# CRANIAL PNEUMATIZATION PATTERNS AND BURSA OF FABRICIUS IN NORTH AMERICAN SHOREBIRDS

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A study of age criteria in some species of North American shorebirds brought us to consider two of the best known techniques of age determination in birds, the size of the bursa of Fabricius and the degrees and patterns of skull pneumatization. The only attempt, known to us, to correlate bursa of Fabricius and gonadal development with the ossification of the skull is that of Davis (1947).

The bursa of Fabricius is a lympho-epithelial organ lying dorsally above the cloaca. At least in some species it has an opening in the cloaca. It reaches its maximum size at 4–6 months and then begins involution (Davis, 1947). By cloacal examination of the bursal pouch, it is possible to distinguish juvenile from adult individuals of some taxa of birds especially Anseriformes and Galliformes (Gower, 1939; Hochbaum, 1942; Linduska, 1943; Kirkpatrick, 1944). Unfortunately, in shorebird species, the bursa of Fabricius has no cloacal opening and thus cannot be used as an age criterion of living birds.

The pneumatization of the skull has been used as a criterion for estimating the age of birds by C. L. Brehm as far back as 1822 (Niethammer, 1968), but it was not generally used until the turn of the century (Serventy et al., 1967). Miller (1946) describes the skull ossification process as follows:

> "The skull of a passerine bird when it leaves the nest is made of a single layer of bone in the area overlaying the brain; at least, the covering appears single when viewed macroscopically. Later the brain case becomes double-layered, the outer layer being separated from the inner layer by an air space across which extend numerous small columns of bone. . . . Externally the skull of an immature bird appears uniform and pinkish in live or freshly killed specimens. The skull of the adult is whitish, due to the air space, and also it is finely speckled as a result of the dense white bony columns between the layers."

Nero (1951) and Serventy et al. (1967), in their respective studies of *Passer domesticus* and *Taeniopygia castanotis*, give examples of the pattern and rate of cranial ossification, from the juvenile to the adult; through a series of stadia ending with the complete pneumatization of the cranial roof in the adult before it is one year of age. This general rule, applied to the Passerines, admits some exceptions as mentioned by White (1948), Chapin (1949), Grant (1966), McNeil and Martinez (1967), and Payne (1969). Chapin (1949) also reported that "swifts and small sandpipers retained a condition throughout life that suggested immaturity. In some other larger birds the pneumatization of the cranial vault seemed to proceed very rapidly." Other workers like Chapin (1949), Verheyen (1953), Harrison (1958, 1964) were interested in the evolutive and adaptive significance of the fully versus incompletely pneumatized skull in birds.

Although cognizant of the fact that adult shorebirds have incompletely ossified cranial roofs, we undertook the present studies to ascertain whether or not the rate of skull ossification can be used as an indication of age in living and dead birds.

## MATERIAL AND METHODS

Series of shorebirds representing 21 species were collected in the Kamouraska region, Quebec, on the south shore of the St. Lawrence River in 1968 (spring, summer, and fall) and 1969 (spring), and on Magdalen Islands, Quebec, in fall 1969. A few specimens also were brought from Venezuela by the senior author in November 1968. These specimens were all prepared as study skins to examine the age characteristics, but the skull roofs were removed and kept separate for further examination of the unpneumatized areas. These skull vaults were then held against a window allowing light to illuminate the unpneumatized areas which were outlined.

The cloaca of each bird was excised and measurements (mm) were taken of the length (A) and height (B) of the fresh bursa of Fabricius; both measurements were used in the approximation of the size of the organ (AB). All birds which had a bursa of Fabricius were considered as immature. However, some birds which had a damaged cloaca were considered as immature if they bore juvenile feathers, especially among the wing coverts. In addition to the above mentioned specimens, we used measurements of the bursa taken by Miss Françoise Cadieux during another study.

## RESULTS AND DISCUSSION

*Bursa of Fabricius.*—The bursa of Fabricius was absent in yearling specimens taken in May and June. Thus the bursa is eliminated within the first year of growth. Moreover, two specimens from Venezuela in November, a Least Sandpiper (*Erolia minutilla*) and a Lesser Yellowlegs (*Totanus flavipes*), had almost fully regressed bursae, though their basic I plumage (first winter) still retained characteristic juvenal feathers. This suggests that, at least in some individuals, the involution of the bursa of Fabricius is completed in less than six months.

