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PTERYLOGRAPHY AND AGE DETERMINATION IN THE ORANGE-CROWNED WARBLER

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In order to provide basic data for a study of molt cycles, I mapped pterylography and developed criteria for age determination in the Orange-crowned Warbler, *Vermivora celata*. The latter investigation made possible the analysis of timing and extent of molt in the various age groups (Foster, 1967). Although the segregation of birds into age classes is of great importance in all branches of ornithology, as has been noted by Davis (1957), age determination is poorly known in Parulidae and in passerines in general.

METHODS AND MATERIALS

Of the 18 specimens used for the study of pterylography, 14 (12 nestlings, 1 immature, 1 adult) were preserved in alcohol. The feathers of these birds were clipped near the base of the shafts to facilitate observation of the tracts. Three birds (2 immatures, 1 first-year) were prepared as dried flat skins, and the projecting calami were observed from the underside of the skin. One juvenal bird was prepared as a study skin with its wings spread.

A series of 150 museum specimens, all birds of known age (juvenile, immature, and adult) and sex, were used to determine criteria for aging.

NATAL DOWN

Preceding the development of the definitive feather tracts, Orange-crowns are very lightly feathered (fig. 1). Of the seven birds examined that still carried natal down, none had more than 59 down feathers. These were variously distributed, as the number of down feathers in any region differs among birds and on the same bird between the members of paired tracts (table 1).

In the alar tract, down feathers are attached to the newly protruding tips of the proximal upper greater secondary coverts. In the capital tract they are located in two areas. A line runs from the anterior region of the eye posteriorly in the superciliary region, and a row in the dorsal occipital region extends antero-laterally around the head. Down feathers in the pelvic region of the spinal tract are arranged in pairs (usually two, rarely one or three) followed by a variable number of solitary feathers. There are also single rows of down feathers running through the humeral and femoral tracts. Feather spacing is quite regular in all regions. Larger gaps, which occasionally exist between feathers, are usually even multiples of the expected distance between them, suggesting that an intervening feather (or feathers) did not develop or has been lost.

Such a limited occurrence of natal down is also characteristic of the Blue-winged Warbler, *Vermivora pinus*, which has patches of down in the capital, spinal, and humeral tracts (Chapman, 1907; Saunders [in Wetherbee, 1957]). In other genera

