J. Field Ornithol., 54(1):58–66

A LABORATORY STUDY OF CRANIAL PNEUMATIZATION IN INDIGO BUNTINGS

By Paul B. Hamel, Jeffery L. Beacham, and Anna E. Ross

Since the early work of Dwight (1900) and Miller (1946), examination of cranial pneumatization has been an important means of aging live passerine birds. Studies of known-age birds (Nero 1951, Serventy et al. 1967, Biur and Thapliyal 1972) show that aging birds with a precision of plus or minus 30 days is unlikely. Consequently, age determinations, on the basis of cranial pneumatization alone, will be limited to specification of the year of hatching (U.S. Fish and Wildlife Service and Canadian Wildlife Service 1978).

Studies of cranial pneumatization (ossification) have been conducted on only a few species. Without systematic examination of the same individuals over time, it is very difficult to detail the pattern of pneumatization. Data for these studies have been gathered in 3 ways: (1) capture/recapture field studies, which have the disadvantage of small sample sizes and uneven distribution of samples over time (Nero 1951, Schneider 1981); (2) studies of serially sampled populations, which have the disadvantage that any individual is examined only once and so cannot yield direct information on the rate of pneumatization (Hogstad 1971, Stewart 1972, Winkler 1979, Yunick 1977, 1979a, 1980, 1981a,b); (3) laboratory studies of known-age individuals killed at regular intervals, which have the same disadvantage of not providing direct information about individual rates (Serventy et al. 1967, Biur and Thapliyal 1972).

Recent work on this subject has been directed toward determination of typical patterns and rates of cranial pneumatization. Yunick (1979b) recognizes 2 patterns of cranial pneumatization, median-line and peripheral pneumatization, suggesting that the patterns may be species-specific in most cases. In median-line pneumatization, the mid-sagittal line pneumatizes before the parietal region, leaving 2 large unpneumatized patches ("windows") on the frontal and parietal bones. In peripheral pneumatization, the posterior parietal region of the cranium pneumatizes before the mid-sagittal line. Winkler (1979), in an extensive review of this topic, presents diagrams of several patterns of pneumatization. His fundamental type (Grundtypus) resembles the peripheral pattern of Yunick (1979b). Pattern or timing of cranial pneumatization has been examined in a few species (Chapin 1949, Hogstad 1971, Johnston 1958, Leberman 1970, Mellencamp 1969, Nero 1951, Schneider 1981, Serventy et al. 1967, Smith 1979, Stewart 1972, Verheyen 1953, White 1948, Yunick 1977, 1979b, 1981a, b).

As a part of studies of the social and migratory behavior of Indigo Buntings (*Passerina cyanea*), this work reports on the pattern and rate of cranial pneumatization based on repeated examinations of crania of captive individuals.

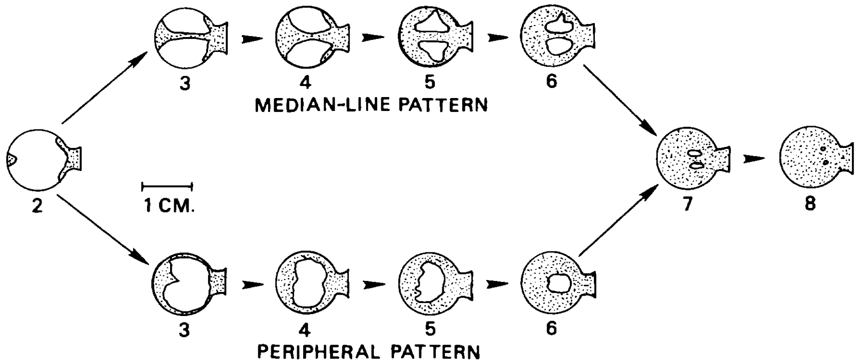

FIGURE 1. A summary of the sequence of cranial pneumatization in Indigo Buntings. Crania are depicted in dorsal view with the anterior to the right. Pneumatized areas are stippled. The numbers identify the pneumatization stages defined in Table 2.

