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3

Molts and Plumages

AN understanding of the molts and plumages of the quails and grouse is of great importance to the applied biologist, for they provide clues that are valuable for determining age and sex of individual birds without resorting to internal examination. They thus offer a means of analyzing wild populations as to sex and age composition, which are basic indices to past and potential reproductive performances and probable mortality rates. Additionally, molts and plumages are generally species-specific traits, which have resulted from pressures of natural selection over a long period of time in a particular habitat and climate. The ecology of the species is of major importance in this regard; species occurring in more northerly regions may undergo their molts more rapidly than those in southerly ones or, as in the case of the willow ptarmigan, certain races may even lack particular plumages that occur in populations existing in other areas having different climates.

From the time they hatch, all grouse and quails exhibit a series of specific plumages, separated by equally definite molts, that are comparable in nearly all species. The only known exception to this occurs in the genus *Lagopus*, which is unique in having an extra molt, and thus a supplementary plumage, intercalated between its summer and winter plumages. This special case will be dealt with as required; the following summary will thus serve to provide the basic sequences and terminology that describe the molts and plumages found in the North American grouse and quails.

NATAL PLUMAGE

All galliform birds hatch covered with a dense coat of down that serves to insulate the body and to provide camouflage for the precocial young, which typically leave the nest shortly after hatching. This natal plumage is generally extremely similar among related species and, because of the lack of known selective pressures for rapid divergence in downy patterns during speciation, often provides more valuable clues to evolutionary relationships than do adult plumage patterns.

POSTNATAL MOLT AND JUVENAL PLUMAGE

Virtually at the time of hatching, or at least within the first week of life, the first indications of the juvenal plumage become apparent through the emergence of the secondary and inner primary feathers and the rectrices (tail feathers). The two outermost juvenal primaries and the innermost of the juvenal secondaries appear later than those situated near the middle of the wing. All native galliform species have ten primaries, which are counted outwardly from the most proximal one, while the number of secondary feathers is somewhat greater and varies among species, with the innermost secondaries sometimes designated as "tertiaries" (although like typical secondaries they insert on the ulna rather than on the humerus). The secondaries are counted inwardly, from the feather nearest the first of the primaries (which insert on the bones of the hand). The third secondary is typically the first to emerge, followed in sequence by the progressively more proximal ones, while the two outermost ones often emerge at about the same time as those near the proximal end. At the same time that the primaries and secondaries are growing, all the upper greater coverts begin growth. The upper coverts for the two outermost primaries actually begin to grow before their associated primaries and possibly serve as functional substitutes for these flight feathers, which are typically delayed in development. Correlated with this, the ninth upper primary covert of the juvenal plumage is often notably more pointed and larger than are the adjoining coverts.

The juvenal remiges (primaries and secondaries) and rectrices (tail feathers) are scarcely fully grown before they begin to be pushed out by the remiges and rectrices of the next plumage, but during the short time they are present the rest of the body is being transformed from a down-covered one to one covered with contour feathers. This transformation is called the *postnatal molt,* and is a complete molt. The feathers which replace the natal down are called *juvenal* feathers, and the associated age category is called the *juvenile* stage.

As the juvenal remiges and rectrices are appearing in the manner described above, other juvenal feathers begin to emerge on both sides of the breast and backwards toward the flanks. Shortly, juvenal feathers also appear on the crown, base of the neck, scapular region, and upper legs, spreading toward the back. The greater and lesser upper wing coverts are fully grown before their associated remiges, and are followed by the median coverts. These upper coverts appear in advance of the lower coverts (Dwight, 1900). Before all the juvenal feathers have appeared throughout the head region, the first signs of the next (post juvenal) molt will be evident in the loss of the inner juvenal primaries and the emergence of new (first-winter) primaries in their places. This occurs as early as eighteen days after hatching in willow ptarmigan and blue grouse and occurs within the first month of life in most or all species. The juvenal primaries are molted outwardly at roughly five-day intervals for the inner ones, and at increasing intervals for the outer ones (table 9). The two outer juvenal primaries (numbers nine and ten) will have just completed their growth shortly before the eighth juvenal primary is dropped. Except in rare instances these two outer juvenal primaries are never normally molted in the species under consideration here. In the ring-necked pheasant this does occur, but it is not typical of the introduced Old World partridges (*Perdix* and *Alectoris*). An important difference between the New World quails and the grouse occurs in association with the postjuvenal molt of the eight inner primaries. In the grouse (as well as in *Perdix* and *Alectoris*) the associated juvenal greater upper primary coverts are also molted in the postjuvenal molt, whereas in all the New World quails so far studied the juvenal greater upper wing coverts of these primaries are not molted but rather are held through the winter and spring until they are molted in the annual (postnuptial) molt (van Rossem, 1925; Petrides, 1942). Since these feathers are marked with more buffy or lighter tips than are the upper primary coverts of adult birds, this difference provides an alternate and more reliable method of determining age in New World quails than the examination of their outer two primary feathers for signs of wear and fading.