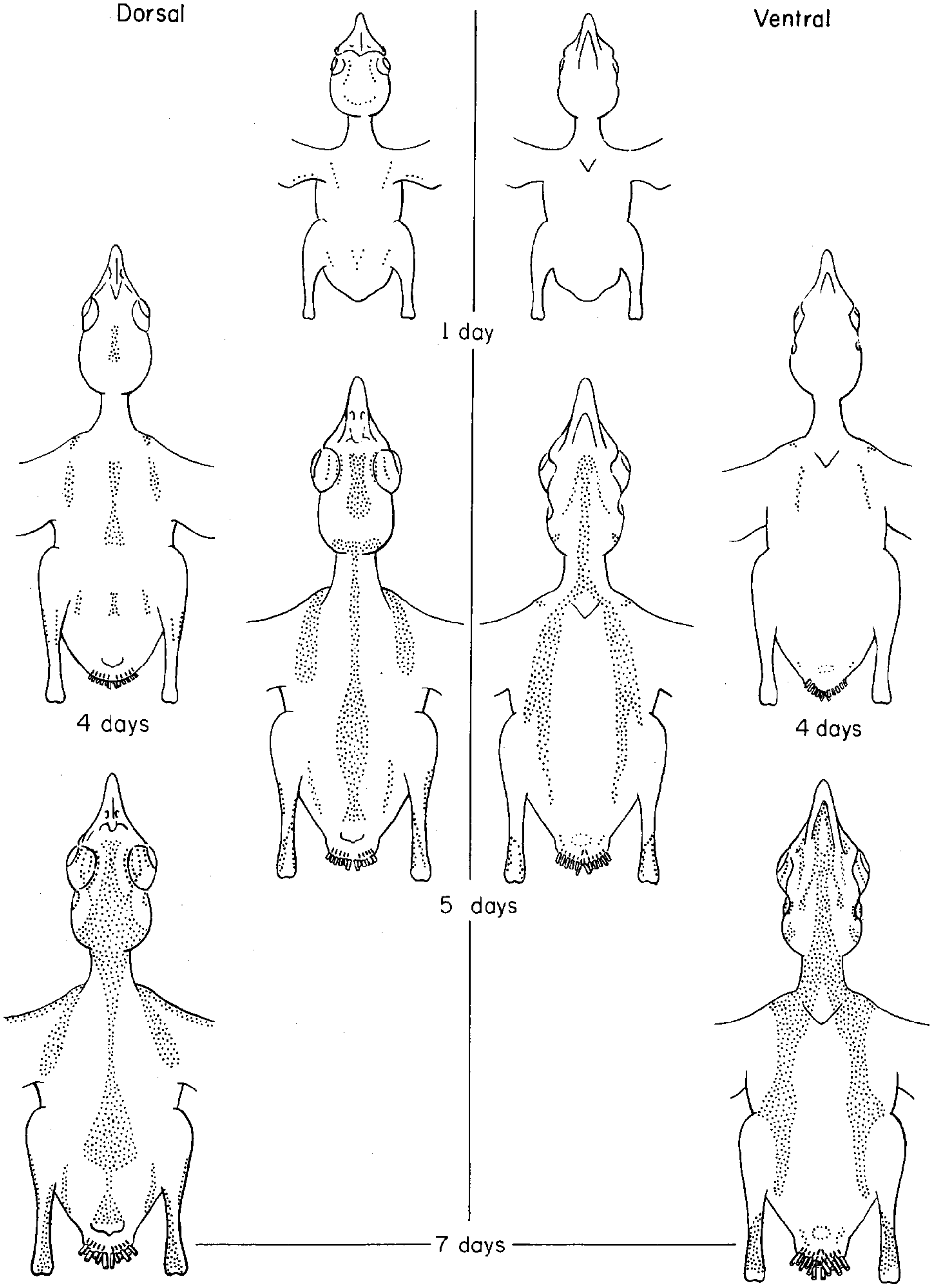

Figure 1. Development of feather tracts in the Orange-crowned Warbler. Stippled areas indicate regions in which feather tips protrude through the skin; regions of visible papillae of feathers that have not broken the skin are not included. No attempt has been made to depict individual feathers.

TABLE 1
VARIATION IN NUMBER OF DOWN FEATHERS IN VARIOUS TRACTS
OF SEVEN NESTLINGS OF *V. c. lutescens*

Region								Average
Superciliary								
right	6	7	8	9	6	9	9	7.7
left	6	7	5	8	6	7	8	6.7
Occipital	8	8	6	8	8	8	8	7.7
Up g s. cov.								
right	6	4	7	4	4	1	–[a]	4.3
left	3	1	6	3	4	3	–	3.3
Humeral								
right	6	6	6	4	6	6	4	5.4
left	6	5	6	6	7	6	4	5.9
Pelvic	8	5	6	6	5	7	3	5.7
Femoral								
right	1	2	4	5	4	4	4	3.4
left	3	2	5	5	4	4	4	3.9
Total	53	47	59	58	54	55	–	54.3

[a] = impossible to determine.

of parulids natal down is also sparse and is often confined to the same tracts as it is in *Vermivora* (Eaton, 1957; Wetherbee, 1957).

DEFINITIVE PTERYLOGRAPHY

The following description of the definitive pterylography, as well as figures 2 and 3, is an approximation intended to represent the shape and extent of feathered areas. No attempt has been made to record each body feather. The description is based on one juvenile of indeterminate sex, one male and two female immatures, one first-year male, and one adult female. All were *V. c. lutescens* except the adult female, which was an *orestera*. Although no conclusive statements can be made because of the small size of the sample, no differences in pattern among the sexes or races were noted. Also, there appears to be little or no difference in pterylography among immatures, first-years, and adults, all of which differ only slightly from juveniles. These differences include narrower interscapular and pelvic regions in the spinal tract of the juveniles, which result in a more abrupt transition from the interscapular to the dorsal region, and from the dorsal to the pelvic region. In addition, juveniles appear to be more densely feathered in all areas.

Alar tract. The Orange-crown has nine well-developed primaries. Distal and slightly anterior to primary 9 is a feather that is shaped like a primary and averages from 3 to 5 mm in length. It is obscured by a covert, 5 to 7 mm long, which lies directly above it and slightly above the level of the adjacent row of primary coverts. This feather and its covert, which molt in sequence after primary 9 and its covert, are probably vestiges of a 10th primary and its upper greater primary covert.