METHODS

Indigo Buntings were captured in mist nets during autumn 1980 on the Clemson University campus, Clemson, South Carolina. Sixty-five presumptive hatching-year birds were kept under artificially maintained, seasonally appropriate photoperiod (from capture until 20 December 1980 at 35°N photoperiod and from 21 December 1980 until 4 March 1981 at 10°N photoperiod). Individually caged, the birds were acclimated to a wild bird seed diet and were transferred gradually to an ad libitum diet of Purina Layena Checkerettes® (Calcium not less than 3.1%) and water. An attempt was made to balance the numbers of males and females in the samples at the time of capture by using the plumage criteria of Johnston (1967) to determine sex. Definitive sex determination was made by examining plumage during or after the prealternate molt in February 1981.

All birds were "skulled" at monthly intervals from the time of capture until 6 April 1981. The birds' feathers were wet with a very dilute solution of isopropyl alcohol in water. The cranium, visible beneath the skin, was examined under a Luxo 1.5 × illuminated magnifier. Unpneumatized "windows" were recorded on life-sized outline drawings of dorsal, lateral, and posterior views of an Indigo Bunting cranium. When unpneumatized "windows" were small enough to be measured accurately, their greatest length and width were measured to the nearest 0.5 mm with a plastic ruler. A subsample of 30 birds was examined weekly. The study was terminated on 6 April, because the extent of pneumatization had not changed for at least 30 days in any of the remaining unpneumatized individuals. Four of 17 birds whose crania were not completely pneumatized on that date were kept and periodically examined in the summer and autumn of 1981 until their crania were completely pneumatized.

TABLE 1. Patterns of cranial pneumatization seen in captive Indigo Buntings.

	Median-line		Peripheral		Total	Percent
Male	13[1]		3		16	53.3
Female	8		6		14	46.7
Total	21	70%	9	30%	30	

[1] Number of individuals in the subsample.

RESULTS

The subsample contained 16 females and 14 males. Of the remainder, 20 were males, 14 were females, and the sex of the last bird could not be determined because it escaped.

A detailed sequence of views of the shape of unpneumatized "windows" is presented in Fig. 1. Indigo Buntings showed both median-line and peripheral patterns of cranial pneumatization (Table 1). The distribution of pneumatization patterns within the sex classes was different. Females showed both patterns of pneumatization in equal proportions. In males, the median-line pattern predominated (the confidence limit at $P = .05$ did not include 50%, Rohlf and Sokal, 1969:208, Table W).

At the completion of the study, the original drawings were examined and grouped into 7 categories (stages) based on extent of completion of pneumatization (Fig. 1). Definition of the stages is presented in Table 2. Stages 2 through 5 are defined visually because the unpneumatized "windows" are too large to measure accurately on a living bird. Stages 6 through 8 are defined by measurement.

The first completely pneumatized cranium in the sample was observed on 11 October 1980, but because of its advanced stage of pneumatization (stage 6) at the time of capture (4 October), we believe this bird was already a year old (see below). Of the hatching-year birds examined, the first date of complete pneumatization was 25 October 1980. By 3 November, three additional birds had completed pneumatization. Figure 2 shows the change in the number of birds at each stage of cranial pneumatization for monthly intervals from October to February.

Twenty birds did not have completely pneumatized crania at the end of the study. Three of these birds had only very tiny "pinhole" (.5 mm or less) unpneumatized "windows" (stage 8) and can be considered to have completed pneumatization. The remaining 17 (26%: 5 female, 12 male) had moderate to very large unpneumatized "windows" (stages 5–7). In these cases, the process may require the 12 months or more to reach completion that Johnston (1967) reports for this species. In fact, none of the 4 birds in this "delayed" group had completed pneumatization when checked on 7 September 1981. By 20 October 1981, 3 of these birds had completed pneumatization. The remaining bird, a female, had not advanced beyond stage 7 (unchanged since 23 February 1981).

TABLE 2. Definitions of stages of cranial pneumatization in Indigo Buntings. See Fig. 1 for diagrams of the stages.

