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EVOLUTION IN THE HOUSE SPARROW. I. INTRAPOPULATION VARIATION IN NORTH AMERICA

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This paper, the first in a series on evolution in the House Sparrow (*Passer domesticus*) in North America and other regions in which it has been introduced since 1850, presents an analysis of individual, age, and sexual variation in external morphological characters undertaken in preparation for studies of geographic variation. A preliminary report on geographic variation in North American populations has appeared (Johnston and Selander, 1964), and a full account will be presented in the second paper of this series (Selander and Johnston, unpublished data).

MATERIALS AND METHODS

Our studies are based on 2877 adult and first-year study skins of specimens collected with Japanese mist nets in 1962, 1963, and 1965 at 37 localities in North America, the Hawaiian Islands, Bermuda, England, and Germany (table 1). Most specimens were collected in October and November, soon after completing the annual molt. Specimens are in the Museum of Natural History of The University of Kansas.

AGE DETERMINATION

In the House Sparrow unossified areas persist in the cranium for from 6 to 12 months (Nero, 1951), thus providing a useful, but not infallible, criterion for distinguishing first-year and adult birds in the fall and early winter. All specimens in our samples with incomplete cranial ossification (labelled "SNCO" = skull not completely ossified) are first-year individuals that had completed the postjuvenal molt. Most specimens showing complete ossification (labelled "SCO") are believed to be one or more years old, but, undoubtedly, some are first-year birds that hatched early in the breeding season. Assuming for the sake of simplicity that the rate of ossification of the cranium is uniform throughout the range of the species, we may expect a northward decrease in the proportion of first-year birds achieving complete ossification by October and November because the breeding season begins later in spring with increasing latitude (see below). At southern localities, such as Austin, Texas, where nesting begins in March, a significant percentage of young birds may be six months old by October, whereas, at northern localities, such as Edmonton, Canada, where nesting may not begin until May, few if any first-year individuals will be six months old by October. Indirect evidence of geographic variation in the proportion of first-year birds achieving complete cranial ossification by October and November is supplied by an analysis of variation in secondary sexual plumage characters in males (see page 241).

In the absence of age-specific characters of plumage or size, there is no objective basis for distinguishing "advanced" first-year birds from true adults. Relying entirely on cranial ossification as a criterion of age, we have included all birds with complete ossification in the "adult" segment of our samples.