The juvenal secondaries, as well as all the juvenal rectrices, are also rapidly lost at about the time that the juvenal primaries are being shed. The juvenal rectrices may be dropped almost simultaneously, as in the bobwhite and rock ptarmigan (Watson, 1962c; Salomonsen, 1939), molted from the lateral follicles toward the middle ones (centripetally), as in the blue grouse (Smith and Buss, 1963), or molted from the central follicles outwardly (centrifugally), as in the California and scaled quails (Raitt, 1961; Ohmart, 1967). The gray partridge also has an imperfectly centrifugal postjuvenal molt of the rectrices (McCabe and Hawkins, 1946). The juvenal

TABLE 9

Average Age (in Days) of Start and Completion of Growth of First-winter Primary Feathers in Representative Grouse and Quails

Species	Primary number (counting from inside); A = starts growth; B = grown								Authority
	1	2	3	4	5	6	7	8	
Grouse	A/B	A/B	A/B	A/B	A/B	A/B	A/B	A/B	
Sage grouse									
males	24/35	29/42+	34/49+	40/56+	47/77+	59/84+	74/105+	102/140+	Pyrah, 1963
females	24/42	27/42	33/49+	38/56+	45/63+	54/77+	66/91+	91/126+	
Blue grouse	17/38	23/44	26/50	35/59	41/68	47/80	59/95	71/113	Zwickel & Lance, 1966
Willow ptarmigan	18/—	25/—	30/—	35/—	40/—	46/—	53/—	65/91	Westerskov, 1956
Ruffed grouse									
New York	14/45	20/49	27/63	35/68	42/77	49/83	61/98	74/119	Bump et al., 1947
Ohio	23/46	27/54	34/54	40/68	47/73	56/88	68/102	85/124	Davis, 1968
Greater prairie chicken	28/56	35/56	41/64	49/77	55/84	60/84+	70/—	82/126+	Baker, 1953
Quails									
Scaled quail	26/50	30/60	35/65	39/75	45/85	57/93	64/115	107/150	Ohmart, 1967
California quail	29/55	32/62	38/70	46/80	52/90	62/108	72/121	100/141	Raitt, 1961
Bobwhite	26–30/ 54–58	33–37/ 56–60	40–44/ 60–64	44–50/ 70–75	52–58/ 81–89	58–63/ 99–107	69–77/ 120–28	97–105/ 146–54	Petrides & Nestler, 1943 Rosene, 1969
Harlequin quail			42/—	49/—	56/—	77/—	98/—	119/ 133–35	Leopold & McCabe, 1957
Partridges									
Gray partridge	24/—	27– 31/—	33– 38/—	39– 45/—	47– 52/—	55– 59/—	67– 73/—	86–87/ 115–25	Petrides, 1951
Red-legged partridge	29/—	34/—	41/—	49/—	58/—	70/—	86/—	105/130	Petrides, 1951

secondaries are lost in about the same sequence as they emerged; starting from the third, the molt proceeds inwardly, with the two outermost secondaries dropping as the more proximal secondaries are being lost.

Body feathers of the juvenal plumage are surprisingly similar in both the grouse and quail groups. Typically white or pale buffy shaft-streaks are conspicuous, especially on the upper parts; these often expand near the tip of the feather to form distinctive hammer-shaped markings. Apparently only the ptarmigans lack these distinctive juvenile markings. Usually the sexes are nearly identical in this plumage.