Stage (code)	Definition developed in this study
2	Little or no pneumatization, or a small triangular pneumatized area in the occipital region. Corresponds to Winkler's (1979) stages 1 and 2.
3	Large triangular pneumatized area in the occipital region; may include completed penumatization along the mid-sagittal line; anteriorly, pneumatization reaches the posterior margin of the orbits. Corresponds to Winkler's (1979) stage 3, in part.
4	Anteriorly, pneumatized area extends posteriorly and laterally to the posterior margin of the orbits; posteriorly, the entire occipital region and posterior portions of the parietals are pneumatized; laterally, the pneumatized area is not visible dorsal to the attachments of jaw musculature. Corresponds to Winkler's (1979) stages 3, in part, and 4, in part.
5	At this stage the entire borders of the unpneumatized "windows" are visible, but accurate measurement is not possible because of the curvature of the skull. Corresponds to Winkler's (1979) stage 4, in part.
6	Unpneumatized "windows" are measurable, and at least 5 mm in their longest dimension. Corresponds to Winkler's (1979) stages 4, in part, and 5, in part.
7	Unpneumatized "windows" are less than or equal to 4 mm in both dimensions. Corresponds to Winkler's (1979) stages 5, in part, and 6, in part.
8	Unpneumatized "window(s)" are less than 1 mm in at least one dimension. Corresponds to Winkler's (1979) stage 6, in part.
9	Pneumatization complete. Corresponds to Winkler's (1979) stage 7.
0	Pneumatization stage undeterminable because of molt, hemmorhage, or other reason.
1	Cranium incompletely pneumatized, Stage unknown.
blank	Cranium not examined.

Based on this information, we suggest the following criteria for aging Indigo Buntings on the basis of cranial examination only:

1. Before 1 October:
   a. Cranium pneumatized (unpneumatized areas .5 mm or less, stage 8–9): age = AHY (after hatching-year);
   b. Length or width of unpneumatized area greater than .5 mm and less than 5 mm (stage 6–8): age = SY (second year);
   c. Unpneumatized area greater than 5 mm (stage 1–5): age = HY (hatching-year).
2. 1–20 October:
   a. Cranium pneumatized (stage 8–9, as above): age = AHY;
   b. Length or width of unpneumatized area greater than .5 mm and less than 5 mm (stage 6–8): age = U (unknown);
   c. Unpneumatized area greater than 5 mm (stage 1–5): age = HY.
3. After 20 October:
   a. Cranium pneumatized (stage 8–9, as above): age = U;

