GEOGRAPHIC AND SEASONAL VARIATION IN THE OCCURRENCE OF INCOMPLETELY PNEUMATIZED SKULLS IN THE HOUSE SPARROW

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The process of skull "ossification" or pneumatization, by which most songbirds obtain a double-layered cranium during the first year or so of life, has received detailed documentation for the House Sparrow (*Passer domesticus*) (Nero 1951; Harrison 1960). House Sparrows commonly achieve the fully double-layered, "adult" cranium by the age of 6 months, with incomplete pneumatization persisting in occasional individuals for a somewhat longer period (up to 221 days in one sparrow seen by Nero).

During each of four seasons in 1968–69, I collected *P. domesticus* at five localities on an east-west transect running from the eastern edge of the Great Plains at Lawrence, Kansas, into the southern Rocky Mountains at Gunnison, Colorado (table 1). These specimens were preserved as flat skins and cleaned skeletons with entire skulls. I collected only individuals which had completed the postjuvenal molt. This restriction, coupled with the observation that all birds collected during spring and summer were in breeding condition, reasonably assures that individuals taken in spring and summer were in at least their second calendar year of life. The occurrence of a few such individuals with skulls not completely "ossified" (this condition is hereafter abbreviated as "snco," the fully pneumatized condition is termed "sco") prompted me to assess the proportions of snco's in each seasonal locality sample. Packard (1967) has studied morphological geographic variation in *P. domesticus* along essentially the same transect.

Chi-square tests of proportional differences in two-way contingency tables provided the statistical foundation for all of the following analyses.

THE AGE OF SNCO'S

Some of the following discussion assumes that, within any seasonal sample, the snco's average younger than the sco's. For the fall samples this is obviously true; skulls of many snco's are but little pneumatized (see Nero 1951: fig. 1, stages 49–93). For later samples the male skins were divided into "brown-cheeked" and "gray-cheeked" categories, the former condition typifying first-year male sparrows and the latter, adults (Selander and Johnston 1967). Especially in worn, summer-taken skins such identification frequently involves a subjective evaluation, but the brown-cheeked group certainly averages younger than the gray-cheeked. The brown-cheeked sparrows include a significantly greater proportion of snco's, in both late winter and breeding season samples, than do gray-cheeked birds (table 2, comparisons 1 and 2; the reason for grouping spring and summer samples into a single "breeding season" set is given below). This does not prove that occasional males in their second year or later do not retain incompletely pneumatized skulls; on the average, though, snco males are relatively young birds. Lacking a similar, age-specific plumage variable for female sparrows, I can only assume that snco females likewise average younger than sco's.

COMPARISON BETWEEN SEXES

Since at no season or locality do the proportions of snco's in males and females show any differences (table 1) I have combined the sexes in all analyses.

SEASONAL VARIATION

For reasons elaborated in the next paragraph, the five localities have been grouped into submontane (Lawrence, Hays, and Kit Carson) and montane (Salida, and Gunnison) subsets. As expected, the proportion of snco's in both subsets declines precipitously from November–December to February–March. From the latter period to the breeding season (May and July–August samples), there is still a relative decrease in the numbers of snco's in both geographic subsets (table 2, comparisons 3 and 4). The May and the July–August samples, however, show similar proportions of snco's. From both of the latter two time periods, virtually all snco's were in a late stage of development comparable to Nero's (1951: Fig. 1) stages 147–181. This suggests that the process of skull pneumatization halts in birds which are breeding (it should be re-emphasized here that all spring and summer snco's were probably in breeding condition—females possessed brood patches; males had fully enlarged testes, swollen seminal vesicles, and black bills). Physiological mechanisms which could halt skull pneumatization during breeding are unknown; in retrospect, however, it is not surprising that the energetically demanding activities of maturation and breeding seem to be mutually exclusive.

GEOGRAPHIC VARIATION

There are no marked differences among the proportions of snco's in the three Great Plains populations at any season; similarly the seasonal proportions at Salida are similar to those at Gunnison (table 1). The two montane samples, however, seem strikingly different from those on the plains to the east. In November and early December a much higher proportion of the montane collection is comprised of snco's than is the submontane collection (table 2, comparison 5). In later seasons, though, the situation changes. In the late winter the proportion of snco's in the two subsets are not statistically distinguishable (table 2, comparison 6). By the breeding season there are almost no snco's included among the montane samples; this is in significant contrast to the situation at lower elevations (table 2, comparison 7).

The November–December differences probably reflect sampling bias. The November collection at Gunnison was from a local concentration at a bird-feeder in an area where breeding density in the preceding summer had been low. Similarly, at Salida the November sample was obtained at stockyards where relatively few sparrows had been found in the previous summer. In contrast, all of the late autumn lowland samples were collected at the location of large breeding colonies. Adult House Sparrows spend most of the year at or near their nest site (Summers-Smith 1963), whereas some first-year birds spend their first fall and winter in flocks away from established breeding colonies (Summers-Smith 1963). Such first-year flocks probably provided all November montane specimens; but the autumn lowland samples must

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TABLE 1. Collection data for skulls of House Sparrows.