The eight upper greater primary coverts are situated dorso-medially between the primaries. Covert number 1 is missing. Directly above them are five or sometimes six upper middle primary coverts; numbers 1, 2, 9, and sometimes 3 are missing. The site of covert 1 is occupied by a carpal

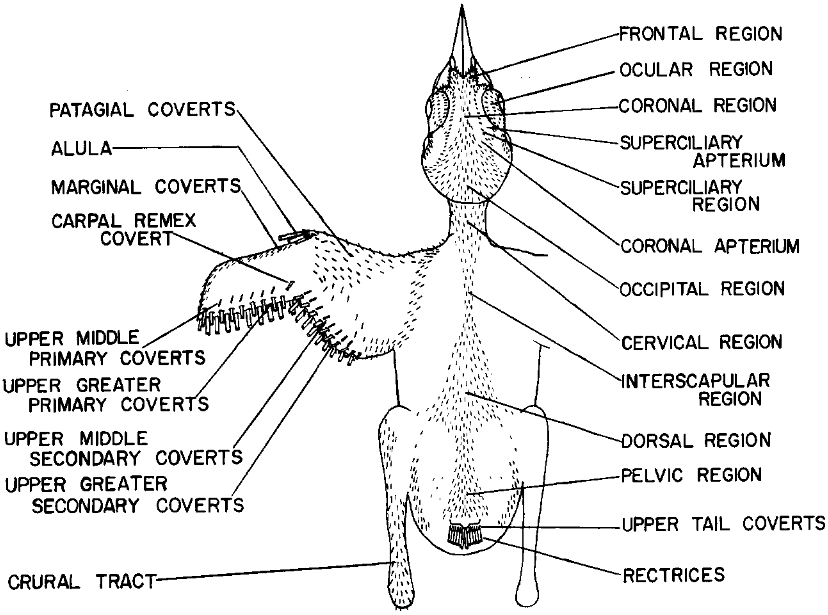

Figure 2. Definitive pterylography of the Orange-crowned Warbler, dorsal view.

remex. This covert grows in an extreme lateral and slightly posterior direction. As with the upper coverts, the under greater primary coverts are situated dorso-medial to their corresponding primaries, and covert 1 is not present. Seven under middle primary coverts are the most that have been noted in any bird. They lie dorsally to their corresponding primaries and approximately in line with them.

The 8th and 9th secondaries are only three-fourths and one-half as long, respectively, as the other seven. There are nine upper greater secondary coverts, each originating directly above its secondary. After the first four coverts, the others gradually decrease somewhat in size so that the last three are approximately the same size as the eight upper middle secondary coverts that lie dorsally and somewhat proximally to their secondaries. When present, the 1st middle covert, which is the same size as both the upper middle secondary coverts, is situated dorsal and distal to secondary number 1. The other coverts are placed dorso-medially between the secondaries; there is no evidence of covert 9. Each of the first eight under lesser secondary coverts is situated directly above the adjacent proximal middle covert, *i.e.*, lesser covert 1 lies over middle covert 2, lesser covert 2 over middle covert 3, and so on. Lesser covert number 9 lies dorso-proximal to secondary nine.

Arising at the proximal, dorso-lateral base of each secondary is an extremely small, downy feather. Its independent nature is emphasized during the postjuvenal molt, at which time it may be found with a sheath, although the secondaries, which do not molt, are without them. Pitelka (1945) found a similar series of feathers at the bases of the 1st primary, the first nine secondaries, and the middle series of greater secondary coverts in several species of *Aphelocoma*.

The alula includes three feathers. The most anterior of these is the longest; the second and third, which lie increasingly proximally and posteriorly to it, are only two-thirds and one-half as long, respectively. The alular coverts merge proximally with the marginal coverts of the patagium, which extend to the humeral tract and merge with it as it extends ventrally over the leading edge of the wing. The upper patagial coverts are concentrated in the anterior-distal region and on the posterior edge of the wing. The under patagial coverts, primarily in the posterior area of the wing, extend sparsely forward to the leading edge and proximally to the sternal region of the ventral tract. Marginal coverts form a narrow band extending the length of the leading edge of the wing.

