pairs emerging nearly simultaneously in the second week. Figure 1 illustrates the general timing of development of this tract. Because of the large amount of wear on the rectrices of these caged birds and because of the occasional accidental plucking of rectrices in handling birds, a detailed analysis of tail feather growth was not possible.

The growth of the body plumage is somewhat complex, each tract developing according to a particular pattern and schedule. Figure 3 summarizes this development by showing the areas of the body that are covered by juvenal feathers at successive intervals during development. Small, isolated patches of pinfeathers appear in the second week on the upper flanks, upper thighs, and scapular area. These patches expand and coalesce with each other and with new centers above and below the tail, and by the fifth week nearly the entire body is covered by juvenal plumage except for the head, which still bears natal down. The down on the head becomes completely replaced in the seventh week.

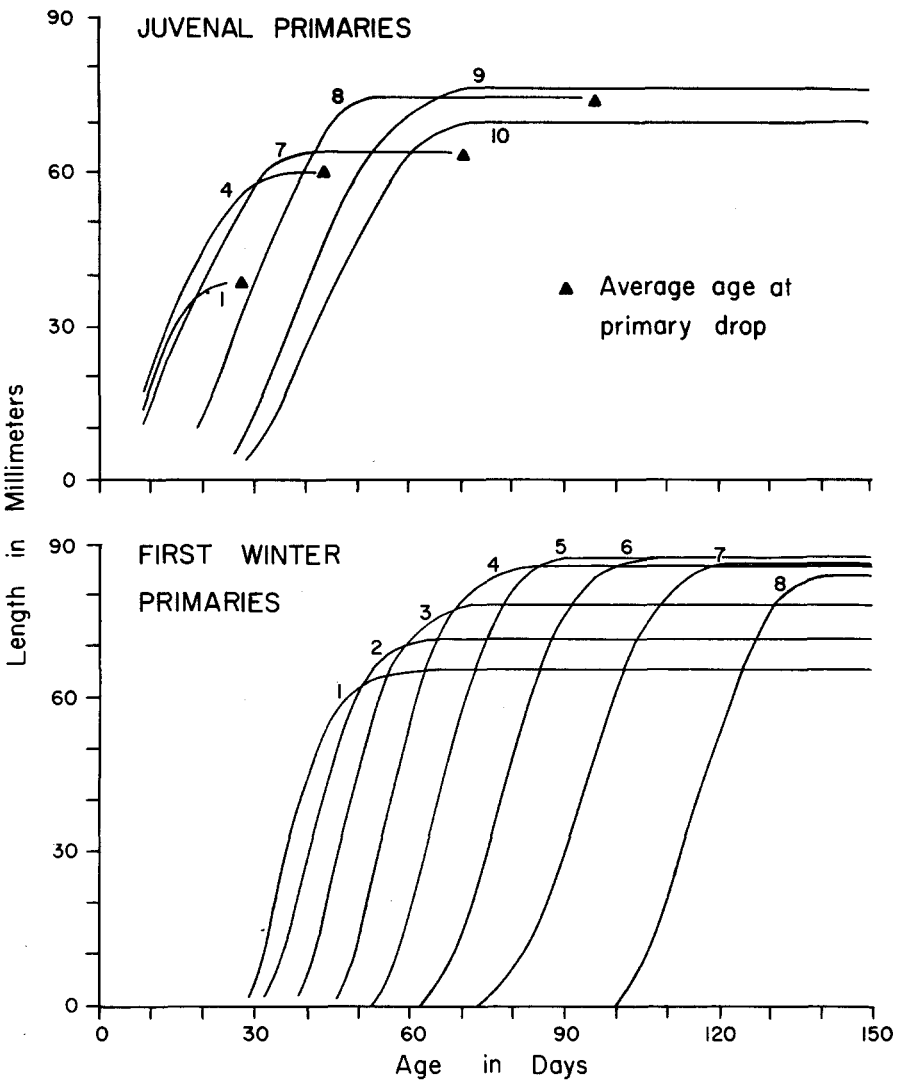

Fig. 2. Growth of individual primaries of California Quail. Each curve is based on mean lengths of several individuals.