The measurements of the average size of the bursa ($\overline{AB}$), as shown in Table 1, indicate that the size of this structure diminishes from July to November. The best examples are the Semipalmated Plover (*Charadrius semipalmatus*), the Ruddy Turnstone (*Arenaria interpres*), the Greater Yellowlegs (*Totanus melanoleucus*), Lesser Yellowlegs, and the Short-billed Dowitcher (*Limnodromus griseus*). The same general trend appears in most of the twelve remaining species, but less clearly because of too small sample sizes.

*Cranial Ossification Patterns.*—All adult as well as immature skulls were characterized by the presence of unpneumatized "windows," the size of which shows great individual variations. Two different patterns of cranial pneumati-

TABLE 1

MEAN SIZE ($\overline{AB}$) (IN MM$^2$) OF THE BURSA OF FABRICIUS FROM JULY TO NOVEMBER IN NORTH AMERICAN SHOREBIRDS

| Species | July | August | | September | | October | | November* |
|---|---|---|---|---|---|---|---|---|
| | 16–31 | 1–15 | 16–31 | 1–15 | 16–30 | 1–15 | 16–31 | 16–30 |
| *Charadrius semipalmatus* | 45.2(2) | 49.0(1) | 37.5(4) | 30.1(5) | 27.6(5) | 20.1(7) | 16.6(3) | 27.5(2) |
| *Charadrius vociferus* | | 86.6(3) | 76.5(1) | 80.0(1) | 88.0(1) | | | |
| *Pluvialis dominica* | | | | 90.0(1) | | 48.0(2) | | |
| *Squatarola squatarola* | | | | | 136.0(1) | | 130.7(17) | 42.0(1) |
| *Arenaria interpres* | | | 82.0(4) | 60.1(6) | | 59.5(2) | | |
| *Capella gallinago* | | | 111.0(4) | | | | | |
| *Actitis macularia* | | 24.6(3) | | | | | | |
| *Totanus melanoleucus* | | | 140.3(6) | 133.5(18) | | | 70.3(4) | |
| *Totanus flavipes* | | 59.3(3) | 58.7(17) | 41.4(18) | | | 38.3(3) | 35.0(2) |
| *Calidris canutus* | | | 113.4(4) | 103.0(3) | | | | |
| *Erolia melanotos* | | | 36.0(1) | | | | 24.6(3) | |
| *Erolia fuscicollis* | | | | | | | 33.1(10) | |
| *Erolia minutilla* | | 26.3(28) | 23.1(24) | 26.9(8) | | | | |
| *Erolia alpina* | | | | | 30.0(1) | | 44.0(16) | |
| *Limnodromus griseus* | | 81.0(1) | 83.9(20) | 47.3(4) | | | | 55.6(5) |
| *Ereunetes pusillus* | 16.0(1) | 23.5(5) | 28.7(16) | 22.6(47) | 14.9(30) | | | 20.9(3) |
| *Crocethia alba* | | 25.0(1) | | 44.5(6) | 36.1(12) | | 40.6(8) | |

* Birds collected in Venezuela by the senior author in November 1968.
Note: Numbers in parentheses represent the sample size.

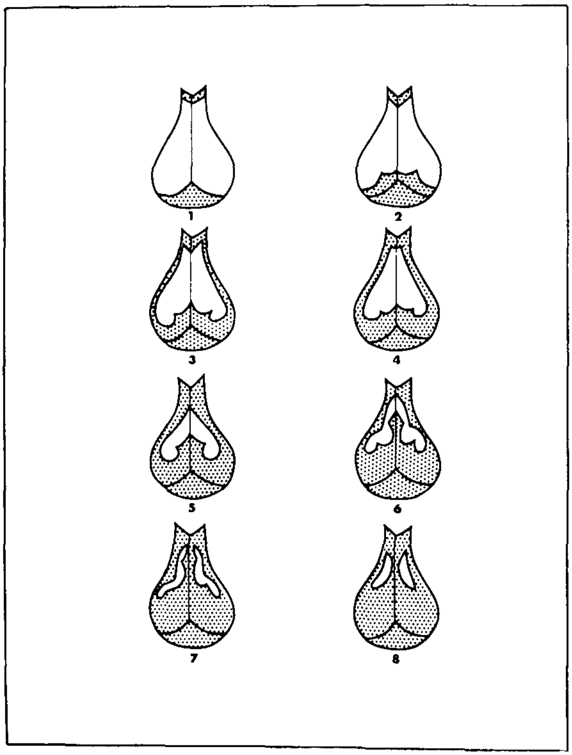

FIG. 1. Different stages of the type I of cranial pneumatization pattern in North American shorebirds. The clear areas represent the absence of pneumatization.

zation are found among the species of shorebirds belonging to the two families that were investigated (Charadriidae and Scolopacidae). The type I (Fig. 1) occurs in the majority of the species of both families (Table 2). It was divided into ten stages of degrees which do not clearly appear to be related to age but may be progressive. Four species had a different pattern that we are designating as type II (Fig. 2), in which we distinguished six consecutive stages. These species were the Common Snipe (*Capella gallinago*), Knot (*Calidris canutus*), Short-billed Dowitcher, and American Woodcock (*Philohela minor*).

