THE CONDOR

VOLUME 69 | NOVEMBER–DECEMBER, 1967 | NUMBER 6

COMPARATIVE MOLT AND PTERYLOGRAPHY IN THE QUAIL GENERA *CALLIPEPLA* AND *LOPHORTYX*

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The aim of this study was to compare the molts and pterylography of four species of quails, Scaled Quail (*Callipepla squamata*), California Quail (*Lophortyx californicus*), Gambel Quail (*L. gambelii*), and Douglas Quail (*L. douglasii*), in order to obtain more information on their phylogenetic interrelationships.

Raitt (1961) has depicted the molts of California Quail, and Raitt and Ohmart (1966) have studied those of Gambel Quail. Although Wallmo (1956a) partially described the molts of Scaled Quail, he presented no data on molting of secondaries, rectrices, and the complete postnatal molt sequence, and therefore it appeared desirable to conduct a more detailed study of molt sequences for comparative purposes. All references made to California Quail pertaining to molt and plumages are from Raitt (1961) unless credited otherwise.

The only study of the pterylography of North American quails was conducted by Clark (1898). Since he had only a few specimens of each species and his descriptions were incomplete, a valid comparison required a thorough reëxamination of *Callipepla* and *Lophortyx*.

MATERIALS AND METHODS

This study of molts was based on captive birds of known age. On 1 July 1962, I obtained 29 eggs of Scaled Quail from the New Mexico State Bird Farm and Hardin McAdoo, both in Carlsbad. Twenty chicks hatched and were reared under artificial light. They were fed Purina Chick Starting Mash and chopped mustard greens until old enough to eat Purina Chicken Growing Mash. I made measurements of the growing remiges on each of the 20 chicks. Data were collected daily until the chicks were 15 days old, and at two-day intervals thereafter. All growing remiges on the left wing were measured. The flight feathers of the right wing were measured intermittently to check symmetry, and only slight differences were found between wings. The rectrices on the left side were measured at the same time as the remiges, except when feather losses necessitated study of the right side.

All measurements were made by placing a celluloid ruler beside the feather. The shaft was then straightened to its greatest length and measured from insertion to tip. The ruler was always placed on the proximal side of the remex to be measured.

Howard Campbell of the New Mexico State Department of Game and Fish kindly loaned 137 wings of immature Scaled Quail, from which I obtained data on fully grown primaries. These wings came from wild birds taken by hunters in southeastern New Mexico in 1961 and 1962. The criterion of Leopold (1939) was used to differentiate between immature and adult wings.

Preserved specimens used in this investigation were obtained as follows:

Callipepla squamata. Scaled Quail. Dona Ana County, College Ranch, 3 miles west, 5 miles north Las Cruces, New Mexico, 7 specimens. Durango, 10 miles north San Juan del Río, Chihuahua, México, 1 specimen. Total number, 8 specimens.

Lophortyx californicus. California Quail. Alameda County, Oakland, California, 4 specimens. San Luis Obispo County, 5 miles east Shandon, California, 4 specimens. Total number, 8 specimens.

Lophortyx gambelii. Gambel Quail. Dona Ana County, Mesilla Dam, New Mexico, 10 specimens. Dona Ana County, 2 miles east, 4 miles south Las Cruces, New Mexico, 6 specimens. Total number, 16 specimens.

Lophortyx douglasii. Douglas Quail. Mazatlan, Sinaloa, México, 3 specimens. Nayarit, 4 miles east, 4 miles north Tuxpan, Nayarit, México, 1 specimen. Total number, 4 specimens.

The birds were preserved in 10 per cent formalin. After a week or more in formalin, they were washed in running water overnight and then placed in 70 per cent ethanol for storage.

I examined the pterylae before and after clipping the specimens. One or two specimens of each species were left unclipped for study of feather morphology in various areas. The pterylae were plotted in full-sized quail outlines.

The number of secondaries was determined by inserting insect pins in the calami and dissecting out this portion of the wing. Dissections were also made on the ventral side of the joint between the humerus and ulna to identify the innermost secondary.

The criteria used to differentiate between the structural types of feathers were those of Chandler (1916) and Stettenheim (personal communication).

MOLTS AND PLUMAGES IN SCALED QUAIL

Natal Plumage

The newly hatched Scaled Quail chicks in this study were fully covered by natal down. Seven juvenal primaries showed as small pinfeathers, as described for California Quail.

Postnatal Molt

Postnatal molt commenced at hatching. Juvenal primaries 1 through 7 were present as pinfeathers, and within a few days after hatching, other regions of the body began to molt, following a definite sequence.

Body. At 10 to 11 days of age, pinfeathers appeared in the pectoral, humeral, and femoral tracts. Also, at this time, the upper and lower tail coverts were visible as pinfeathers. Around the twelfth day, the pinfeather sheaths ruptured, showing early brushes. By the fifteenth or sixteenth day, the area from the occiput to the upper tail coverts was covered by the brush tips of juvenal feathers, and the femoral and humeral tracts had well-developed plumage. Ventrally, in the anterior portion of the pectoral tract, the ruptured sheaths showed as large brushlike feather tips. During this period, the down along the leading edge of the wing was replaced with feathers. Both dorsal and ventral wing surfaces, between the leading edge and the developing secondary coverts, were still covered with down. Auricular pinfeathers appeared during the twenty-second and twenty-third days. The area between the leading edge of the wing and the secondaries had early brushes. Small pinfeathers were visible from the posterior end of the culmen back to the nape along the midline.