TABLE 1

SAMPLES OF HOUSE SPARROWS COLLECTED IN 1962, 1963, AND 1965

Sample code number	Locality	Date	Number of study skins	
			Male	Female
1	**Edmonton**, Alberta, Canada	23–26 Oct. 1963	49	34
2	**Montreal**, Quebec, Canada	16–21 Oct. 1963	40	41
30	**Middlebury**, Addison Co., Vermont	17–26 Nov. 1963	19	12
39	**Pittsburgh**, Pennsylvania	20 Oct. 1965	37	26
40	**Delmont**, Westmoreland Co., Pennsylvania	21 Oct. 1965	59	47
3a	**Detroit** (1963), Michigan	19 Oct. 1963	13	30
3b	**Detroit** (1965), Michigan	23 Oct. 1965	57	55
37	**Ann Arbor**, Michigan	25 Oct. 1965	21	16
38	**Salem**, Washtenaw Co., Michigan	24 Oct. 1965	19	10
4	**Roodhouse**, Green Co., Illinois	29–30 Nov. 1963	11	13
5	**Salt Lake City**, Utah	31 Oct. 1963	106	68
6	**Lawrence** (Lawrence and Eudora, Douglas Co.), Kansas	8 Oct.–3 Nov. 1962	74	43
7	**Vancouver**, British Columbia, Canada	30 Oct.–9 Nov. 1963	40	43
8	**Oakland**, California	28–29 Oct. 1963	44	26
9	**Sacramento** (Elk Grove and Franklin, Sacramento Co.), California	27–30 Oct. 1962	52	51
36	**Stockton**, San Joaquin Co., California	28 Oct. 1962	20	9
10	**Los Angeles** (City of Industry), California	22–23 Oct.–1–2 Nov. 1962	68	51
11	**Death Valley** (Furnace Creek Ranch), California	19–21 Oct. 1962	21	21
12	**Phoenix** (Peoria and Gila Bend Air Base), Arizona	29–31 Oct. 1963	26	20
13	**Las Cruces**, New Mexico	28 Oct.–6 Nov. 1962	56	37
14	**Bastrop**, Bastrop Co., Texas	2 Oct.–15 Nov. 1962	71	58
15	**Austin**, Texas	2–3 Jan. 1963	26	11
16	**Devine**, Medina Co., Texas	17 Nov. 1962	15	9
41	**Del Rio**, Uvalde Co., Texas	16 Nov. 1965	54	55
18	**Nueces Co.** (Bishop and Robstown), Texas	8–9 Feb. 1964	21	15
19a	**Progreso** (1963), Hidalgo Co., Texas	14–15 Dec. 1963	116	66
19b	**Progreso** (1965), Hidalgo Co., Texas	17, 20 Nov. 1965	54	49
17	**Houston**, Texas	13–14, 31 Oct. 1962	57	56
21	**Baton Rouge**, Louisiana	28 Oct. 1962	11	4
20	**Zachary**, East Baton Rouge Parish, Louisiana	28–30 Oct. 1962	18	6
28	**Birmingham**, Alabama	30 Oct.–27 Nov. 1963	29	22
29	**Camilla**, Mitchell Co., Georgia	1 Nov. 1963	11	17
22	**Gainesville**, Florida	18–24 Nov. 1963	39	37
23	**Mexico City**, México	14–15 Nov. 1963	44	21
24	**Oaxaca** de Juárez, Oaxaca, México	8–9 Nov. 1963	50	22
25	**Oahu** (Honolulu), Hawaiian Islands	21 Oct. 1963	86	39
27	**Bermuda** (Nonsuch Island)	12 Oct.–11 Nov. 1963	30	32
26	**Oxford**, England	22–26 Oct. 1962	53	40
35	**Ludwigsburg** (near Stuttgart), Germany	1–4 Oct. 1962	34	14
		Totals:	1651	1226

Analysis of Plumage Color

Adventitious soiling. Specimens from Oxford, England, and downtown Detroit, Michigan, Pittsburgh, Pennsylvania, and Birmingham, Alabama, were conspicuously and uniformly darker in color than those from other localities as a result of being soiled with coal dust and soot (Johnston and Selander, 1963). Specimens of samples collected in rural areas appeared to be clean, but test washings revealed that all were discolored with soil or soot. Contrary to the claim of Keve (1965:56), adventitious soiling affects all populations of House Sparrows, including those in rural areas; and even individuals in late stages of the annual molt, and thus in very fresh plumage, may be discolored (Johnston and Selander, 1963). Because this type of discoloration affects the entire plumage and is similar in all members of a sample, it is deceptive, being easily mistaken for feather pigmentation (Harrison, 1963b). Comparable degrees of discoloration are apparent in museum specimens of Horned Larks (*Eremophila alpestris*), towhees, juncos, and other species that have terrestrial habits or inhabit urban and industrial areas.

All study skins were thoroughly cleaned by washing for five minutes in hot water and a liquid detergent (uncolored "Joy"), rinsing several times in hot water and a final time in white gasoline, and drying over a forced-air steam radiator. Although much of the discoloring soil (but not soot) may be removed by washing specimens in white gasoline, petroleum ether, or carbon tetrachloride, thorough cleaning can be obtained only with a detergent.

Before washing the study skins, we measured the color of the breast and pileum in a series of females from each sample and the pileum of males from several samples. By comparing color determinations before and after washing, we are able to assess the degree to which soil and soot modify colors produced by feather pigments in these plumage areas. The reason for our concern with color variation in unwashed material is the fact that to some degree the adventitious soiling masks the feather pigments from the action of selection.

Colorimetric techniques. Several characters of color and pattern of the plumage were analyzed by matching specimens to series of scored reference specimens representing segments in total spans of variation. Comparisons were made under a Macbeth Super Color Matching Skylight (Model BX 848A), which provides light of a color temperature of 7500° K and an intensity of 200 foot-candles on the floor of a Munsell gray viewing chamber.