Caudal tract. The Orange-crown has 12 equally developed rectrices. The central pair (1-1) is displaced dorsally and lacks upper tail coverts, one of which is placed directly over each of the other 10 rectrices. The outer five pairs of the seven pairs of under tail coverts lie in a row directly under their corresponding rectrices, 2 through 6. The next proximal pair is under the central pair of rectrices but is displaced ventrally, while the central pair of coverts is slightly proximal to the central rectrices and is displaced dorsally. Conceivably, this central pair of coverts could be the original middle upper coverts that have migrated to a ventral position phylogenetically.

The anus is ringed by a single row of feathers ranging from 8 to 12 mm in length in the region dorso-lateral to the anus, and gradually decreasing in size to 3 to 5 mm ventral and dorsal to it. Small numbers of postventral feathers approach the ventro-lateral anal circlet as well as the outermost under tail coverts.

Capital tract. Both the frontal and loral regions are well feathered. Each loral region gives rise to several widely spaced rows that run over the upper eyelid and merge at its posterior edge. From the frontal region arises a central coronal area that extends posteriorly to merge with the occipital region, and a right and left line of superciliary feathers. Each superciliary row appears to be distinctly separated from the coronal region by a coronal apterium, and from the ocular feathers, with which it merges posterior to the eye, by a less well-defined superciliary apterium. Each ocular-superciliary row joins the occipital region, which extends postero-laterally around the head. Posteriorly, the occipital region merges with the cervical region of the spinal tract; laterally, each side merges with the postero-dorsal tip of an auricular region, and below that with a postauricular region. Antero-dorsal to the occipital–auricular junctions are the temporal apteria. These junctions also partially bound the postauricular apteria, which lie on each side of the head between the auricular region, which surrounds the ear, and the postauricular region. Each auricular region connects with the loral region antero-ventrally and with the ventral ocular feathers antero-dorsally. Each postauricular region runs ventro-anteriorly and joins the malar region.

Spinal tract. The spinal tract arises imperceptibly from the posterior occipital region, gradually narrowing and grading into a very narrow interscapular region. The dorsal region arises rather abruptly at the level of the posterior edge of the wing. It tends to be triangular with rounded corners, with the apex placed anteriorly. The posterior-lateral corners run out as a single row of widely spaced feathers and meet the anterior femoral tract. A truncate band slightly narrower than the dorsal region extends posteriorly as the pelvic region and then gradually flares laterally over the oil gland.

Humeral tract. This tract originates ventrally from the sternal region of the ventral tract. It passes dorsally over the leading edge of the wing and then runs posteriorly to the trailing edge where it meets the posterior patagial coverts.

Femoral tract. The femoral tract is a band three to four feathers wide that runs posteriorly around the body from the level of the anterior pelvic region to the level of the rectrices. It is ventral and approximately parallel to the main axis of the body.

Ventral tract. The well-feathered interramal region gives rise to a central band of feathers, the submalar region, which extends posteriorly and then splits into three bands at the level of the ear. Each distal extension merges laterally with the malar region, which arises from the distal undersurface of the bill and extends posteriorly. The resultant band extends dorsally and connects with the postauricular region. The midmalar region also merges weakly with the ventral auricular region. The malar and submalar regions are separated on each side by a submalar apterium. The central submalar division extends posteriorly along the neck where it merges with the cervical region. This region splits shortly into two ventro-lateral bands, which are weakly differentiated into three regions. The sternal region runs postero-laterally merging with the axillar region, which dips slightly beneath the wing and then rises to a small peak behind it. The abdominal region, after dipping slightly under the thigh, terminates posteriorly at the level of the anus.

Crural tract. The posterior surface of the tibia is well feathered ventrally and dorso-laterally. The sides and the medio-dorsal anterior surface are less densely feathered.