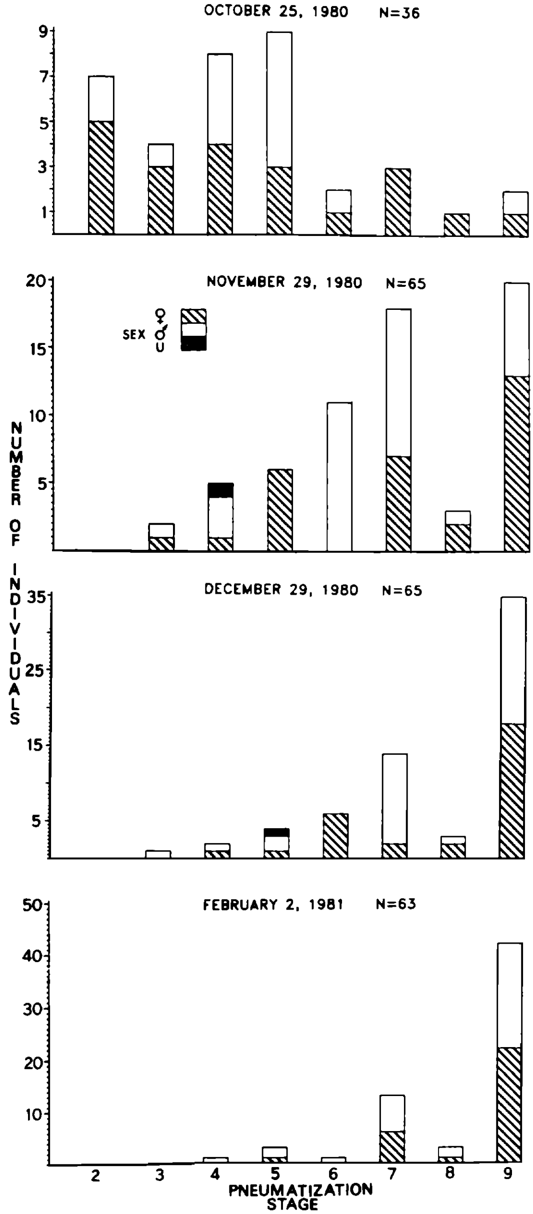

FIGURE 2. Proportion of captive Indigo Buntings at each stage of cranial pneumatization for monthly intervals from October to February. Numbers on the horizontal axis identify the stages defined in Table 2. Vertical axis = number of birds at each stage. Open portion of the histogram = male birds; slanted lines = female birds; dark = one bird of unknown sex. N = sample size.

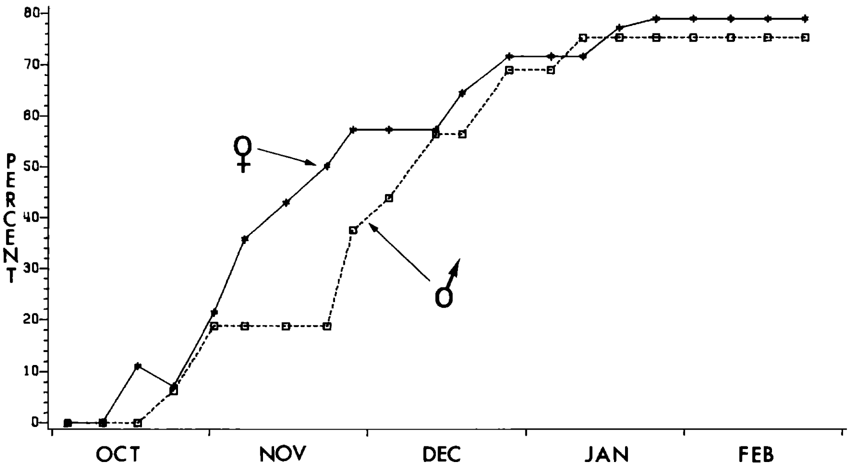

FIGURE 3. Percent of captive Indigo Buntings with completely pneumatized crania on each sampling date. Horizontal axis = date; vertical axis = percent of birds (sample sizes: females = 16; males = 14) with pneumatized crania (stage 9). Solid line = female birds; dashed line = male birds.

   b. Unpneumatized area larger than .5 mm (stage 1–8): age = HY (One of 65 birds in our sample was incorrectly aged here, see above).
4. After 1 January:
   a. Cranium pneumatized (stage 8–9, as above): age = AHY;
   b. Unpneumatized area larger than 0.5 mm: age = SY.

Additional information can be inferred from examination of the plumage as well (Johnston 1967).

Figure 3 shows the percent of birds in the subsample whose crania were completely pneumatized at each sampling date during the study. Regression analyses of the proportions of crania pneumatized in males and females were performed. The rates of pneumatization of males and females were not different (the slopes were not significantly different), but male cranial pneumatization was delayed compared with that of females by about 12 days (y intercepts significantly different at $P = .05$).

DISCUSSION

Yunick (1979b) identifies 2 patterns of pneumatization and lists species for which each pattern is typical. Several studies have also reported apparently species-specific patterns (Biur and Thapliyal 1972, Hogstad 1971, Nero 1951, Smith 1979, Verheyen 1953). Nero's results for House Sparrows (*Passer domesticus*) and those of Biur and Thapliyal for Baya Weavers (*Ploceus philippinus*) conform to the idea of species-specific pneumatization patterns. Thirty of 36 crania depicted by Nero (1951:

Fig. 1) exhibit the median-line pattern. The remaining 6 could not be assigned to a particular pattern. The Baya Weaver skulls drawn by Biur and Thapliyal (1972) depict a median-line pattern.

Our results did not indicate a single pattern for Indigo Buntings. One third of the subsample exhibited the peripheral pattern. Likewise, the results of Serventy et al. (1967) differ from Yunick's suggestion. Thirty-two of 49 Zebra Finch (*Taeniopygia castanotis*) crania shown in Serventy et al. (1967: Figs. 1 and 2) could be assigned to one of the pneumatization patterns. Seventy-five percent of those assigned exhibited the peripheral pattern.