FIRST WINTER PLUMAGE

The first winter plumage, which is attained during the postjuvenal molt, is similar to that of the adult and is retained until the first postnuptial molt. With the dropping of juvenal primary number 1 on about the twenty-eighth day, the postjuvenal molt begins. Development of the first winter plumage is not completed until about 24 weeks of age. Thus, the full period required for development is over 19 weeks, as opposed to the ten-week period of juvenal plumage growth.

As in the study of the development of the juvenal plumage, most emphasis in the study of growth of the first winter plumage was given to the remiges, particularly the primaries. Composite growth curves were obtained for all of the primaries (fig. 2). In

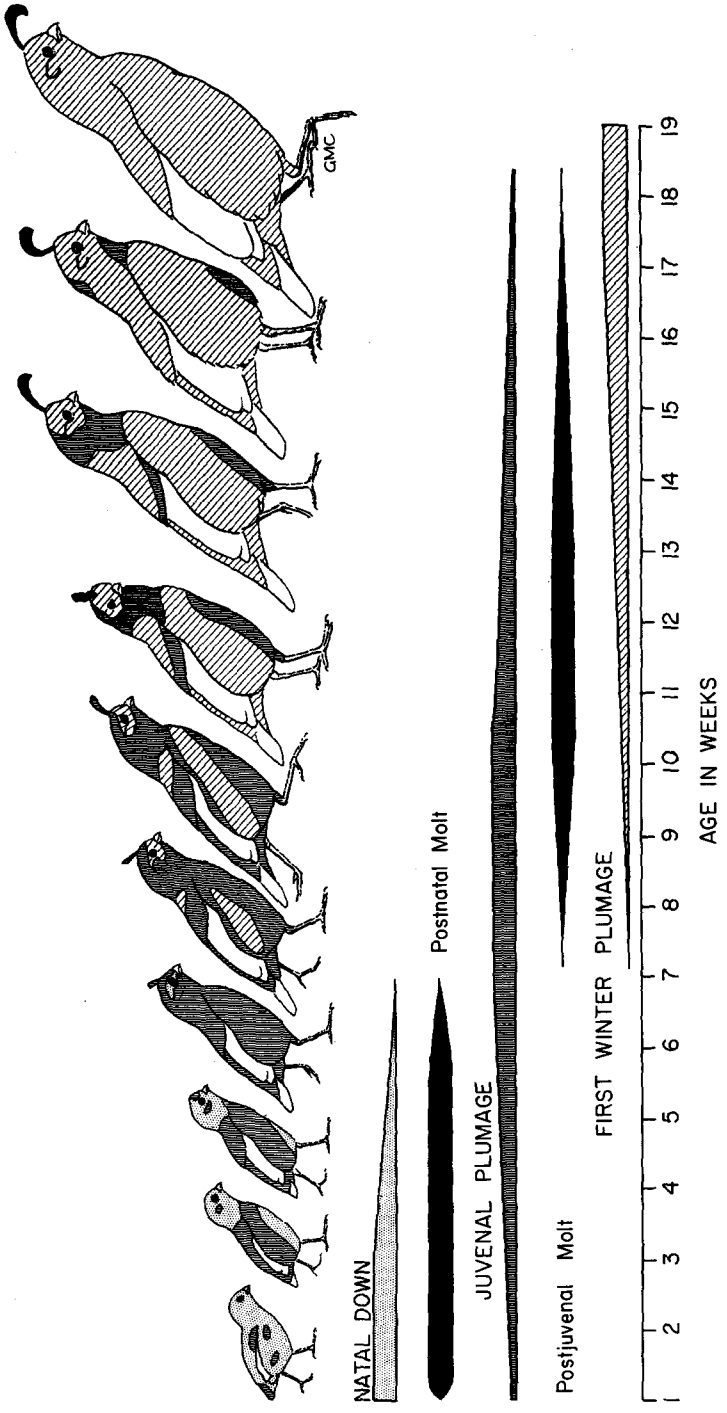

Fig. 3. Development of body plumage of California Quail. Stippling indicates areas bearing natal down; vertical hatching, areas covered by juvenal feathers; oblique hatching, areas covered by first winter plumage.

general the middle portions of the curves are based upon more individuals and are more likely to be typical. The complete curves available for these feathers are all of a roughly sigmoid shape, which is typical for growth curves in general. The growth rates of the eight first winter primaries are very similar, with a slight decrease in rate in the later ones. The interval between the molting of the successive primaries lengthens progressively from a period of about four days between numbers 1 and 2 to one of over 20 days between numbers 7 and 8.