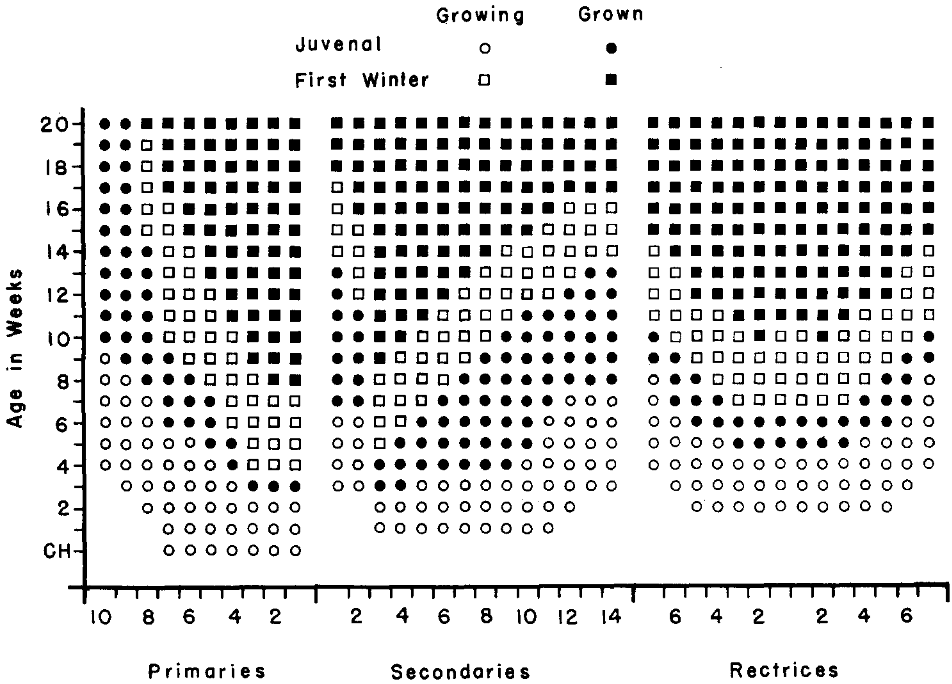

Figure 1. Summary of postnatal and postjuvenal molts of remiges and rectrices in Scaled Quail (*Callipepla squamata*). "CH" is condition at hatching. Method of presentation after Leopold (1943) and Raitt (1961).

The sides of the head remained covered with down. Pinfeathers developed around the periphery of the down-covered area of the head and progressively appeared toward the center. The region was not fully covered by juvenal plumage until the bird was about nine weeks old. The sides of the head were the last places to acquire juvenal plumage. A similar sequence has been reported for California Quail.

Secondaries. Pins of secondaries 3 through 10 were visible during the first week after hatching (fig. 1) with 11 becoming visible in the sixth to eighth day. Secondary growth in Scaled Quail was like that described for California Quail. Secondaries number 1 and 2 did not appear until the latter part of the second or early in the third week, while numbers 3 through 12 were present the second week. Secondaries 13 and 14 erupted about the same time as 1 and 2 (fig. 1). All juvenal secondaries were fully grown by the end of the seventh week.

Rectrices. In Scaled Quail the central 5 pairs appeared during the second week, whereas in California Quail 4 pairs erupted in the second week. There were 14 rectrices (7 pairs) in Scaled Quail. Pairs 6 and 7 erupted the third and fourth week, respectively. The inner 3 pairs reached full growth near the end of the sixth week, the other 4 pairs within the next three weeks, and all were grown by the end of the ninth week.

Primaries. The 20 Scaled Quail raised from hatching and 3 juveniles collected on the College Ranch all had 10 juvenal primaries. Wallmo (1956b) reported that ". . . in Scaled Quail, only the outer 7 primaries develop in the juvenile plumage."