Variation in the color of unpatterned areas of the plumage was analyzed with a Bausch and Lomb Spectronic 505 recording spectrophotometer equipped with a visible reflectance attachment (see Bowers, 1956; Lubnow and Niethammer, 1963; Selander, Johnston, and Hamilton, 1964; Kniprath, 1965; and Dyck, 1966, for discussion of colorimetric techniques). Flatness of the 100% line was maintained within limits of 0.5% peak-to-peak, and flatness of the 0% line, within 0.25%. Wavelength accuracy of the Spectronic 505 is 0.5 mμ, and repeatability, 0.2 mμ; photometric accuracy and repeatability are $\pm$ 0.5% (transmittance) and $\pm$ 0.3% T, respectively. The Spectronic 505 was modified for the present work by reducing the size of the monochromatic beam spot at the reference and sample ports to 5 $\times$ 7 mm and decreasing the diameter of the sample port to 11 mm. To prevent light leaking into the integrating sphere, the reflectance attachment was enclosed in a light-tight box.

White standards of 100% reflectance were prepared from magnesium sulfate (Bausch and Lomb Lot No. 26037) in a Bausch and Lomb powder press.

From curves of percentage diffuse spectral reflectance in the wavelength range from 400 to 700 mμ, trichromatic coefficients (x, y, z) were derived by the 10 selected ordinate method (Hardy, 1936: 49–51), which involves a total of 30 readings from each curve. From the coefficients, we computed dominant wavelength (Λ_d), relative brightness (Y), and excitation purity (P_e), corresponding, respectively, to the psychological attributes of hue, value (brilliance), and saturation (chroma). Excitation purity was used in preference to colorimetric purity on the recommendation of Judd (1950:18).

(1) Λ_d (to the nearest mμ) was determined by reference to table 6 of Judd (1933). The slope of the dominant wavelength on the chromaticity diagram is given by $\frac{x_s - x_w}{y_s - y_w}$ where x_s and y_s are trichromatic coefficients of the sample, and x_w and y_w are coefficients of I.C.I. Illuminant C.

(2) Y (in %) = $100\ y_s$.

(3) P_e (in %) = $\left(\frac{x_s - x_w}{x_l - x_w}\right) 100$, where x_l is the trichromatic coefficient of the point on the chromaticity diagram where a line from the white point (I.C.I. Illuminant C) extended through the sample point intersects the spectrum locus.

Replicate reflectance curves are essentially identical provided the specimen remains positioned at the sample port between runs, but they vary slightly when the specimen is repositioned between runs (table 2).

Linear Dimensions and Body Weight

The following linear measurements (millimeters) were taken by one of us (R.K.S.) from study skins: (1) wing length: chord of unflattened wing; (2) tail length: distance from point of insertion of central pair of rectrices (tail feathers) to tip of second rectrix (rectrices numbered from central pair, 1-1, to outer pair, 6-6); (3) bill length: distance from anterior surface of nostril to tip of bill; (4) bill width: distance between lateral surfaces of rami of lower mandible immediately posterior to horny covering of mandible; (5) tarsus length: diagonal from posterior midpoint of joint of tibiotarsus and tarsometatarsus to distal edge of distalmost undivided scute on anterior surface of tarsometatarsus near its junction with middle toe.

Body weights (grams) obtained within a few hours of death are available for most specimens. Because of individual, age, and other variation in amount of subcutaneous and visceral body fat, it seemed desirable to adjust the weights. Descriptive designations of amounts of body fat made by specimen preparators were grouped into five scored categories, ranging from 0 ("no fat") to 4 ("extremely fat"). Because most specimens were assigned to category 2 ("moderately fat"), we elected to adjust the weights of specimens in other categories to values that would be expected if they were in category 2. Adjustment values were obtained from unbiased estimates of intrapopulation differences in mean weight of female specimens in the various fat categories, using 17 large samples ($n = 638$). Weights of males and females in category 1 were increased by 0.8 g, and weights of birds in category 3 were reduced by 0.9 g. Adjustments for birds in categories 0 and 4 were 1.6 g and -1.7 g, respectively.