The program of primary molt illustrated in figure 2 agrees in general with that of Williams (1959:204–205), except with regard to the growth rate of number 8. His figure 1 indicates a markedly lower growth rate and a concomitantly greater age for completion of primary development—25 weeks as opposed to 21 weeks in the present study. Although the curve for primary 8 is based on only seven birds, there is high uniformity within the sample, only ten days separating the two extremes in age of completion of growth. Furthermore, Genelly (*op. cit.*:281), using 19 known-age California Quail, found an average age of completion of growth of number 8 to be slightly over 21 weeks. Williams' curve is based on a comparable sample of 21 birds. Hence, it appears that there may be a real difference in the rate of development between California and New Zealand populations of this species.

There are 15 feathers in the secondary series of the first winter plumage. As in the juvenal series, number 3 is the first to erupt. Number 2 emerges at about the same time as number 11, and numbers 1, 13, 14, and 15 erupt after number 12 (fig. 1). The intervals between the eruptions of secondaries 3 through 10 are five to seven days. Numbers 11 through 15 erupt in rapid succession after number 10. These innermost secondaries are much shorter than the others, except number 1 which is nearly the last to erupt and is the last to complete its growth. It is shorter than the other more distal ones, and its growth rate appears to be slower. With the attainment of full length by number 1 at about 130 days of age, secondary development is completed; this is only shortly before the completion of primary growth.

Petrides and Nestler (*op. cit.*:777) report that, in Bobwhites, secondary number 1 (axial) is not completely grown until two to seven days following full primary growth. Thus, although timing of the primary molt is quite similar in the two species, the secondary molt in the Bobwhite starts at a slightly greater age and requires more time than in the California Quail. This difference is the only significant one discovered in comparison of plumage development of the two species.

The greater primary coverts of the juvenal plumage are not molted but are retained throughout the first year just as are the outer two primaries. These coverts, the first seven of which are mottled brown in color in contrast to the plain gray of their adult counterparts, provide the most obvious and reliable means of separating first-year birds from adults. The greater secondary coverts of the first winter plumage erupt along with the secondaries. The middle and lesser coverts develop in turn after the greater coverts are in, those of the primaries preceding those of the secondaries. The under wing coverts develop last.

In the seventh week the inner juvenal alular feather is molted, and the new, first winter replacement begins its growth. About a week later the middle feather follows suit. The third molts in about 12 weeks, and by 15 weeks of age the alular development is complete.

The order of tail molt is again centrifugal in the postjuvenal molt, and the number of rectrices, namely 12, is the same as in the juvenal plumage. The central four pairs of first winter rectrices appear in rapid succession at about ten weeks of age, and the

outer pair erupt at about 14 weeks. The completion of development is reached by about 18 weeks.

The development of the first winter body plumage follows much the same course as does that of the juvenal body plumage, except that the head begins to molt at the beginning of the sequence. Various stages in this development are illustrated in figure 3. Whereas the juvenal body plumage requires five weeks to complete its growth, the first winter body plumage develops from the age of seven weeks to beyond the age of 23 weeks, a total of over 16 weeks.

At the end of the sixth or the beginning of the seventh week of age, first winter feathers begin to appear below the eye. This is the first area in which sexual dimorphism of plumage becomes evident. In the male these feathers are black, and in the female they are brown. Since the juvenal feathers in this area are brown, it is not possible to be certain of the sex of a female until a few days later (in age) than one can sex a male with certainty.

AGE DETERMINATION

The growth curves of figure 2 provide a means of estimating the chronological ages of young California Quail. The drawings of body plumage development (fig. 3) might also be used in age determination, but the growth of the primaries is more regular and is subject to measurement. Because it was felt that the addition of criteria based on the growth of secondaries might increase the accuracy of age determination, growth rates of secondaries were obtained in this study. However, secondary development proved to be somewhat more variable, and therefore less useful in aging than is primary development. Hence, the detailed data are not included here.