Four studies either have involved birds of known age or have reported detailed sequential sampling of individuals (Nero 1951, Serventy et al. 1967, Biur and Thapliyal 1972, this study). In 2 of these studies (Serventy et al. 1967, this study) neither pattern of cranial pneumatization could be considered typical of the particular species involved. Yunick (1981b) has suggested that the size of the cranium is an important determinant of pneumatization pattern, such that small crania exhibit the peripheral pattern and large crania the median-line pattern. Indigo Bunting crania (ca. 16.5 × 13.5 mm) are within the size range of species exhibiting the peripheral pattern (Yunick 1981b: Fig. 2). Further detailed studies are needed to determine whether the occurrence of the median-line, peripheral, or other pattern is species-specific or represents individual variation (cf. Winkler 1979).

Our study demonstrated sex differences in pattern and timing of cranial pneumatization. Possible explanations of the sex differences in timing include: (1) sex differences in metabolism because of female physiological adaptations for egg-laying; (2) the prolonged maturation of males relative to females in Indigo Buntings; and (3) some laboratory-specific effect. Clearly, these are not mutually exclusive alternatives. Sex differences in metabolism may exist but no differences in the rates of cranial pneumatization were demonstrated in this study. Prolonged maturation is implicated because males do not achieve definitive alternate plumage until after their second prealternate molt. The sex differences in cranial pneumatization that we have observed may be another aspect of this prolonged maturation of males; Yunick (1979a) reports a similar situation in Purple Finches. Winkler (1979) suggests that delayed breeding and slow pneumatization may be related. A laboratory-specific effect cannot be ruled out but is considered unlikely (see below). Discrimination among these possibilities will require further study.

Johnston (1967) notes that Indigo Buntings may require 12 months or more to complete cranial pneumatization. In our study, 26% of the birds required at least a year and possibly as much as 16 months (assuming a 1 June hatching date). Possible explanations for the delay include: (1) anomalies in the development of these particular individuals; (2) prolonged maturation characteristic of this species; and (3) some laboratory-specific effect. Johnston's results suggest that (2) or (3) are possible, while the large proportion of birds showing the delay suggests that (1) is unlikely. Possibility (1) is believed unlikely because the majority of the incompletely pneumatized Indigo Buntings showed typical median-line pneumatization that was proceeding along a normal pattern, although slowly. Two birds showed a nearly completed peripheral pattern, also proceeding slowly along a normal pattern. The remaining 3 birds (about 5%) exhibited patterns that appear anomalous. Possibilities (2) and (3) cannot be separated on available data because both the Johnston study and the present one used laboratory-held birds and did not involve field controls. Winkler (1979) reviews evidence that elevated temperatures (25°C) may prolong the pneumatization process in laboratory-held birds. However, a male Indigo Bunting with an unpneumatized cranium was captured in the Clemson area in December 1978 (Hamel et al. 1980) leading us to believe possibility (3) unlikely.

The timing of cranial pneumatization may be related to the annual cycle of these birds. Indigo Buntings held over the summer showed little progress in pneumatization until after the prebasic molt when they began to pneumatize at a much accelerated rate.

Further studies of cranial pneumatization should involve simultaneous laboratory and field data collection. Such methodology will permit the identification of possible effects of captivity on rates and timing of cranial pneumatization.

SUMMARY

Repeated observations of the crania of individually-caged Indigo Buntings indicated both peripheral and median-line cranial pneumatization patterns. Female buntings completed pneumatization earlier on average than did males. Aging criteria based on cranial pneumatization are discussed.

ACKNOWLEDGMENTS

These birds were kept under authority of US-FWS Permit Number PRT 2-679-NV MBC. We gratefully acknowledge the assistance of Alan Avakian, Claire Filemyr, Harry LeGrand, Kathy McCarthy, and Skip Missimer in the capture and maintenance of the birds. Helpful criticism on an earlier draft of the manuscript was provided by Sidney A. Gauthreaux, Jr., Carl W. Helms, David W. Johnston, M. Kathleen Klimkiewicz, and Robert Yunick. We are indebted to Janet Hinshaw and J. M. Turbeville for providing and for translating, respectively, the Winkler paper. The work has been made possible by support from the Clemson University Department of Zoology.