Locality	Elevation (ft)	Dates	No. snco/ No. sco[a] ♂♂	♀♀
Lawrence, Douglas Co., Kansas	800	4–5 Dec.	19/3	15/8
		24–27 Feb.	4/17	4/18
		23–24 May	0/22	1/20
		25 July–2 Aug.	3/13	3/17
Hays, Ellis Co., Kansas	2000	30–31 Nov.	18/6	17/2
		2 Mar.	3/21	0/21
		9–10 May	1/19	3/23
		20–21 July	2/21	2/17
Kit Carson, Cheyenne Co., Colorado	4300	28–29 Nov.	18/13	16/6
		19 Feb.	9/27	3/17
		18 May	3/19	3/20
		22–23 July	5/18	0/26
Salida, Chaffee Co., Colorado	7000	12–13 Nov.	6/1	11/0
		13–15 Feb.	2/8	0/12
		16–17 May	0/4	0/5
		15 July–8 Aug.	0/14	1/14
Gunnison, Gunnison Co., Colorado	7900	15–16 Nov.	7/0	5/1
		17 Feb.	0/15	2/9
		15 May	0/10	0/7
		13 July–10 Aug.	0/14	0/9

[a] snco = birds with skulls not completely ossified. sco = birds with skulls completely ossified.

have contained some sco adults netted near their nest sites.

The late winter and breeding season samples, both montane and submontane, were collected at breeding localities. On noting the virtual absence of snco's in spring and summer at montane colonies, I hypothesized that most or all montane first-year birds probably did not breed in contrast to many lowland first-years. This idea seemed reasonable in view of the relatively rigorous climate (Packard 1967) and probably low summer insect biomass of montane Colorado. Even in lowland areas some first-year sparrows probably do not breed (Summers-Smith 1963; Weaver 1939) and are probably less efficient than adults when they do (Selander and Johnston 1967). However, as judged by cheek color of males, as great a proportion of first-year birds occur among montane breeding sparrows as are found among lowland breeders (table 2, comparison 8). Seemingly, then, the proportion of snco's and sco's differ between montane and plains breeding populations because montane first-year sparrows more often achieve full skull pneumatization by the breeding season than do their plains counterparts. The explanation may be that lowland first-years begin breeding (and, hence, stop pneumatization) earlier than montane birds. I have no direct data, but note that along climatic gradients similar to that running from the plains up into the mountains (though latitudinal rather than elevational), House Sparrows begin breeding later in regions of relatively cold, seasonally retarded climates than in regions of moderate or warm climates (Selander and Johnston 1967).

SUMMARY

Some populations of first-year and older House Sparrows will include snco birds at any season. The average age of these snco's is lower than that of sco's from the same population. The proportions of snco's do not differ between sexes. The proportion of snco's declines from fall, through winter, to spring; but it remains constant through the following breeding season. Very few snco sparrows were taken at breeding colonies in montane Colorado, contrasting with numbers of actively breeding snco's collected at colonies in eastern Colorado and Kansas. Speculatively, these differences can be because Great Plains sparrows begin breeding and stop pneumatization earlier in the year than do montane birds.

TABLE 2. Tests of proportional differences in skull ossification and plumage of House Sparrows.

Comparison	sco	snco	χ^2
1. Brown cheek, late winter	29	12	4.742 ($P \leqslant 0.05$)[a]
Gray cheek, late winter	36	4	
2. Brown cheek, breeding season	48	10	4.208 ($P \leqslant 0.05$)[a]
Gray cheek, breeding season	65	4	
3. Late winter, submontane	121	23	3.152 ($P \leqslant 0.10$)[a]
Breeding season, submontane	235	26	
4. Late winter, montane	44	4	3.877 ($P \leqslant 0.05$)[a]
Breeding season, montane	77	1	
5. Submontane, fall	38	103	5.983 ($P \leqslant 0.05$)[b]
Montane, fall	2	29	
6. Submontane, late winter	121	23	1.783 (ns)[b]
Montane, late winter	44	4	
7. Submontane, breeding season	235	26	6.172 ($P \leqslant 0.05$)[b]
Montane, breeding season	77	1	
	montane	submontane	
8. Brown cheek, breeding	18	58	0.039 (ns)[a]
Gray cheek, breeding	23	69	

[a] One-tailed test.
[b] Two-tailed test.

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CLIFF SWALLOW COLONY IN ARCTIC ALASKA

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With one exception there appear to be no previous records of the breeding of the Cliff Swallow (*Petrochelidon pyrrhonota*) north of the timber line in the Brooks Range. Gabrielson and Lincoln (The Birds of Alaska, Stackpole Co., Harrisburg, Pa., p. 603, 1959) give no instances of breeding to the north of these mountains. However, Irving (U.S. Natl. Mus. Bull. 217:90, 1960) mentions that in the winter of 1908 or 1909 near the head of the west fork of the Kuparuk River at 68°35′ N, 149°20′ W over a hundred nests, containing frozen young birds, were found built against rock cliffs. A study of the relevant literature reveals no other mention of breeding by this species north of the Brooks Range.

On the evening of 23 June 1970, I saw eight Cliff Swallows hawking over a small lake above the south side of the Atigun Canyon at an elevation of about 2900 ft. This canyon lies to the east of Galbraith Lake in the Brooks Range. The following morning at least 7–10 pairs of these swallows were located at a nearly vertical cliff face overlooking a tributary of the Atigun River near the eastern end of the canyon at an elevation of about 2800 ft (fig. 1). A number of mud-built nests, some of which were apparently unoccupied, were seen under slight projections on the cliff face. The majority of these nests were gourd-shaped, but three were of open cup construction and at least one of these was occupied. This locality is approximately 5 miles SE of the Kuparuk River site mentioned by Irving.

It is quite possible that other breeding colonies of this species are present in canyons and valleys on the north side of the Brooks Range, where they could easily be overlooked. Even with the present relatively high level of activity in these mountains and on the Arctic Slope of Alaska generally, there are large areas that remain unvisited by ornithologists.

FIGURE 1. Site of a breeding colony of Cliff Swallows above a tributary of the Atigun River on the north side of the Brooks Range in the Atigun Canyon.

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