Although the timing of the development of the primaries is well correlated with the age of the bird, the correlation is not perfect. Petrides and Nestler (1943:781) report maximum errors in aging, due to deviation from mean lengths of primaries at given ages, of from four days to thirteen days, the magnitude of maximum error increasing roughly with age. They point out that the data indicate that the true ages of a majority of birds will fall within a period of a week in either direction of the indicated age. Thompson and Kabat (1950), using the table of Petrides and Nestler (*op. cit.*), analyzed discrepancies in age indicated by different growing feathers on the same wing and variation in indicated age of birds of the same brood. This work on wild birds revealed a standard deviation in error of aging of about two days, a variation less than that found by Petrides and Nestler on captive quail.

Wallmo (1956) finds a similar degree of accuracy in Scaled Quail by comparing intervals indicated by primary molt with known intervals in individual wild birds retrapped after varying periods. Using this method and also that of comparing true age with age indicated by primaries in captives of known age, Williams (1959) obtained results agreeing with the others cited.

In this study, deviations of the age indicated by various remiges from the actual known age were ascertained in order to obtain a measure of the reliability of the curves of figure 2 as aging criteria. Ages were chosen that would make use of the middle portion of each growth curve because these portions are probably more nearly true reflections of the samples.

The maximum amount of error in the use of primaries for aging was as follows: juvenal number 1, two days; juvenal 4, four days; first winter 1 and 2, three days; first winter 3, five days; first winter 4 and 5, four days; first winter 6 and 8, eight days; and first winter 7, nine days. Thus, the curves of figure 2 provide a standard for aging which are accurate to within four days up to the age of 70 days and to within nine days

up to 125 days of age. This degree of accuracy is approximately that found by the other workers on age determination in quail.

Another fact emerging from the study of the deviations in apparent age from true age is that individuals tend to deviate in the same direction at various ages. Of the 14 birds used, ten showed a significant departure (by chi square test) from an equal amount of positive and negative deviation. Thus, if a bird were slow in development at one age, it tended to be slow at a later stage, and the same was true for birds tending to be ahead of average development. Therefore, it is doubtful whether accuracy of aging can be increased by using growth stages of more than one primary at a time, as all primaries of any one bird tend to give similar errors as to true age.

The first winter secondaries are more variable in their growth than are the primaries. The maximum range in age of eruption of primaries is 11 days (primary 6). The minimum range in secondaries is 11 days and the maximum is 21. Thus the primaries provide the most reliable criteria of age, and the analysis of variation in aging was confined to them.

Although the growth of primary number 8 is nearly complete at 130 days and the curve is no longer accurate for age determination, the presence of a portion of the growing sheath at the base of this feather indicates an age of less than 145 days and may be used to estimate roughly the age of birds at 20 and 21 weeks. Growing contour feathers may be detected on the medial surfaces of the legs after the sheath of primary number 8 has disappeared. Presence of such feathers denotes an age of less than 165 days.

ADULT MOLT

Adults, including birds at the end of their first year, undergo a complete molt at the end of each breeding season. The course of this molt is regular and similar to that of the postjuvenal replacement.

Dwight (1900) reports a prenuptial replacement of feathers in the facial area in addition to the complete postnuptial molt; however, examination of about 30 museum skins collected in late winter and early spring failed to confirm the existence of this prenuptial molt. Live birds in the study area were not checked specifically for prenuptial molting, but many birds were handled during this period and no molting was noted. At any rate there is but a single complete, or nearly complete, molt each year, the postnuptial molt.

Data on the annual molt were obtained from examination of birds captured in the regular trapping program. Since the molt of the entire plumage is included in the period of primary replacement (Genelly, 1955:281), the lengths of growing primaries were estimated or measured on each molting bird in order to obtain an index as to the extent of molting. Thus, in the primary molt series there are ten major stages corresponding to the dropping of the ten primaries. For each primary, substages may be recognized, according to the amount of growth. In all, forty stages were used in this study, four for each primary; these are plotted against a time scale in figure 4. Males and females are plotted separately. The males begin molting earlier than the females, but the two groups complete the molt at about the same time. These findings agree with those of Genelly (*op. cit.*:282) as to timing and differences between the sexes.