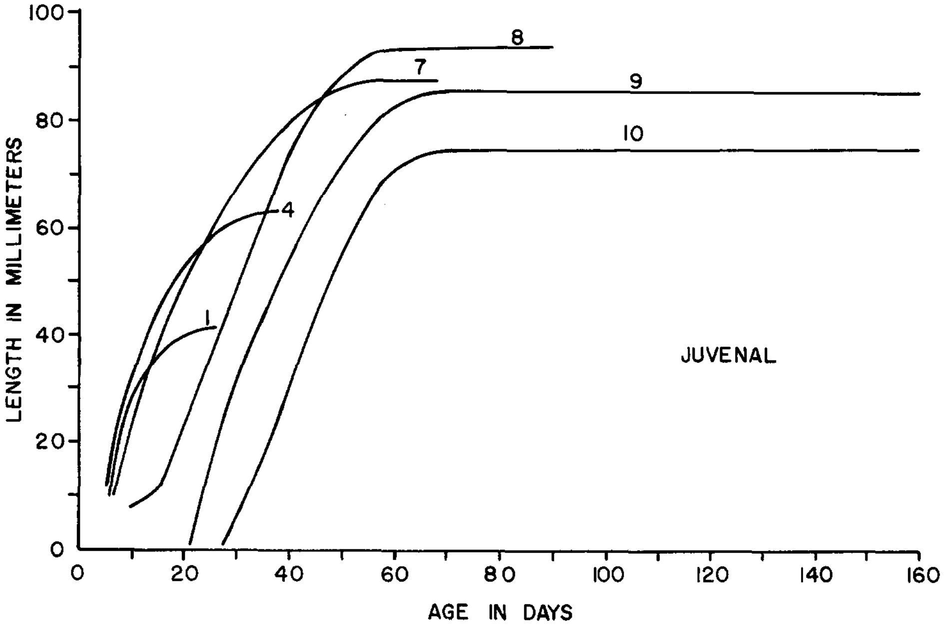

Figure 2. Growth curves of juvenal primaries of Scaled Quail. Each curve is based on mean data from 20 birds.

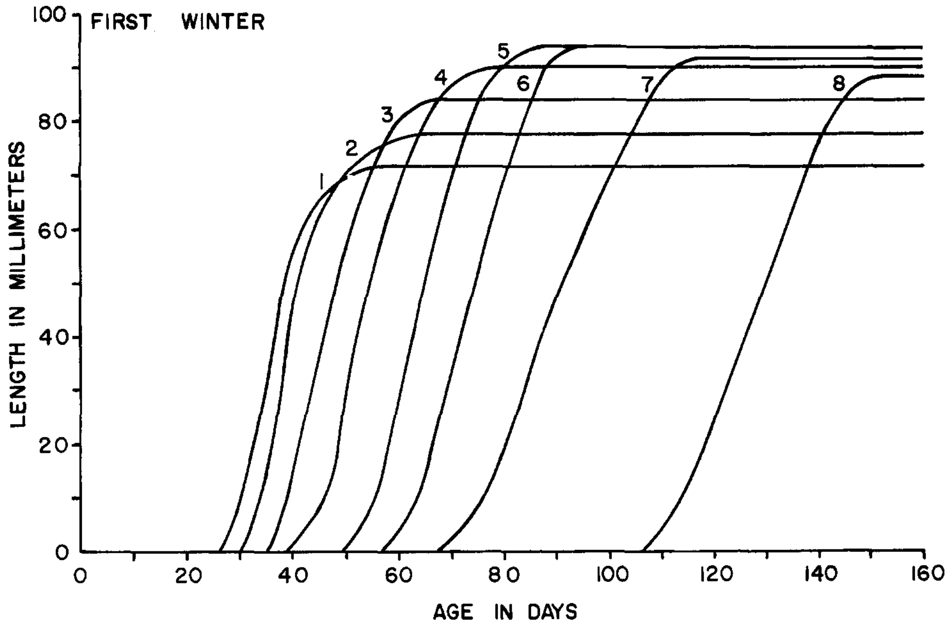

Figure 3. Growth curves of first winter primaries in Scaled Quail. Each curve is based on mean data from 20 birds.

TABLE 1

MEAN LENGTH OF FIRST WINTER PRIMARIES IN SCALED QUAIL

Primary no.	Source of data		
	Wallmo (1956a)	This investigation	
		Captives[a]	Hunter-kills[b]
1	81 mm	72.9 mm	72.5 ± 6.25 mm
2	86	78.6	78.1 ± 6.42
3	92	86.1	84.5 ± 6.15
4	105	90.4	91.1 ± 5.46
5	107	94.0	94.1 ± 5.11
6	108	95.4	94.0 ± 5.31
7	109	92.9	92.7 ± 5.58
8	108	87.6	89.1 ± 5.95
9	100	85.3	84.6 ± 4.88
10	91	75.6	74.4 ± 4.52

[a] Hand-reared captives; n = 20.
[b] Wings from SE New Mexico; mean ± 95% confidence interval, n = 137.

He also reported that juvenal primaries 4 through 7 were grown by the fourth week; but this was not the case with the 20 birds I studied. Primary number 4 reached full growth at a mean age of 28 days, 5 at 35 days, 6 at 38 days, and 7 at 42 days.

Juvenal primary remiges of all birds in this study were grown by the tenth week. Wallmo (1956a) reported growth of juvenal remiges as not complete until the twelfth week.

AGE DETERMINATION

The growth curves in figures 2 and 3 can be used for aging young Scaled Quail. Wallmo (1956a) published aging criteria for Scaled Quail, but lacked data to age birds in juvenal plumage.

POSTJUVENAL MOLT

Before the postnatal molt was completed in the head region, the postjuvenal molt commenced with the dropping of number 1 juvenal primary.

Body. The postjuvenal molt was found to agree with data reported by Wallmo (1956a) for Scaled Quail and by Raitt and Ohmart (1966) for Gambel Quail.