POSTJUVENAL MOLT AND FIRST-WINTER PLUMAGE

The postjuvenal molt (or "prebasic," according to Humphrey and Parkes) gradually replaces the juvenal body feathers with the more distinctly species-specific feathers of the first-winter (or "basic") plumage. The postjuvenal molt is virtually complete in all the species considered here, involving all the body feathers and all the flight feathers with the exception of the two outermost (primaries nine and ten) and their coverts. Additionally, the upper greater (and possibly other) coverts of the more proximal primaries are retained in the New World quails, as earlier mentioned.

Because the outer two juvenal primaries are retained during the postjuvenal molt, they will normally be carried by the bird until its next complete molt, which occurs after the next breeding season. This is the case at least in the species considered here, although Petrides (1942) reports that in the chachalaca (*Ortalis vetula*) these primaries are retained only until February or March, when a complete wing and tail molt occurs. Because of their relatively long persistence, the outer two primaries are usually subjected to considerable fading and wear; they thus provide a basic method of age estimation, especially in grouse, which do not retain distinctive juvenal upper primary coverts. Limitations to their value in determining age come from two sources; possible difficulties in estimating their wear relative to that of the more proximal primaries and from occasional aberrations in wing molt. This latter problem may result from a precocious molting of one or both of the outer juvenal primaries during the first fall (as regularly occurs in pheasants) or from an abnormally arrested molt in which the juvenal remiges are retained longer than normally. Several examples of each of these aberrant variations have been reported, and are important to note because of their obvious implications in the accuracy of age estimation techniques (table 10).

The gradual loss of the eight inner juvenal primaries, and their replace-

ment by primaries of the first-winter plumage, provides an excellent method of estimating the ages of young grouse and quail between about three and fifteen or twenty weeks of age, by which time the last of these primaries will have completed their growth. Growth rates of representative species of all the United States genera of grouse and quails have been studied and for these an estimation of age is possible by determining the extent of primary replacement and growth during this period (table 9). Undoubtedly there may be some population variations in growth rates of these species, and hand-reared birds may develop at somewhat different rates from wild ones, but the availability of such ageing criteria is extremely valuable for back-dating probable hatching periods based on the examination of young birds.

First-winter secondaries replace juvenal secondaries at the same time this process occurs in the primaries or slightly later, and by the time the last of the juvenal secondaries have been shed the young bird will be well into its acquisition of the *first-winter* plumage. By the time the bird is four or five months old it should have completed growth of all its first-winter flight feathers and lost all its juvenal feathers other than those few wing feathers that are carried through the winter. With the loss of its juvenal body feathers the bird can be classified as an *immature* rather than a juvenile. Except in the ptarmigans, no further molt will occur until at least the following spring among the species considered here. However, the three ptarmigan species present a special case, for which an additional plumage stage and molt cycle must be mentioned.

SUPPLEMENTARY POSTJUVENAL MOLT AND SUPPLEMENTARY PLUMAGE

In at least the North American species of ptarmigans, a special plumage situation exists that must be mentioned here. One unique fact is that when the two outer juvenal primaries emerge (at two or three weeks of age) they do not resemble the other brownish primaries, but rather have the white vanes typical of the first-winter primary. Indeed, Salomonsen (1939) considers them to represent first-winter rather than juvenal primaries, but to do so is to accept the view that a major evolutionary difference between the primary molt of ptarmigans and all other grouse exists, and it seems more reasonable to believe that the coloration of the two outer juvenal primaries has only been adaptively modified in the genus *Lagopus* in relation to ecological requirements for concealing coloration. The postjuvenal molt of the body feathers of young ptarmigans likewise begins unusually early,

at about four or five weeks of age, and the first feathers of preliminary winter plumage begin to appear. These initially consist of vermiculated or mottled feathers rather than pure white ones. Some juvenal feathers are retained for a time, including ones on the throat, breast, and hindneck. As this postjuvenal molt is being completed, a second stage of molt ("supplementary postjuvenal molt") begins, which replaces the last of the juvenal body feathers with pure white feathers and which also replaces the grayish or brownish feathers grown during the earlier stages of the postjuvenal molt with new white feathers. The body plumage held during the first winter thus includes both some of those feathers acquired during the preliminary postjuvenal molt, such as those on the abdomen, the under tail coverts, under wing coverts, legs, and toes, as well as others acquired during the later or supplementary postjuvenal molt, all of which are white (Salomonsen, 1939).