LITERATURE CITED

BIUR, K., AND J. P. THAPLIYAL. 1972. Cranial pneumatization in the Indian weaverbird, *Ploceus philippinus.* Condor 74:198–200.

CHAPIN, J. P. 1949. Pneumatization of the skull in birds. Ibis 91:691.

DWIGHT, J. 1900. The sequence of plumages and moults of the passerine birds of New York. Ann. N.Y. Acad. Sci. 13(1):73–360.

HAMEL, P. B., E. D. KETTERSON, AND V. NOLAN, JR. 1980. Second winter record of Indigo Bunting in South Carolina. Chat 44:108–109.

HOGSTAD, O. 1971. Age determination of Goldcrests *Regulus regulus* in early summer and early autumn. Ornis. Scand. 2:1–3.

JOHNSTON, D. W. 1958. Sex and age characters and salivary glands of the Chimney Swift. Condor 60:73–84.

———. 1967. The identification of autumnal Indigo Buntings. Bird-Banding 37:211–214.

LEBERMAN, R. C. 1970. Pattern and timing of skull pneumatization in the Ruby-crowned Kinglet. Bird-Banding 41:121–124.

MELLENCAMP, W. R. 1969. Skull ossification in the White-throated Sparrow. EBBA News 32:109–111.

MILLER, A. H. 1946. A method of determining the age of live passerine birds. Bird-Banding 42:33–35.

NERO, R. W. 1951. Pattern and rate of cranial "ossification" in the House Sparrow. Wilson Bull. 63:84–88.

ROHLF, F. J., AND R. R. SOKAL. 1969. Statistical tables. W. H. Freeman and Co., San Francisco, Ca.

SCHNEIDER, K. J. 1981. Age determination by skull pneumatization in the Field Sparrow. J. Field Ornithol. 52:57–59.

SERVENTY, D. L., C. A. NICHOLLS, AND D. S. FARNER. 1967. Pneumatization of the cranium of the Zebra Finch *Taeniopygia castanotis*. Ibis 109:570–578.

SMITH, W. P. 1979. Timing of skull ossification in the kinglets. North Am. Bird Bander 4:103–104.

STEWART, R. M. 1972. The reliability of aging some fall migrants by skull pneumatization. Bird-Banding 43:9–14.

U.S. FISH AND WILDLIFE SERVICE AND CANADIAN WILDLIFE SERVICE. 1978. Bird Banding Manual. Vol. 2. Washington, D.C. and Ottawa, Ontario.

VERHEYEN, R. 1953. Contribution a l'étude de la structure pneumatique du crâne chez les oiseaux. Bull. Inst. R. Sci. Nat. Belg. 29:1–24.

WHITE, C. M. N. 1948. Skull ossification in certain Passeriformes. Ibis 90:329.

WINKLER, R. 1979. Zur pneumatisation des schädeldachs der vögel. Der Ornithologische Beobachter 76:49–118.

YUNICK, R. P. 1977. Timing of completion of skull pneumatization in the Pine Siskin. Bird-Banding 48:67–71.

———. 1979a. Timing of completion of skull pneumatization of the Purple Finch and the Common Redpoll. North Am. Bird Bander 4:53–55.

———. 1979b. Variation in skull pneumatization patterns of certain passerines. North Am. Bird Bander 4:145–147.

———. 1980. Timing of completion of skull pneumatization of the Black-capped Chickadee and the Red-breasted Nuthatch. North Am. Bird Bander 5:43–46.

———. 1981a. Skull pneumatization rates in three invading populations of Black-capped Chickadees. North Am. Bird Bander 6:6–7.

———. 1981b. Further observations on skull pneumatization. North Am. Bird Bander 6:40–43.

Department of Zoology, Clemson University, Clemson, South Carolina 29631.
Received 16 Dec. 1981; accepted 1 Nov. 1982.