Primaries. Postjuvenal molt of the primaries began with the shedding of number 1 juvenal primary when the birds were 25 to 28 days old. About four days later, 2 was dropped, followed shortly by number 3. Postjuvenal primary molt progressed distally from 1 through 8 (fig. 1). Primaries 9 and 10 were not replaced in post-juvenal molt, but remained as juvenal remiges the first year.

Postjuvenal molt and primary growth were found to be similar to those of California Quail except that mean primary lengths were longer in Scaled Quail.

Mean lengths of immature Scaled Quail primaries reported by Wallmo (1956a) did not agree with measurements obtained in this study or those from 137 wings from southeastern New Mexico (table 1).

Secondaries. Numbers 3 through 6 were replaced in the postjuvenal molt before

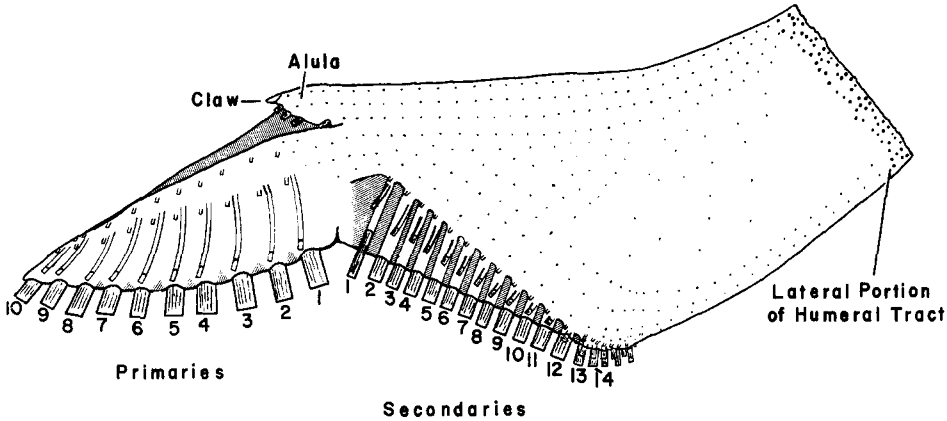

Figure 4. Dorsal view of a clipped wing showing feather relationships of the species in *Callipepla* and *Lophortyx*.

all juvenal secondaries were grown. Numbers 7 through 14 were replaced in the following weeks, and 2 was replaced in the twelfth week. Number 1 was molted and replaced in the fourteenth week.

Rectrices. Postjuvenal molt commences in the tenth week. The tail molt was centrifugal, with the seventh pair completing growth about the fourteenth week (fig. 1).

PTERYLOGRAPHY

For the pterylographic study a total of 36 alcoholic specimens of *Callipepla squamata*, *Lophortyx californicus*, *L. gambelii*, and *L. douglasii* were examined. Primarily, information on the above four species is presented in this paper, but two specimens of the Barred Quail (*Philortyx fasciatus*), two of Bobwhite (*Colinus virginianus*), two of Blackthroated Bobwhite (*C. nigrogularis*), and four of Montezuma Quail (*Cyrtonyx montezumae*) were examined.

Alar tract. The alar tract was the most difficult to study because of the large number of feathers and the proximity of one feather to another. Feather arrangements were the same in Scaled, California, Gambel, and Douglas Quail. A dorsal view of a wing showing feather relationships is shown in figure 4.

Primaries. Ten primary feathers were observed in all specimens examined. Relationships of the primaries to the wing bones are shown in figure 5.

Upper wing coverts. Ten upper greater, 10 upper middle, and 10 upper lesser primary coverts were found in the four species. Sharp (1957) reported only 9 greater primary coverts in the Bobwhite. Examination of two subspecies of Bobwhite Quail and two specimens of the Black-throated Bobwhite revealed 10 greater primary coverts. The tenth greater covert does not occupy interprimary space as do the other 9, but lies along the calamus of the tenth primary on the leading edge of the wing.

Middle primary coverts lie in the spaces between insertions of the greater primary coverts (fig. 4). Lesser primary coverts insert anterior to the middle coverts and cover the spaces formed by the insertion of the middle coverts.

The row of greater secondary coverts of the specimens in both genera continues around the bend formed by the ulna and humerus and up onto the humerus, as

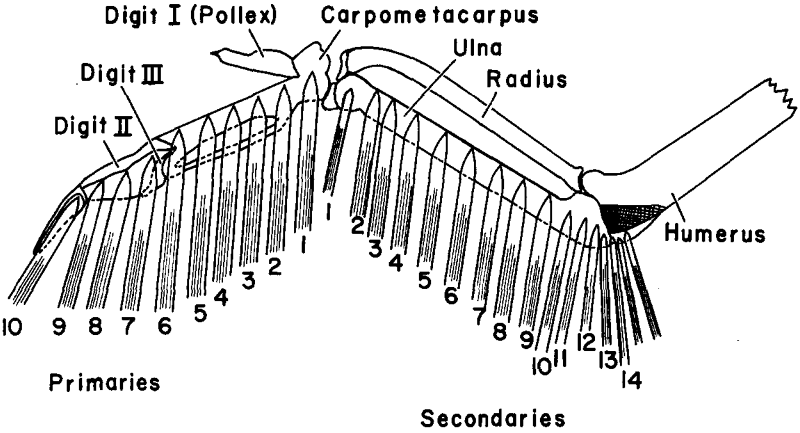

Figure 5. Dorsal view of remex relationships with wing bones found in *Callipepla* and *Lophortyx*. Nomenclature from Humphrey and Clark, 1961, but homology of digits is questionable (Montagna, 1945).

discussed by Van Tyne and Berger (1959:83–84). The middle secondary coverts and under greater secondary coverts converge with the secondaries and upper greater secondary coverts in the humerus-ulna articulation, making orientation and counts difficult.