PRENUPTIAL MOLT AND FIRST NUPTIAL PLUMAGE

In most grouse and quail relatively little and possibly no additional molting occurs after the assumption of the first-winter plumage and the first breeding season. Dwight (1900) reported that in the genera *Colinus*, *Callipepla*, and *Cyrtonyx*, and possibly also in *Oreortyx*, there is a restricted renewal of feathers in the face and throat regions of these quail prior to the onset of breeding. The occurrence of such a prenuptial molt in the New World quail has been questioned by later investigators (Raitt, 1961; Raitt and Ohmart, 1966) but observations on hybrid quail support its existence (Johnsgard, 1970). Dwight reported a correspondingly restricted chin and head molt in species of the genera *Tympanuchus* and *Bonasa* and possibly but not definitely in species of *Dendragapus*. A fairly extensive prenuptial ("prealternate") molt was reported by Watson (1962c) in Cuban bobwhites. He also mentions that whereas the head is the last site to complete the postjuvenal molt, it is the first to begin the prenuptial molt in this species.

In the ptarmigan species there can be no question about the occurrence of a prenuptial molt ("pre-alternate" according to the classification of Humphrey and Parkes, 1959) and a distinctive nuptial (or "alternate") plumage. The extent of this molt may vary with age, sex, and latitude, but at this time the males first become markedly different from females. The male willow ptarmigan thus assumes its characteristic rusty brown upperparts, while male rock ptarmigan acquire vermiculated grayish feathering, and females of both become decidedly barred in appearance. The molt of the female

may proceed somewhat more rapidly and be more extensive than in the male. However, at least in the rock ptarmigan, both sexes retain through the summer at least some portions of the preceding winter plumage, including feathers of their legs, toes, under wing coverts, and some upper wing coverts (Salomonsen, 1939).

POSTNUPTIAL MOLT AND SECOND WINTER PLUMAGE

Except in those species such as sage grouse in which sexual maturity may not be attained the first year, the bird will normally have attempted to breed while still in its first nuptial plumage. The timing of the following postnuptial molt is generally associated with endocrine changes related to changes in gonadal activity. In any case, it is typical for all the species considered here to begin a complete body molt in late summer, with the males generally somewhat in advance of the females. At this time the primaries will begin to be molted in outward sequence from the first through the tenth, the secondaries will be dropped starting with the outermost ones and proceeding proximally, and the rectrices will begin a gradual or rapid molt. The adult tail molt of grouse, like that of most pheasants (Beebe, 1926), is generally centripetal, as reported by Bendell (1955b) for blue grouse, and by Bergerud, Peters, and McGrath (1963) for willow ptarmigan, but may be virtually simultaneous, as indicated by Salomonsen (1939) for the rock ptarmigan and Stoneberg (1967) for the spruce grouse. In the bobwhite (Watson, 1962c) and probably in most or all other New World quails, the adult tail molt is centrifugal, providing an apparent basic difference in the molting sequences of grouse and quail. This may not be universal however; Baker (1953) mentions a greater prairie chicken specimen that was undergoing an apparent centrifugal tail molt.

At the same time the wing and tail feathers are being molted, the body feathers are being renewed, approximately in the same order that they originally grew in during the postjuvenal molt. Except in the ptarmigan, all of the feathers that grow in during the postnuptial molt will be carried through the following winter and represent the second winter plumage. It is of interest to note that only at this time will the last traces of the juvenal plumage be lost—namely, the two outermost primaries, their coverts and, in the case of the New World quails, the upper greater coverts of the other primaries as well. There are also a few cases of arrested molt known in which these outer primaries are not dropped but are carried through a second winter, as noted in table 10.