Although means of unadjusted and adjusted weights for samples differ generally by less than 0.5%, the adjustment was useful in reducing apparent age variation and strengthening correlations between weight and linear dimensions.

TABLE 2

REPLICATE DETERMINATIONS OF BREAST COLOR IN 25 UNWASHED FEMALE HOUSE SPARROWS FROM SALT LAKE CITY

Determination	Brightness		Dominant wavelength		Purity	
	Mean	SD	Mean	SD	Mean	SD
First (1 July)	25.61	2.22	578.6	0.7	22.84	2.59
Second (10 July)	25.70	2.31	578.7	0.6	22.92	2.71
Significance of mean difference[a]:	$t = 0.324$		$t = 0.225$		$t = 0.246$	
Average individual difference:	1.04		0.6		0.85	

[a] t-test of difference between correlated means (Steel and Torrie, 1960:78–79).

Computations and statistical analyses were performed at the computation centers of The University of Texas, Austin, and the University of California, Berkeley. Levels of statistical significance are specifically identified in the tabular presentations that follow. In the text and footnotes, a single asterisk (*) indicates significance at the 5% level of probability ($P \leq 0.05$), and a double asterisk (**) indicates significance at the 1% level ($P \leq 0.01$).

SEASONAL AND OTHER NONGENETIC SOURCES OF VARIATION

Our major objective in studying morphological variation in the House Sparrow is to determine the degree to which populations derived from introductions and exposed to new environments and selective pressures have come to differ from the parental Old World populations and among themselves. Considering the short period since introduction of the species to the New World in the mid-19th century, for any character the genetically determined interpopulation component of the total variance may, understandably, be relatively small. Therefore, we have been especially concerned with the problem of minimizing or, at least, recognizing other sources of variation that might obscure the genetically determined variation or lead to erroneous conclusions regarding the extent of the genetic contribution to interpopulation variation in means and variances of character values. The considerable variation dependent upon age and sex is analyzed below; here we consider some sources of variation in certain characters arising indirectly from individual and geographic variation in timing of events in the annual cycle and from regional variation in periods of sampling relative to the reproductive and molt phases of the cycle.

Our purpose in sampling populations in October and November was to obtain material in fresh plumage, thereby minimizing variation in wing length and tail length and in color and pattern of the plumage resulting from abrasion. Our schedule of collecting was arranged to avoid sampling populations too early or too late in the fall, since neither molting nor abraded specimens can be used in analyzing these characters. The material shows some degree of intersample variation in average feather condition, but at most localities we obtained an adequate number of individuals that have completed the molt but do not show marked feather abrasion.

That our samples are relatively uniform in condition of the plumage is due in part to the fact that the timing of reproductive and molt cycles is not greatly variable regionally, at least in temperate North America. Studies of testis volume and

spermatogenic activity at London, Ontario (Threadgold, 1960a); Minneapolis, Minnesota (Kirschbaum and Ringoen, 1946); Lawrence, Kansas (Selander and Johnston, unpublished data); Norman, Oklahoma (Allender, 1936a, 1936b); Austin, Texas (Selander and Johnston, unpublished data); Pasadena, California (Davis and Davis, 1954); and Belfast, Ireland (Threadgold, 1960a) demonstrate surprisingly little geographic variation in timing of the reproductive cycle, especially with regard to testicular regression, which occurs in August in all populations studied. As noted by Threadgold (1960a), the cycles are not uniformly retarded from south to north as would be expected if daylength were the overriding environmental factor influencing the cycle; and the experimental demonstration of testicular development under very short photoperiods (Threadgold, 1960b; Middleton, 1965) suggests that the testis cycle is only partially controlled by daylength.

The length of the breeding period is shortened toward the north by delay in time of vernal recrudescence of the gonads. On the basis of "rather broad statements culled from the literature," Summers-Smith (1963:68–69) indicates that in North America and Europe the breeding season begins about two months later at 60° N than at 35° N. At London, Ontario, Threadgold (1960a) found that vernal recrudescence of the testis is delayed about six weeks compared with southern localities in the United States, and at Minneapolis the delay is about four weeks. We have found a delay of at most two weeks in time of reaching full testis development at Lawrence, Kansas, compared with Austin, Texas.