Secondary coverts perform the same function as primary coverts in covering the spaces formed by insertions of the calami posterior to them.

Under wing coverts. Under coverts resemble upper coverts in number and arrangement.

Secondaries. Ventral and dorsal dissection revealed 14 secondaries in each of the species studied. Clark (1898) reported 15 secondaries for the species in *Lophortyx*, and Raitt (1961) reported 15 secondaries in California Quail. Secondary 14 lies at the articulation of the humerus and ulna. Feather number 15 either lies partially in the articulation or on the humerus. Dissection and examination of wings of the four species revealed the same feather arrangement (fig. 5).

Alula. Clark (1898:643) reported four flight feathers on the alula for all North American Quail. Sharp (1957), however, stated that there are 3 feathers on the alula in the Bobwhite, and Raitt (1961) implied the presence of 3 feathers on the alula in California Quail. Clipped specimens revealed 4 feathers on the alula, the first near the junction of the alula and the wing, the remaining 3 (numbers 2–4) close together just posterior to the claw (fig. 4). Number 1 feather was slightly smaller in diameter than the 3 more-distal ones and was inconspicuous (fig. 4). Numbering of feathers 1 through 4 was proximal to distal (Van Tyne and Berger, 1959).

Humeral tract. The humeral tract lies in the proximal portion of each wing (fig. 4). Feathers in this tract were arranged in irregular rows. No interspecific differences were apparent.

Dorsopelvic tract. The dorsopelvic tract was composed of the dorsal and pelvic tracts (fig. 6). They were continuous and were considered as one tract.

Clark (1898) reported for the North American Odontophorinae that the dorsal tracts and the upper cervical were continuous and do not form a dorsal apterium, but

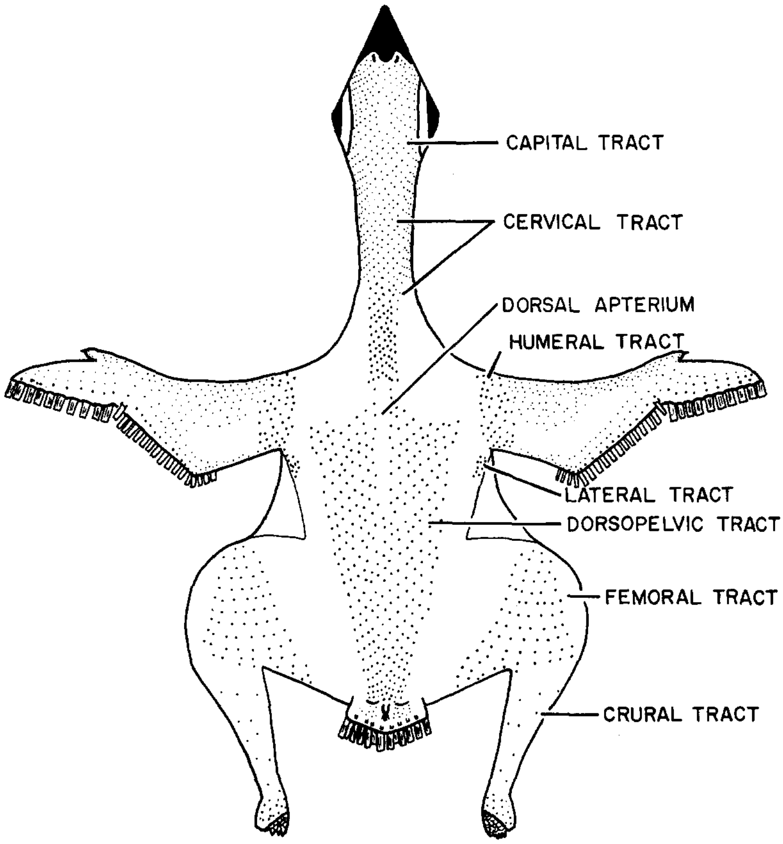

Figure 6. General dorsal view of pterylography in *Callipepla* and *Lophortyx*. Rectrices on right side show the condition in *Lophortyx*, those on left side show condition in *Callipepla*.

that some specimens of *Lophortyx* had a trace of a dorsal apterium. Brewer (1961) found a dorsal apterium in the Bobwhite. All species examined in this study possessed a dorsal apterium, which lies in the junction of the cervical and the dorsopelvic tracts.