TABLE 10

Reported Aberrations in Primary and Secondary Molt of Grouse and Quails

I. Examples of Precocious Molt

A. Molt of ninth juvenal primary in first autumn, or of both ninth and tenth juvenal primaries

1. Chukar partridge: Reported in six of eighteen early-hatched birds by Smith (1961).
2. Interior bobwhite: Reported in two Wisconsin specimens by Thompson & Kabat (1950).
3. Florida bobwhite: Loveless (1958) reported that 33.4 percent of 138 south Florida birds molted beyond the eighth primary, with 30.4 percent molting their ninth, and 3.0 percent both their ninth and tenth. Further, 5.1 percent of the birds molted some of the upper primary greater coverts, starting distally, and two males molted all but one of these coverts. Precocial primary and covert molt was also noted in South Carolina bobwhites by Rosene (1969).
4. Cuban bobwhite: Reported in eight of eighty-one specimens by Watson (1962c).

II. Examples of Arrested Molt

A. Retention of one or more secondaries abnormally long

1. Chukar partridge: One female retained two juvenal secondaries through the first autumn (Watson, 1962c).
2. Blue grouse: Two adult males retained all but two secondaries for at least thirteen months and through the postnuptial molt (Bendell, 1955b).

B. Retention of primaries abnormally long

1. Scaled quail: One specimen retained tenth juvenal primary through second autumn (Wallmo, 1956a).
2. Bobwhite: Late-hatched birds frequently retain seventh juvenal primary (as well as ninth and tenth) through first autumn (Thompson and Kabat, 1950). Adults may retain ninth or tenth primaries through postnuptial molt and at least until midwinter (Rosene, 1969).
3. Blue grouse: Two adults retained their ninth and tenth primaries through the postnuptial molt (Bendell, 1955b).
4. White-tailed ptarmigan: Retention of juvenal primaries through a second autumn reported (C. Brown, quoted in Ellison, 1968a).

SUPPLEMENTARY POSTNUPTIAL MOLT AND SUPPLEMENTARY WINTER PLUMAGE

As noted, the ptarmigans differ from the other grouse in the postnuptial molt sequence, and they exhibit an early or preliminary postnuptial fall molt in adults that corresponds to the early postjuvenal molt of young birds. In this mixed white and grayish plumage adult male rock ptarmigan closely resemble females, and both can hardly be differentiated from immature birds (although the old birds will be replacing their two outer primaries at this time). This stage is referred to as the preliminary second winter plumage. A few body feathers will still be retained at this time from the summer plumage, including (in males) some greater wing coverts or tertiaries and some mantle or hindneck feathers. Females retain many lower breast or flank feathers, some inner median and greater coverts, some tertiaries, and some scattered upper breast, throat, and mantle feathers. These summer feathers, plus the grayish fall feathers just acquired and including some of the upper parts, some flank feathers, the tertiaries, and some upper wing coverts, are now quickly replaced with white feathers by a special supplementary postnuptial molt (Salomonsen, 1939). Observations by Höst (1942) on captive willow ptarmigan clearly indicate the importance of photoperiod not only in regulating the timing of molt in willow ptarmigan but also in influencing the pigment characteristics of the new feathers. Höst found that by exposing birds in winter plumage to artificially long photoperiods starting in November, he could induce the precocious assumption of the spring nuptial plumage and even stimulated a female to lay a clutch of eggs in December and January. One of the males that had acquired a nuptial plumage at the beginning of February was then exposed to a seven-hour photoperiod, upon which it molted directly back into a white winter plumage without passing through an intervening fall plumage. However, five birds that had their daylight reduced in August passed through a short fall plumage before assuming their winter plumage.

SECOND NUPTIAL PLUMAGE

The second nuptial plumage is acquired in the same manner as the first nuptial plumage, and later plumages and their intervening molts are repetitions of the earlier ones. Once the juvenal outer primaries have been lost in late summer, it is generally almost impossible to recognize birds in their second fall of life from older age categories.