Cranial pneumaticity cannot be used as an indication of the age of shorebirds. In fact, no clear correlation exists between the age of the birds and the extent to which their skulls are ossified (Tables 2 and 3); some immature (first year) birds have a skull roof as pneumatized as that of some adults.

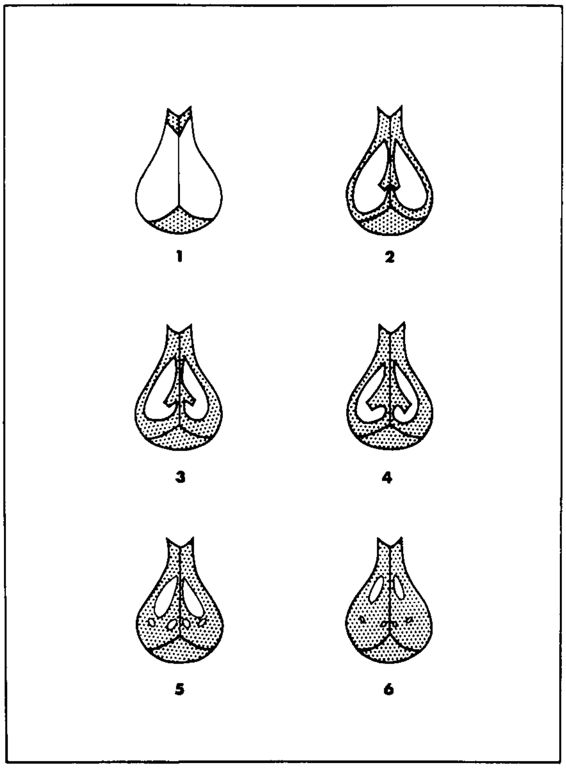

FIG. 2. Different stages of the type II of cranial pneumatization pattern in North American shorebirds. The clear areas represent the absence of pneumatization.

However, the different stages found in each type of cranial ossification are probably time progressive. Categories 7 and 8 in Table 2 are found almost exclusively in the adult age class, which suggests that there may be some age significance.

The extent of skull ossification attained in the shorebird species following the type I of cranial pneumatization (Table 2) varies between the genera and species. It seems obvious that the genera of Charadriidae attain a higher degree of cranial ossification than the genera of Scolopacidae. The stages or categories numbered 6, 7 and 8 are found almost exclusively in *Charadrius*, *Pluvialis*, *Squatarola*, and *Arenaria*, while the stages numbered 1 and 2 are found almost exclusively in the genera of Scolopacidae, especially in *Erolia*, *Ereunetes*, *Limosa*, and *Crocethia*. The two *Totanus* species seem to be intermediate between the two groups. It would be hazardous to draw conclusions about *Numenius*, *Actitis*, and *Tringa* because of the small sample sizes.

## Table 2

## Variation in the Extent of Skull Ossification in Shorebird Species Following the Type I of Cranial Pneumatization[a]

| Species | Age Status[b] | Stages of cranial pneumatization | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 |
| *Charadrius semipalmatus* | A | | 2.1(3) | 24.4(34) | 14.3(20) | 24.4(34) | 27.3(38) | 6.4(9) | 0.7(1) |
| | B | | | 17.5(7) | 17.5(7) | 50.0(20) | 15.0(6) | | |
| *Charadrius melodus* | A | | | | | | 100.0(1) | | |
| | B | | | | | | | | |
| *Charadrius vociferus* | A | | | | | 22.0(9) | 44.0(18) | 12.0(5) | 22.0(9) |
| | B | | | | 25.0(2) | 37.5(3) | 37.5(3) | | |
| *Pluvialis dominica* | A | | | | 100.0(1) | | | | |
| | B | | | 40.0(2) | 40.0(2) | 20.0(1) | | | |
| *Squatarola squatarola* | A | | | 36.3(12) | 48.4(16) | 6.0(2) | 6.0(2) | 3.0(1) | |
| | B | | | | 44.4(8) | 22.2(4) | 16.6(3) | 16.6(3) | |
| *Arenaria interpres* | A | | | 20.3(13) | 59.3(38) | 17.7(11) | 1.5(1) | 1.5(1) | |
| | B | | | 30.0(3) | 50.0(5) | 10.0(1) | | 10.0(1) | |
| *Numenius phaeopus* | A | | | | | 100.0(2) | | | |
| | B | | | | | | | | |
| *Actitis macularia* | A | | 16.6(1) | 16.6(1) | 33.3(2) | 33.3(2) | | | |
| | B | | 25.0(1) | 50.0(2) | 25.0(1) | | | | |
| *Tringa solitaria* | A | | | 50.0(2) | 50.0(2) | | | | |
| | B | | | | | | | | |
| *Totanus melanoleucus* | A | | | 22.5(16) | 57.7(41) | 14.1(10) | 4.2(3) | 1.4(1) | |
| | B | | | 16.0(4) | 72.0(18) | 12.0(3) | | | |