The mean length of the dorsal apterium for Scaled Quail was 36 mm, for California Quail 37 mm, for Gambel Quail and Douglas Quail 33 mm. The width of the dorsal apterium in each of the four species was 4 mm. From 4 to 8 semiplumes split the apterium in each of the four species studied. Chandler (1916) reported that in Galliformes semiplumes are present only in the apteria. Thus the presence of semiplumes confirms that this region was an apterium.

The posterior portion of the interscapular tract was split by the dorsal apterium in each of the four species (fig. 6). The feathers lie in chevron patterns with 6 to 7 feathers composing a chevron. The absence of 3 feathers in the center of the chevron results in a 3 to 4 mm split in the posterior portion of this tract, forming the anterior portion of the dorsal apterium (fig. 6).

Partial or complete loss of the triangle-shaped areas on the anterolateral portion of the dorsal tract occurs in some individuals of each species. The pelvic tract was

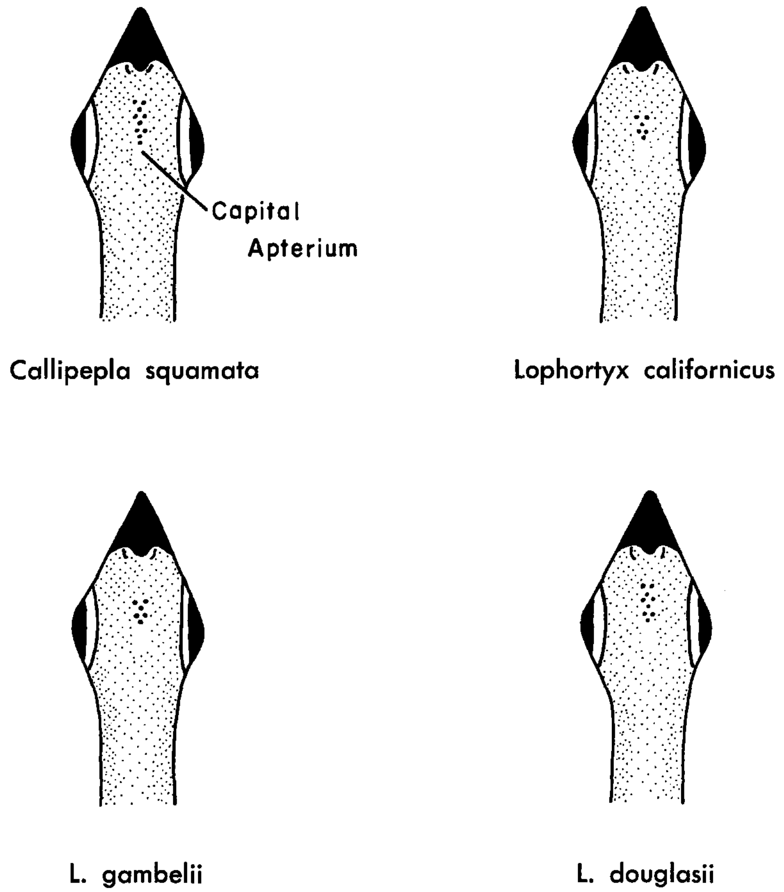

Figure 7. Crest pterylography in *Callipepla* and *Lophortyx*.

not demonstrable as a discrete unit. There were no differences between the pelvic tracts in the four species.

Down was found only on the oil gland and anal circlet on birds in first winter or adult plumage. All specimens in *Callipepla* and *Lophortyx* were alike in this respect.

Femoral tract. Feathers in the femoral tract were arranged in a roughly linear or semicircular pattern. Feathers were farther apart in the anterior portion of the tract, and the calami and shafts were not as heavy as those in the posterior region.

Lateral tract. Six to 10 feathers lying anteriorly to the femoral tract form the lateral tract (fig. 6). It showed no regular pattern among the species.

Cervical tract. This tract forms the anterior apex of the dorsal apterium and is a continuation of the posterior part of the capital tract. No interspecific variation in this tract could be found.

Capital tract. One of the few differences among the species was in the crest pterylography of the capital tract (fig. 7). Crest patterns in California and Gambel Quail were alike; both males and females exhibited the same pattern as found by

Clark (1898). It appeared that the calami and shafts of the plumes of California Quail were heavier than those in Gambel Quail. Clark (1898) reported 7 plumes forming the crest of Douglas Quail, but apparently ignored the 2 mottled brown and red feathers lying anterior to the main crest and posterior to the smaller black and white feathers which form a bridle behind the culmen. These 2 additional feathers should be considered crest feathers because they did not form part of the bridle, nor did they have the same coloring as the feathers lying laterally to the crest. Thus there were properly 9 feathers in the crest of Douglas Quail (fig. 7). Clark (1898) reported that in the crest of Scaled Quail ". . . there is, however, no special tract made by the feathers of the crest, which are always more numerous and softer than in the crest of the *Lophortyx*." I found a definite crest pattern in Scaled Quail (fig. 7). Feathers lateral and anterior to the crest were longer than the other feathers composing the capital tract, but the longer feathers were gray in color and were less marked than the white feathers forming the crest. The only difference in pterylographical arrangement between Scaled and Douglas Quail was the extra feather in Scaled Quail at the posterior portion of the crest. Douglas Quail differed from California and Gambel Quail in having 3 more crest feathers anteriorly.