A summary (figures 9 and 10) of the foregoing information with respect

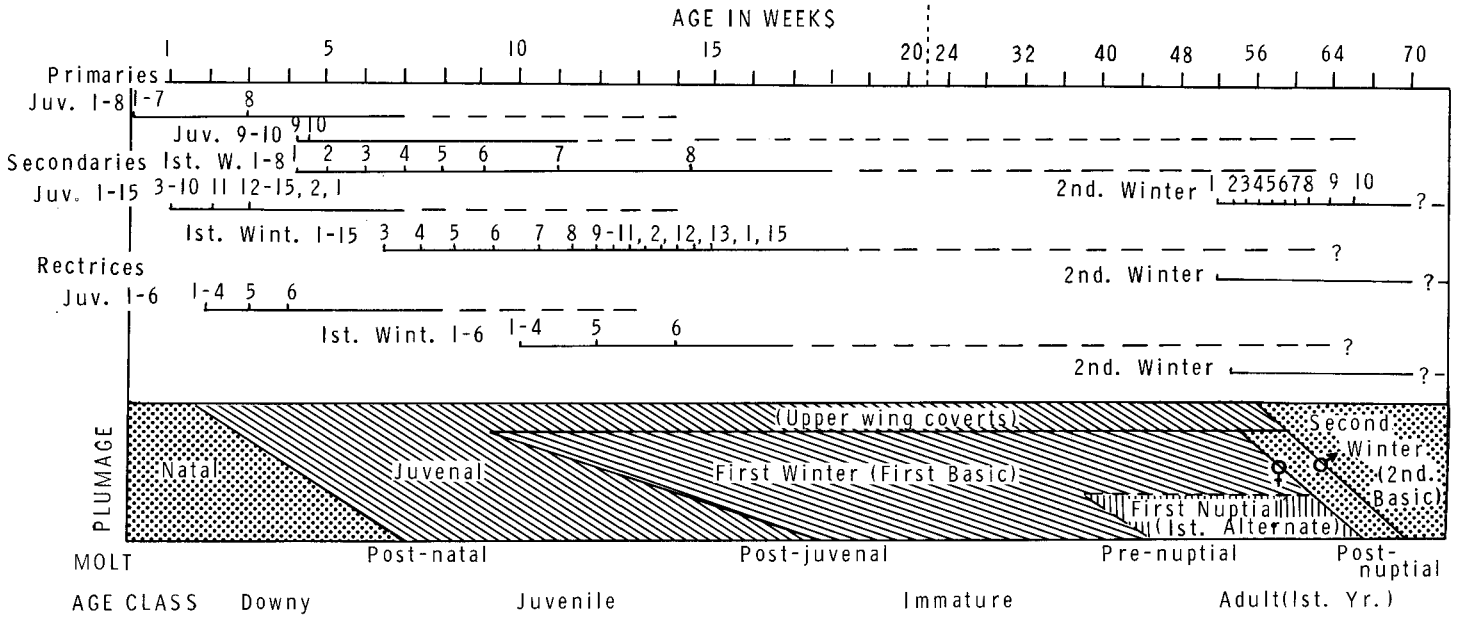

FIGURE 9. Sequence of molts and plumages in the California quail.