TABLE 2 Continued

| Species | Age Status[b] | Stages of cranial pneumatization | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 |
| *Totanus flavipes* | A | | | 61.5(24) | 28.2(11) | 7.7(3) | 2.6(1) | | |
| | B | 3.1(1) | | 62.5(20) | 25.0(8) | 7.7(3) | | | |
| *Erolia melanotos* | A | | | | 100.0(1) | | | | |
| | B | | | | 100.0(3) | | | | |
| *Erolia fuscicollis* | A | | 4.0(4) | 20.0(20) | 61.0(61) | 15.0(15) | | | |
| | B | | | 11.1(1) | 55.5(5) | 33.3(3) | | | |
| *Erolia minutilla* | A | 2.8(5) | 14.8(26) | 26.3(46) | 36.6(64) | 18.2(32) | 0.5(1) | 0.5(1) | |
| | B | 7.0(4) | 24.5(14) | 24.5(14) | 36.8(21) | 7.0(4) | | | |
| *Erolia alpina* | A | | | | 100.0(2) | | | | |
| | B | 6.3(1) | | 25.0(4) | 68.7(11) | | | | |
| *Ereunetes pusillus* | A | | 26.6(66) | 42.3(105) | 29.1(72) | 2.0(5) | | | |
| | B | | 47.3(45) | 34.7(33) | 17.9(17) | | | | |
| *Limosa haemastica* | A | 35.0(14) | 5.0(2) | 15.0(6) | 32.5(13) | 12.5(5) | | | |
| | B | | | | | | | | |
| *Crocethia alba* | A | | | 65.8(23) | 17.1(6) | 17.1(6) | | | |
| | B | 20.0(2) | 40.0(4) | 10.0(1) | 10.0(1) | 20.0(2) | | | |

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[a] The variation is expressed in percentage (and number of examined skulls) falling in each stage of cranial pneumatization.

[b] A = Adult birds without bursa of Fabricius; B = First year birds with bursa of Fabricius.

TABLE 3

VARIATION IN THE EXTENT OF SKULL OSSIFICATION IN SHOREBIRD SPECIES FOLLOWING THE TYPE II OF CRANIAL PNEUMATIZATION[a]

| Species | Age Status[b] | Stages of cranial pneumatization | | | | | |
|---|---|---|---|---|---|---|---|
| | | 1 | 2 | 3 | 4 | 5 | 6 |
| *Capella gallinago* | A | | | | 33.3(1) | 33.3(1) | 33.3(1) |
| | B | | | | | 100.0(4) | |
| *Calidris canutus* | A | 2.3(1) | 45.5(20) | 25.0(11) | 6.8(3) | 20.5(9) | |
| | B | 42.8(3) | 28.6(2) | | 14.3(1) | 14.3(1) | |
| *Limnodromus griseus* | A | | 31.8(8) | 23.8(5) | 28.5(6) | 9.5(2) | |
| | B | 0.7(1) | 21.2(30) | 29.1(41) | 34.0(48) | 12.1(7) | 2.8(4) |

[a] The variation is expressed in percentage (and number of examined skulls) falling in each stage of cranial pneumatization.
[b] A = Adult birds without bursa of Fabricius; B = First year birds with bursa of Fabricius.