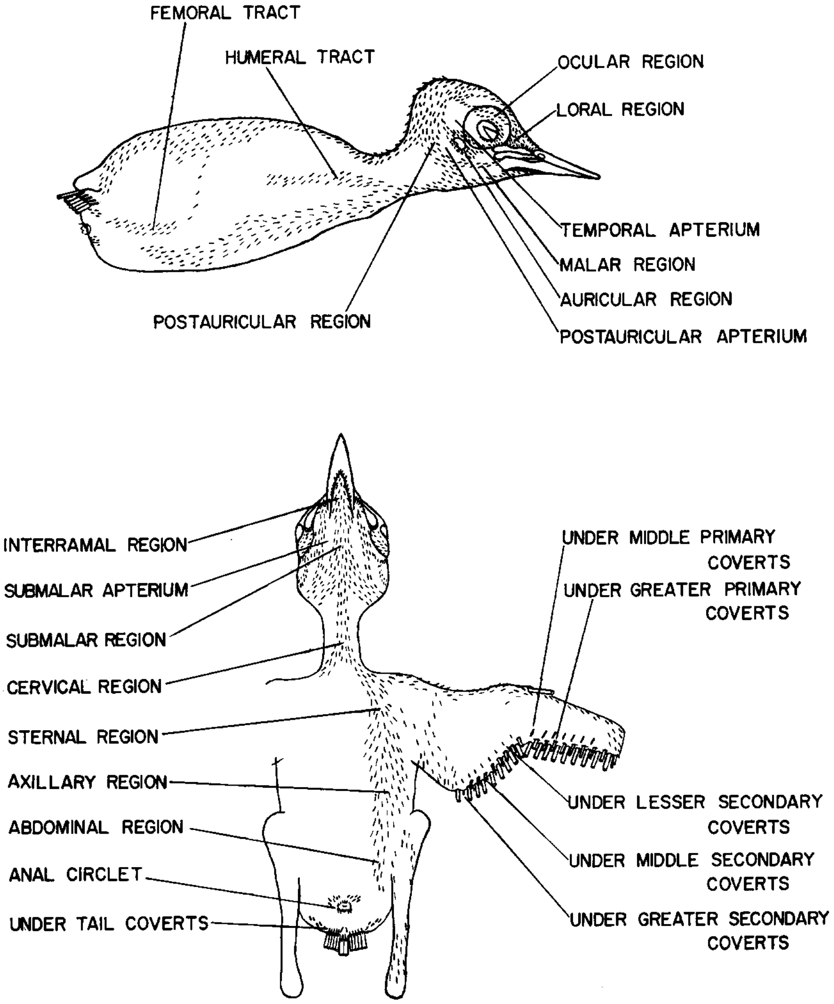

Figure 3. Definitive pterylography of the Orange-crowned Warbler. Above, lateral view; below, ventral view.

Comparison with the Yellow-throat

Stewart (1952) studied the Yellow-throat (*Geothlypis trichas brachidactylus*) in some detail. Its pattern of feather distribution is approximately the same as that of the Orange-crown. Many differences noted between the two probably result from the diagrammatic nature of Stewart's drawings. For example, a vestigial 10th primary and its covert, downy feathers at the base of the secondaries and the feathers in the postventral region are not pictured.

Other differences in alar pterylography are perhaps more real. The Yellow-throat has one more upper greater, one more under greater primary covert, and three to four more upper middle and two more under middle primary coverts than does the Orange-crown. Variation in under secondary coverts may be the result of interpretation. The under middle and under lesser secondary coverts described for the Orange-crown seem to correspond in position to the under greater and middle secondary coverts of the Yellow-throat. These were so designated in the Orange-crown because of the presence of an inconspicuous row of feathers alternating with the secondaries on the trailing edge of the wing. These small feathers, which were assumed to be under greater secondary coverts, could easily be overlooked. Only eight upper middle secondary coverts were noted in the Yellow-throat, however; despite any interpretation, this is one less than in the Orange-crown. There are seven pairs of upper tail coverts in the Yellow-throat as compared with five pairs in the Orange-crown.

The variation in the larger tracts is slight. The crural tract is more densely feathered in the Yellow-throat, but the upper and under patagial membranes are somewhat more naked. The humeral tract does not meet the sternal region ventrally, nor do the submalar, malar, and postauricular regions merge ventro-laterally. In the capital tract there is a corresponding absence of the superciliary apteria and the presence of the midcoronal apterium. There is a slight difference in the shape of the spinal tract; the cervical region is narrower, the dorsal region more rounded, and the pelvic region less flared posteriorly in the Yellow-throat.