A capital apterium occurs posterior to the crest in each species. This apterium measured about 4 mm long and 3 mm wide for the four species.

Crural. Feathers in the crural tract appeared to be circularly arranged around the leg, being farther apart anteriorly and closer together posteriorly. No interspecific differences in pattern were observed in this tract.

Rectrices. The numbers of rectrices differed among the four species. All Scaled Quail were found to possess 7 pairs, and all California Quail had 6 pairs. Among Gambel Quail that I examined, one female possessed 7 pairs, but the remaining 15 specimens had 6 pairs of rectrices. Each Douglas Quail had 6 pairs.

Arrangement of rectrices was alike in the four species. Pair number 1 was borne on a higher plane than the others. The remaining pairs, 2 through 7 (in Scaled Quail) or 2 through 6 (in *Lophortyx*), were on the same plane. Pair number 2 partially underlaid pair number 1 (fig. 6).

Upper rectrix coverts. Upper rectrix coverts varied in number from 4 to 6. They were arranged asymmetrically in some specimens.

A small group of feathers lying between the oil gland and rectrices may be considered lesser upper rectrix coverts, or a post pelvic tract. The pterylographic pattern and number of these feathers varied widely.

Under rectrix coverts. The under rectrix coverts also varied in symmetry, and number from 4 to 6.

Anterior to the under coverts and posterior to the cloaca was a tract termed by Clark (1898) as the post anal tract. This and the post pelvic tract varied in pattern and numbers of feathers.

Ventral pterylae. Four paired tracts comprise the ventral pterylae: ventral cervical, pectoral, sternal, and abdominal. These tracts were continuous with one another.

The ventral cervical tract was continuous anteriorly with the submalar and interramal region (terminology of Pitelka, 1945). Posteriorly, the ventral cervical divides a short distance anterior to the sternum, forming paired pectoral tracts which end just anterior to the leg attachment (fig. 8).

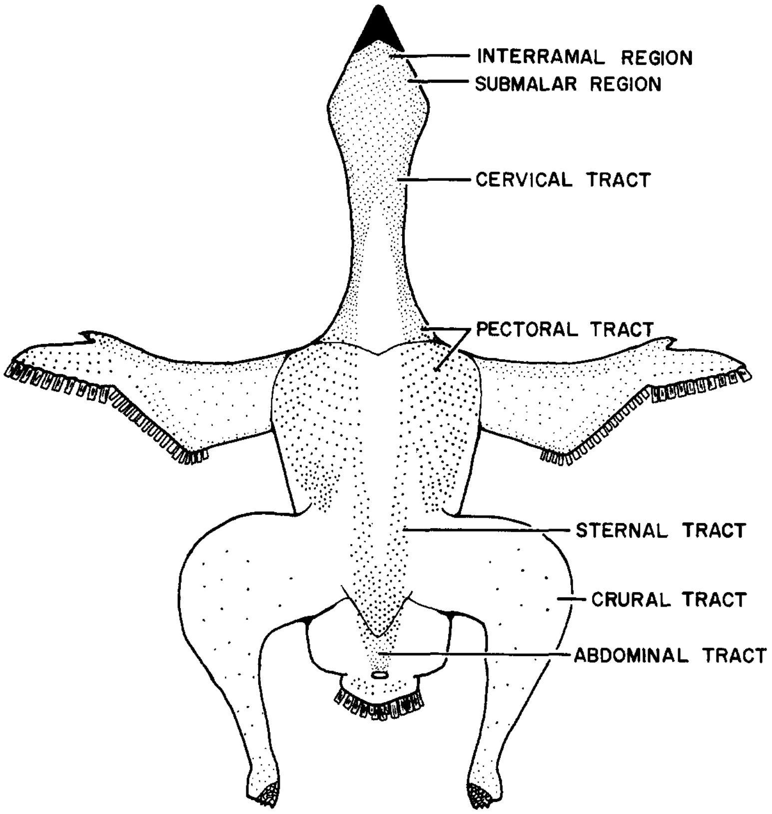

Figure 8. General ventral view of pterylography of the species in *Callipepla* and *Lophortyx*. Rectrices on left side show the condition in *Callipepla*, those on right side show condition in *Lophortyx*.

The abdominal tract extends anteriorly from the cloaca toward the sternum, where it bifurcates, forming paired sternal tracts. The sternal tracts continue anteriorly to connect with the pectoral tracts. Clark (1898) reported that "only the species in the genus *Cyrtonyx* had the ventral pterylae connected . . . the ventral tract (sternal) runs up on the breast so far as to connect with the anterior part of the sternal tract (pectoral) by 2 rows of feathers on each side." Sharp (1957) diagrammed the sternal tracts not connecting with the pectoral tracts in the Bobwhite. She also showed the abdominal tract ending at the posterior portion of the sternum. However, in the four species of this study, this was not the case (fig. 8). Two specimens of Bobwhite and two of the Black-throated Bobwhite showed patterns similar to those that I found in *Callipepla* and *Lophortyx*.