A few workers have attempted to find the evolutionary and/or adaptive significance of the fully versus incompletely pneumatized skull vault in birds. Chapin (1949) mentioned that "the skull-roof of most woodpeckers is composed of single layer of bone, thicker and stiffer than that seen in the young of Passeres." He "considered this as a direct adaptation to their hammering and the use of the beak as a chisel." As far as Verheyen (1953) is concerned:

> "les os dermiques pneumatiques présentent . . . l'avantage de mieux résister aux vibrations et de mieux amortir les secousses que les lames épaisses qui manquent de souplesse. Aussi la plupart des espèces arboricoles (donc celles qui, au cours de leurs évolutions aériennes, peuvent se cogner la tête contre divers obstacles) possèdent-elles un crâne pneumatique tandis que celles qui vivent sur l'eau ou qui évitent les terrains boisés ont un dermatocrâne incomplètement pneumatisé."

On the other hand, according to Harrison (1958), the skull pneumaticity of birds is related to their mode of life, depending upon whether they are swimming or diving birds, hammering species, swift or slow fliers. Harrison (1964) believed that birds "showing diminished pneumatisation can be loosely classified as "swift fliers" and include such species as the gallinaceous birds (Galliformes) which accelerate rapidly, sandgrouse (Pteroclididae), most of the limicoline birds (Charadrii), and the swifts *Apus apus* and *A. affinis.* An exception among the Charadrii is the slow-flying Jack Snipe *Lymnocryptes minimus*, which develops complete pneumatization." The present results indicate that the Killdeer, American Woodcock, Common Snipe, Knot, and Short-billed Dowitcher are the shorebird species that show less unpneumatized skulls: some specimens of these species had almost fully ossified skulls, almost as pneumatized as that of the Jack Snipe. One fact is against Harrison's theory of swift versus slow fliers. The Common Snipe, while performing its aerial nuptial evolutions, dives to the ground from at least a hundred yards and then suddenly, before swooping down upon the ground, turns back abruptly and starts again the same aerobatics. The Killdeer, American Woodcock, Common Snipe, Knot and, even the Jack Snipe (Bent, 1927, 1929), also perform aerial evolutions at the time of breeding, although they are less spectacular. This means that these species are subjected to a heavy acceleration followed by an equal deceleration, and according to Harrison's theory, a much less fully ossified skull would be advantageous.

On the other hand, we would be tempted to make a comparison between the incompletely ossified skull of shorebirds and the ones of the woodpeckers. According to Harrison (1964), "the partial absence of skull pneumatization in woodpeckers suggests that this type of skull may be relatively heavier and therefore a more effective hammer." Shorebirds, excluding plovers and turnstones, feed by probing and making series of holes in sand and/or mud, so it may be that a heavier type of skull could possibly be of some advantage.

## SUMMARY

The involution of the bursa of Fabricius begins in the autumn and is fully achieved by the end of the winter in all studied species. The presence of this organ may be used as an age criterion in shorebirds collected during fall migrations. The degree of cranial ossification does not permit distinguishing young birds from adults, since large "windows" persist generally in adult was well as in juvenile shorebirds. Two different patterns of cranial ossification are found in shorebirds; one applies to most species while the other one is found in the American Woodcock, Common Snipe, Knot, and Short-billed Dowitcher. The genera of Charadriidae attain a higher degree of cranial ossification than the genera of Scolopacidae. The authors also discuss the adaptive value of the skull pneumaticity.

## ACKNOWLEDGMENTS

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## REQUEST FOR INFORMATION: SANDERLING

For the past two years, the Long Point Bird Observatory has undertaken a study on the relationship between fat deposition and fall migration in the Sanderling. In conjunction with this study, a large number of birds have been color-marked and sightings of these marked birds away from Long Point have indicated that most of the birds fly directly from the study area to the East Coast.

During 1972, the Observatory hopes to individually color-mark and color-code several hundred Sanderling in order to further investigate this phenomenon.

Birds will be feather-dyed on the breast and abdomen with one of four colors: red, yellow, green, or white (no color) ; according to the percentage of the bird's total body weight attributable to fat.

The birds will be wing-tagged on *each* wing with semi-permanent wing tags of the following colors: black, blue, brown, green, red, orange, yellow, and white. The wing-tagging will individually identify each bird.

Birds banded on the right leg will be adults and those banded on the left leg will be immatures.

The Observatory would be pleased if anyone sighting these birds would report the following information to us: Date of sighting; Location (including nearest city or town) ; Color of feather-dye on the breast and abdomen; Color of the wing tag on the right wing; Color of the wing tag on the left wing; Leg on which the bird is banded.

Co-operators will receive a short note explaining the project's application to the preservation of the Long Point peninsula in a natural state and the date on which the bird was last seen on Long Point. Reports of marked birds should be sent to: Long Point Bird Observatory, Long Point, Ontario, CANADA.