DEVELOPMENT OF THE DEFINITIVE FEATHER TRACTS

For this study, two Orange-crowned Warbler (*V. c. lutescens*) nests were found in Tilden Park, Alameda County, California. They contained four and five unhatched eggs, respectively. The nests were examined frequently until the eggs hatched, and then once each day thereafter. Two nestlings were collected at one day of age, and one was collected each day thereafter until nine days, with the exception of the eighth day. These observations were supplemented by the examination of 18 study skins of individuals undergoing the postnatal molt. In contrast to the situation in the Blue-winged Warbler (Chapman, 1907), in which the down feathers do not begin to appear until the third day after hatching, young Orange-crowns possess their full complement of down at hatching. Therefore, developmental pterylography, or the ontogeny of the definitive feather tracts, consists essentially of the sequence of the postnatal molt. This molt is summarized in table 2, which lists the first observation of (1) pigment outlines of feathers that show prominently through the skin, (2) feathers breaking through the skin, and (3) feathers breaking their sheaths. The stages listed in the table are those most representative of the region at the time and do not necessarily describe the condition of every feather, nor do they imply any particular degree of advancement in relation to other regions of the same tract. For example, all regions of the spinal tract had broken through the skin by the fourth day after hatching. However, the degree of development of the protruding feathers showed clearly that the dorsal region was more advanced than the pelvic and cervical regions, which were more advanced than the interscapular. In earlier stages of development, rows of feathers may be recognized by small bumps made by the feather papillae in the skin. The outlines of the major feather tracts are quite distinct by the first day after hatching.

It is interesting to note that the rectrices, which are first to break the skin, are some of the latest feathers to break their sheaths. Feathers of regions of the head, postventral area, and under wing are also slow in breaking the sheaths. The under greater primary coverts have not yet appeared on the ninth day after hatching, though they are quite well developed in juvenal birds. Their failure to appear, at least as pigment lines, can probably be attributed to the fact that they are a pale yellow and

TABLE 2
SEQUENCE AND TIMING OF THE POSTNATAL MOLT

Days after hatching	1	2	3	4	5	6	7	9
Alar tract								
Primaries	P	1–6 S	7–9 S			T		
Up g p cov.			S			T		
Up m p cov.			S			T		
Un g p cov.								
Un m p cov.							S	
Secondaries	P		S		T			
Up g s cov.		P	1–4 S	5–8 S		T		
Up m s cov.			P	S			T	
Un g s cov.						P	T	
Un m s cov.					S		T	
Alula		P	S		T			
Carp. rem. cov.			S		T			
Marg. cov.			P	S				T
Patag. cov.			P			S		T
Caudal tract								
Rectrices	S							T
Up tail cov.				S			T	
Un tail cov.				P	S		T	
Anal circlet					S			
Postven. reg.				S				
Capital tract								
Frontal		P			S			
Loral							P	S
Superciliary		P			S		T	
Ocular			P		S			
Coronal		P		S			T	
Occipital		P		S			T	
Auricular				P		S		
Postauricular				P	S		T	
Malar				P		S		T
Spinal tract								
Cervical		P		S		T		
Interscapular		P		S		T		
Dorsal		P		S		T		
Pelvic		P		S			T	
Humeral tract		P		S		T		
Femoral tract		P		S		T		
Ventral tract								
Interramal				P		S		
Submalar			P		S			T
Cervical		P			S		T	
Sternal		P		S			T	
Axillary		P			S	T		
Abdominal				P	S	T		
Crural tract			P		S		T	

P indicates feathers visible under the skin as dots or lines of pigment; S, feather tips breaking through the skin; T, feather tips breaking their sheaths.

do not present enough contrast to be seen through the skin. Development of each region within all tracts begins centrally and proceeds laterally. Therefore, within some of the wider regions, as many as three of the four developmental stages may be seen at any one time. Also, as development proceeds there is a gradual change in the shape of the tracts (fig. 1).

When the young leave the nest approximately nine days after hatching, most of their feathers retain at least a basal sheath except the wings, which are more heavily sheathed, and the tail, which is still little more than a stub. In a study of the Blue-winged Warbler, Burns (in Chapman, 1907) found that pin-feathers were not obvious until the fifth day after hatching, although the birds were "well feathered" by the seventh day and "fully fledged" on the eighth.

In view of the great similarities between the definitive pterylographies of the Orange-crown and Yellow-throat, it is of significance to compare the developmental pterylography or postnatal molt between them. The Yellow-throat has well-developed down by the first day. In general, however, development begins later than in the Orange-crown, although it does not necessarily take longer to reach the stage of broken sheath tips. The timing and duration of development are approximately the same in both the alar, spinal, femoral, and crural tracts; it is earlier in the Yellow-throat humeral tract, later in the capital tract, and very much later in the caudal tract, especially the rectrices. This late development may be related to the extremely slow development of the rectrices in the Orange-crown, so that, presumably, definitive tail length is reached at approximately the same time in both. Different regions of the ventral tract develop before, after, and at the same time as the corresponding regions in the Orange-crown.