In pheasants, Kabat, Thompson, and Kozlik (1950) found that there is a similar lag of about one month in the beginning of molt in hens as compared to the beginning of molt in cocks. They found that the individual hens molt at the same time as their chicks and they believe, therefore, that hens do not begin to molt until after their broods hatch. Genelly (*loc. cit.*) gives evidence for a similar situation in California Quail. In the pres-

ent study hatching occurred late in 1956, and the molt of the hens was likewise later than in other years. However, the timing of the molt in cocks was similar in all four years. Thus, the situation in pheasants, with the males molting at a regular time each

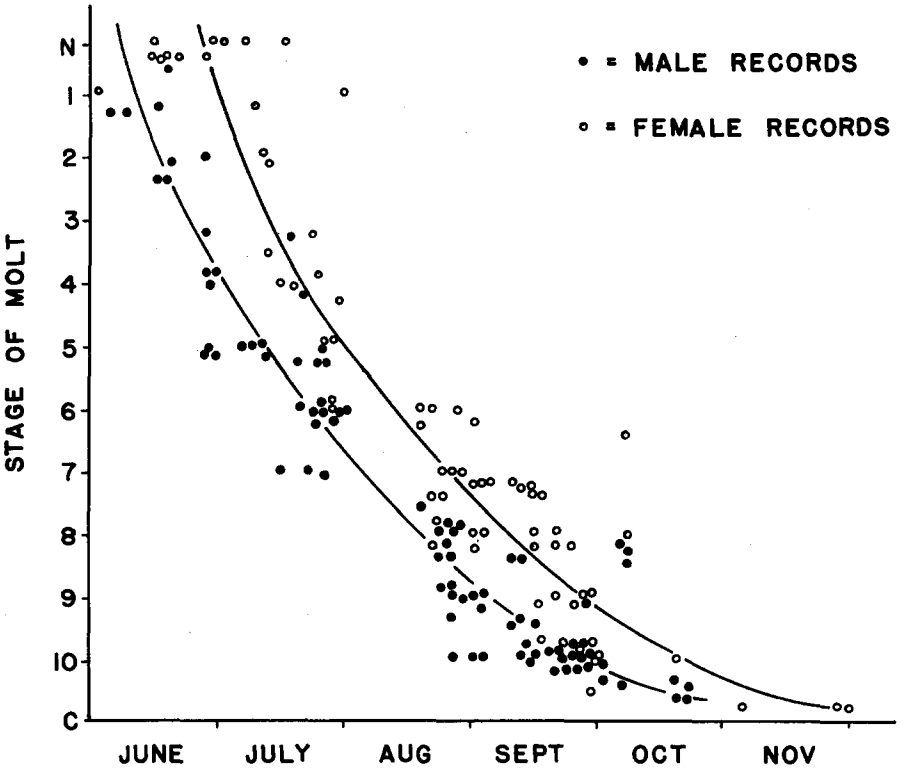

Fig. 4. Timing of adult molt in California Quail. Data from four years are combined. Each circle represents one molting bird. Stages of molt correspond to the number of the primary last molted. The letter "N" signifies that molt had not begun; "C" signifies molt completed.

year and the females not molting until their clutches are hatched, is apparently duplicated in this population of California Quail.

The convergence of the two curves of figure 4 suggests that females molt more rapidly than males. Genelly (*loc. cit.*) found a similar convergence but was not able to conclude whether or not individual females actually complete their molt in a shorter time than individual males. The recapture of various birds of each sex several times during the period of molt in this study has made it possible to estimate roughly the time required for the individual bird to replace its plumage completely. These data indicate that males take over a month longer to complete the molt than do females.

SUMMARY

Young California Quail (*Lophortyx californicus*) are hatched with a covering of natal down. This down is replaced in a regular sequence by the juvenal plumage during the postnatal molt. Juvenal plumage development lasts from the time of hatching until the age of about 11 weeks. The juvenal plumage is replaced by the first winter plumage during the postjuvenal molt, which commences at the age of four weeks. The first winter plumage is fully developed by the age of 21 to 23 weeks. The greater primary coverts

and primaries 9 and 10 of the juvenal plumage are retained for about a year and are molted in the first postnuptial molt. The sequence of feather replacement is similar in all molts except that the head plumage is replaced late in the postnatal molt whereas the head begins molting early in the postjuvenal, and presumably in the postnuptial, molt.

The regular replacement of the series of remiges, especially the primaries, may be used as a gauge to determine the age of the young quail.

Adult quail undergo one complete molt each year at the end of the breeding season. The adult males begin to molt early in June, and the females follow about a month later. Inception of molt in individual hens is apparently governed by the hatching of their young. Females replace their plumage in a shorter time than do males; both sexes complete the molt in late October.

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