Measurements were made from the fork of the abdominal tract to the lip of the cloaca to determine if any difference existed between species. In Scaled Quail the mean distance was 30 mm, 21 mm in California Quail, 21 mm in Gambel Quail, and 21 mm in Douglas Quail. On the only specimen of Douglas Quail from Nayarit, México, the division of the abdominal tract was 8 mm from the cloaca. For all practical purposes, these quail are of equal size.

DISCUSSION

Postnatal and postjuvenal molt sequences in Scaled, California (Raitt, 1961), and Gambel Quail (Raitt and Ohmart, 1966) are similar, except for slight differences in timing and mean primary lengths.

It is unlikely that the disparities between results of this study and information reported by Wallmo (1956a and b) are due to geographic differences, because his sample of five birds came from the same source as part of the 20 birds used in this study. The 137 quail wings used to obtain mean primary lengths were of the same subspecies as those birds measured by Wallmo (1956a).

Differences in pterylography among the species of *Callipepla* and *Lophortyx* were found in the number of rectrices, crest, and the length of the abdominal tract. Clark (1898) found that "the number of rectrices is constantly 12, but in 2 skins of *L. californicus* (both females) there were only 10, and in 2 other females of the same species, there were 14." His report of two specimens of California Quail with 7 pairs of rectrices and the single Gambel Quail in this study with 7 pairs indicate the variability of rectrix numbers in the *Lophortyx* group. This variability in rectrix number lessens the generic strength of the character.

The crest pterylography of Douglas Quail resembles that of Scaled Quail more closely than does that of California or Gambel Quail. The plumes in the crest of Douglas Quail are not club-shaped and stiff as they are in California and Gambel Quail, but were softer and more like those of Scaled Quail. In California Quail and Gambel Quail barbs of the crest plumes were convoluted, but no convolution was exhibited in the crest feathers of Douglas Quail. The plumes were partially overlapping, but the barbs showed no convolution.

The difference in length of the abdominal tract between *Callipepla* and *Lophortyx* was apparently not reported previously. Some individual and/or geographic variation occurs in the length of the tract as was shown by the one specimen of Douglas Quail from Nayarit, México.

Ridgway and Friedmann (1946:265, 275) separated *Callipepla* from *Lophortyx* on three principal criteria: number of rectrices, convolution of crest plumes, and sexual dimorphism. They also reported that the sexes were alike in Scaled Quail, but differences were apparent when the birds were carefully examined. Females were brownish gray, whereas the males were deep blue on the back and nape. The male was bluer on the sides of the neck and breast than the female. The throat difference reported by Wallmo (1956a) also aids in sex identification. The degree of sexual dimorphism is not as great in Douglas Quail as it is in California and Gambel Quail. With added information, the generic strength of these characters is reduced.

Sibley (1957) discussed the excessive splitting of groups characterized by strong sexual dimorphism. He stated, "hybridization should be given far more weight as an indicator of close relationship than is given to secondary sexual characters as evidence of diversity." Intergeneric hybrids of *Callipepla* and *Lophortyx* have been found in the wild as well as produced in captivity (Jewett *et al.*, 1953; Gray, 1958).

More information is needed on comparative behavior, ecology, and hybridization, but in view of the similarities between *Lophortyx* and *Callipepla* in molt and pterylography, plus the formation of wild hybrids, it appears that generic separation of the two groups is questionable. Phillips *et al.* (1964) recently combined the two genera. Perhaps this is the best solution, but combining *Lophortyx* and *Callipepla* avoids the question of relationships of other closely related groups such as *Colinus*.

The taxonomic problems posed by relationship among these four species cannot be resolved without consideration of other related species presently included in still other genera.

SUMMARY

Molt data were obtained from 20 Scaled Quail (*Callipepla squamata*) chicks raised from hatching. Postnatal and postjuvenal molt sequences of the species are described.

Pterylographic data were obtained from eight clipped alcoholic specimens of Scaled Quail, eight of California Quail (*Lophortyx californicus*), 16 of Gambel Quail (*L. gambelii*), and four of Douglas Quail (*L. douglasii*). The only pterylographical differences among the four species were in crest patterns, rectrix numbers, and lengths of abdominal tract. A dorsal apterium, not previously recognized, was found in each of the four quail species examined.

Callipepla and *Lophortyx* should perhaps be combined, but not without consideration of related species in other genera.

ACKNOWLEDGMENTS

I am especially indebted to Ralph J. Raitt, Jr., for his advice and encouragement throughout the investigation. Grateful acknowledgment is extended to Gene M. Christman and Ward C. Russel for help in obtaining the California Quail used in the study. Thanks go to Howard Campbell for the loan of Scaled Quail wings from which measurements were made. David W. Francis provided an incubator and supplied valuable advice and literature. Hardin McAdoo furnished quail eggs for the study, and without this help I could not have obtained the molt data. I would like to thank Ralph J. Raitt, Stephen M. Russell, Roger C. Hungerford, and Lyle K. Sowls for suggestions and comments during the preparation of the manuscript.

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