AGE DETERMINATION

The classes used in this study were delimited as follows. (1) Juvenile: a bird from hatching to the completion of the postjuvenal molt. This class includes birds in both the natal and juvenal plumages. (2) Immature: a bird that has completed the postjuvenal molt but not the first prenuptial molt. (3) First-year bird: a bird that has completed the first prenuptial molt but not the first postnuptial molt. Immatures that do not undergo a prenuptial molt are also designated as first-year birds after the completion of the prenuptial molt period for the species, and before the completion of their first postnuptial molt. (4) Adult: a bird that has completed at least one postnuptial molt.

Birds feathered only by the sparse natal down or by the juvenal plumage are easily recognized. The latter plumage is a grayish-white tinged with brown in *celata* and *orestera*, and so is obviously distinct from the other plumages that contain major amounts of yellow and green. The juvenal color of *sordida* and *lutescens*, although much more like that of the other age classes, is nevertheless distinct, being a grayer or "muddier" green. The difference in plumage color between the juveniles of each of the two pairs of subspecies is quite distinct. Such intraspecific variation in juvenal plumage color has also been noted in the Eastern Savannah Sparrow, *Passerculus sandwichensis savanna* (Sutton, 1935), although there it involved individuals of the same subspecies. In all subspecies of the Orange-crown, the juvenal feathers lack the luster found in immatures and adults and display a characteristic lax quality due to a reduced density of barbs along the shaft.

Subsequent age classes are not so easily recognized since "after the postjuvenal molt, immatures and adults are indistinguishable on the basis of plumage characters"

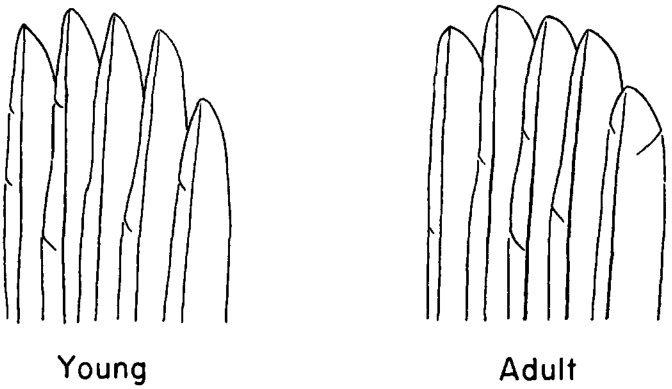

Figure 4. Dorsal view of primaries in the Orange-crowned Warbler, showing narrow, pointed feather tips of young (juvenal, immature, and first-year) birds, and wide, blunt tips of adults.

(Dwight, 1900). The use of degree of skull ossification, another common criterion for aging, is also of limited utility, primarily because so few study skins carry this information. Of the 2155 bird skins examined during a study of molt (Foster, 1967), the labels of only 33 carried skull-ossification data. The usefulness of this method is further limited in early-fall birds in which an ossified skull may signify either an immature or an adult. If six months is considered to be the minimum time necessary for ossification (Dwight, 1900; Chapin, 1917), this process may be completed as early as October, at least in *sordida* and *lutescens*, which breed earlier than the other races. Eggs of *lutescens* have been found as early as 2 April, and nestlings by 19 April. Eggs of *sordida* have been found on 26 March, and nestlings by 15 April. A fully feathered juvenal *sordida* was taken on 25 April (Chicago Natural History Museum, No. 148567); allowing three to four weeks for the postnatal molt, which may have been completed for a variable length of time, the hatching date may be placed no later than early April.

Although no data are available on the time required for skull ossification in the Orange-crown, a minimum period of six months is, if anything, too generous an allowance. A *lutescens* taken on 22 August that had completed approximately half of the postjuvenal molt showed a skull two-thirds ossified. If a two-month period is assumed to elapse between hatching and the beginning of the postjuvenal molt, and two months are allowed for the duration of the molt (Foster, 1967), then this bird may be assumed to have completed two-thirds of the skull ossification by three months of age. One *celata* taken on 9 September and two *lutescens* taken on 12 September had completed the postjuvenal molt and showed the skull two-thirds ossified.