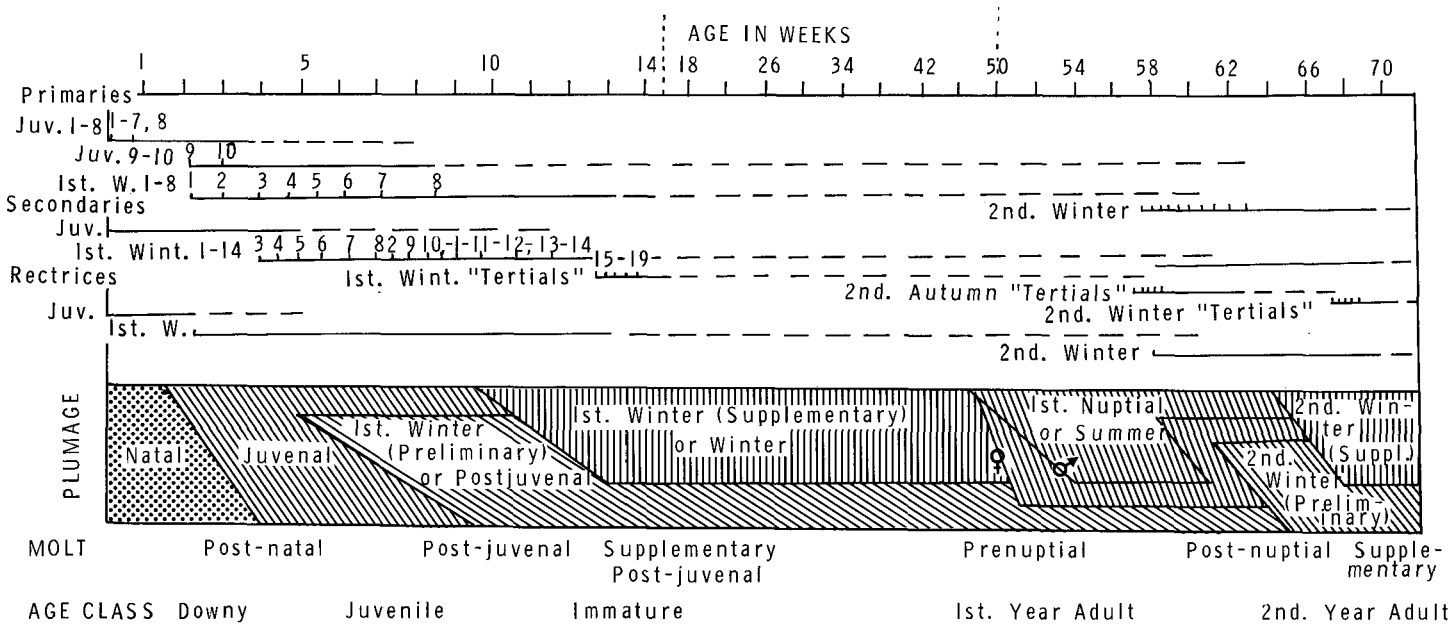

FIGURE 10. Sequence of molts and plumages in the rock ptarmigan.

to a representative species of quail (based mainly on information on the California quail by Raitt, 1961) and the rock ptarmigan (based mostly on data provided by Salomonsen, 1939). The relatively greater complexity of the ptarmigan plumages and the compression of the natal and juvenal plumages into the minimum possible time spans are apparent in these diagrams.

ENDOCRINE AND ENVIRONMENTAL CONTROLS OF MOLTING

Timing of the postnatal and postjuvenal molts can probably be regarded as age-dependent, progressing as rapidly as food supplies and general bodily development allow. Additionally, in the ptarmigan, ecological requirements for coloration changes related to the seasons may place special demands on molt timing in young birds. Watson (1962c) found that Cuban bobwhites apparently have more prolonged postjuvenal and prenuptial molts than do Florida populations of the same species, which he suggests might be related to differences in midwinter temperatures of the two regions. Watson suggests that, although gonadal hormones may help to regulate molt timing by their temporary inhibiting effects, thyroid activity is probably responsible for the initiation of molting and that breeding and molting are not under the same hormonal control. Raitt and Ohmart (1966) likewise suggest that there is no directly causative relationship between the regression of gonadal activity and the onset of the postnuptial molt they observed in Gambel quail.

Although the thyroid hormone is most commonly implicated in molt initiation, recent evidence (summarized by Sturkie, 1965, and by Lofts and Murton, 1968) indicates that molting may be relatively independent of thyroid activity, or at least the increased metabolic activity associated with molting may not indicate direct thyroid control of the latter. Juhn and Harris (1955, 1968) found that injected progesterone can initiate molt in adult female domestic fowl, and that prolactin stimulates molt in capons when given alone or in conjunction with progesterone. Shaffner (1955) and Adams (1956) also reported on the molt-stimulating effects of progesterone. Jones (1969b) found that progesterone injection alone did not stimulate defeathering associated with incubation patch development in the California quail, but that this hormone in conjunction with prolactin has such effects.

Although molt might be initiated by progesterone alone in various year-round breeders, this effect evidently does not occur among seasonally breeding birds (Kobayashi, 1958). In seasonally breeding forms there may instead be a synergistic relationship between progesterone and thyroxin relative to molt control, since Kobayashi found that thyroidectomy had the effect of inhibiting molt induction through progesterone treatment in such species.

In addition to direct endocrine controls, external factors such as photoperiod changes may be additional regulators of molt, as suggested by Höst's (1942) early experiments with willow ptarmigan. Lofts and Murton (1968) have reviewed the evidence on this point and have confirmed that at least some north-temperate photoperiodic species of birds require a postnuptial exposure to reduced photoperiod not only to regain their photosensitivity relative to reproduction but also for the normal temporal completion of their molt.