Studies of other birds have also shown that skull ossification may be completed in six months or less. The skull of the House Sparrow (*Passer domesticus*) may be ossified in as little as three and one-half months (Harrison, 1960, 1961), although the majority complete ossification in six months (Nero, 1951; Harrison, 1960, 1961). The average time for total ossification in the Starling (*Sturnus vulgaris*) is six months, in the magpie (*Pica pica*) four to five months, in the Carrion Crow (*Corvus corone*) two and one-half to three months, and in the Rook (*Corvus frugilegus*) three to four months (Harrison, 1960, 1961).

Because of the lack of obvious plumage differences and the limited availability of reliable skull data, an attempt was made to develop other criteria for segregating adult and immature birds during the fall and spring. Since the juvenal flight feathers are retained until the first postnuptial molt (Foster, 1967), it was thought that they might exhibit characteristics different from those of flight feathers gained after a postnuptial molt. Dwight (1900) and Bent (1953) had previously used wear and fading as criteria to estimate the age of several species of parulids, especially in the spring and early summer.

In this study, Orange-crowns in juvenal plumage, or undergoing the postjuvenal molt, and those marked "skull unossified" provided a series of reliably aged fall young. Birds undergoing the postnuptial molt, the tips of whose flight feathers had broken from their sheaths, as well as birds in fresh plumage that were taken before 1 October and marked "skull ossified" provided a series of reliably aged fall adults.

The only consistent difference noted that could be used to segregate young and adults was the shape of the tips of the primaries (fig. 4). Immature birds have primaries with tips narrower and more centrally pointed than those of the adults, whose primaries tend to be both wide and blunt (almost truncate in *sordida*). There is also a tendency for the tips of the rectrices to be narrower and more pointed in immatures. These differences are found in all races. Also, within both age classes, the females tend to have primaries with wider tips than those of the males.

In addition to the differences in shape of the flight feathers, the plumage of immature and first-year birds wears much more extensively than that of adults. This is most evident in the flight feathers, although it also applies to body plumage. Immatures taken as early as late October and early November may show initial signs of wear in the broken and frayed barbs at the edges of the flight feathers. In contrast, comparable wear may appear in adults only as late as late April or May. Consequently, two categories, coincident with those defined on the basis of wing shape, may be defined on the basis of wear. In conjunction with wear, immature and first-year birds tend to fade to a greater degree than adults and to become paler and more "washed out" in appearance. New adult feathers also have a dull sheen or luster that is lacking in immatures.

The differences in luster, degree of fading, and durability between adult feathers and immature and first-year feathers possibly can be explained by a difference in their structure, such as Norris (1952) found in the Pine Warbler (*Dendroica pinus*), or may be due to the fact that juvenal flight feathers are carried for more than one year and may be from two to four months older than those of the adults. Juvenal flight feathers begin to break their sheaths between five and nine days after hatching in April, May, and June. Adults do not attain their new flight feathers until late July or August. Although there is no evidence that indicates it, differential wear due to different habits and habitats of the age groups is possible.

Preliminary analysis indicates that at least in certain subspecies, the age categories separated on the basis of the aforementioned criteria are verified by differences in wing and tail length. Additional information on size differences of age groups within the various races will be presented elsewhere.

SUMMARY

Down feathers of Orange-crowned Warblers (*Vermivora celata*) are variously distributed, the number in any region differing among birds and on the same bird between members of paired tracts. In each developing feather tract, growth begins centrally and moves laterally. The tracts are nearly completed when the stub-tailed young leave the nest approximately nine days after hatching, although most feath-

ers carry at least a basal sheath. Slight variations occur in definitive pterylography between juveniles and the older age groups. The pterylography of this species also differs from that of the Yellow-throat (*Geothlypis trichas brachidactylus*), the only other parulid whose pterylography has been studied in detail. Differences between these two species occur in the number of wing coverts, number of tail coverts, density of feathers in the crural and patagial areas, and configuration of several of the major tracts.

A method of aging the birds by use of plumage characteristics was established. Immature and first-year birds have primaries with tips narrower and more centrally pointed than those of adults, whose primaries tend to be both wide and blunt. Furthermore, feathers of immature and first-year birds wear much more extensively than do those of the adults.

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