On the likely assumption that adult individuals begin molting at the time of gonadal regression, we surmise that postnuptial molt begins in August in most populations in temperate North America; and our data indicate that most adults have completed the molt by mid-October. For our material collected in October and November, it seems probable that the span of intersample variation in average elapsed time since completion of the postnuptial molt is less than two months. In first-year birds the intersample span of variation in elapsed time since completing the postjuvenal molt apparently is somewhat greater.

In addition to intersample variation in average degree of feather abrasion, we have noted regional differences in the degree of intrasample variation of this wear, especially in first-year birds. This latter variation is undoubtedly related primarily to geographic variation in the length of the annual molt period, which for first-year birds is in turn correlated with regional variation in the length of the period of the breeding season over which young are fledged from nests. Variation in degree of feather wear may be especially great in samples from tropical localities where breeding extends through most of the year; molting individuals are taken in the same mist nets with individuals in moderately worn plumage that apparently had completed the annual molt five months previously.

Asynchrony of annual cycles among colonies at the same sample locality may also contribute to intersample and intrasample variation in degree of feather abrasion. As noted by Summers-Smith (1963:73) and confirmed by our observations, "breeding within colonies tends to be closely synchronized, though different colonies in the same area may differ by as much as two weeks or more. . . ." Correspondingly, we have found some variation in timing of molt among different winter flocks in the same area. The most notable example comes from work at Lima, Perú (Selander, unpublished data). Most of 95 specimens collected on 18 April 1965 from a large flock at chicken pens two miles east of Lima were in moderately heavy molt, and only 10% had completed the molt. Yet over 50% of 150 specimens taken the next day,

19 April, at a dairy five miles west of Lima had completed the molt. Possibly at some localities in North America we sampled flocks derived from a single breeding colony, while at other localities we took specimens from flocks composed of individuals from two or more slightly asynchronous breeding colonies.

Wing length and tail length. The length of the wing and tail in birds decreases progressively following the annual molt as the tips of the outer primaries and the rectrices are gradually abraded. The rate of wear varies markedly among different species and, to a lesser degree, among populations of the same species, depending upon several factors, including, importantly, the frequency and duration of contact of the feathers with vegetation. In general, forms that, like the House Sparrow, do not inhabit dense vegetation, do not experience excessive wear, but the seasonal decrease in length of the remiges and rectrices is appreciable and must be considered in studies of variation.

Although Calhoun (1947a:211) in his study of wing length in North American House Sparrows did not measure any bird showing "obvious wear" to the primaries, there remained a statistically significant difference between mean wing lengths of birds taken in the fall and those collected in the spring. Series of specimens taken in October, November, and December were compared with those taken in February, March, and April, with the following results: mean wing length of 225 "fall" males was greater than that of 397 "spring" males by 0.43 mm ($P = 0.001$), and for 173 "fall" females and 272 "spring" females, the difference was 0.35 mm ($P < 0.05$).

By collecting samples in October and November we have all but eliminated variation in wing length and tail length due to wear of the feathers; in specimens of these samples the primaries and rectrices are uniformly unworn. In specimens taken later in the year a slight abrasion of the flight feathers is apparent, as demonstrated by comparing mean wing lengths and tail lengths in our two samples from Progreso, one taken in November and the other in December (table 3).

Bill length. The House Sparrow and many other birds that are largely granivorous in the winter and insectivorous in the summer exhibit seasonal changes in bill length resulting from variation in rate of wear experienced by the constantly growing horny tip (Clancey, 1948; Davis, 1954; Selander, 1958). In samples of House Sparrows from Berkeley and Pasadena, California, Davis (1954) found mean bill length significantly greater in May, June, and July than in December and January; the seasonal difference was 5% for the Berkeley sample and 3.5% for the Pasadena sample. A small decrease in bill length from November to December is shown in our samples from Progreso (table 3). In a study of 433 specimens from Germany, Steinbacher (1952) found a 10% increase through June, July, and August. Bill length remained almost constant from October through May and was less variable individually in this period than in the summer. Seasonal variation was greater in females than in males, as also reported for the Tree Sparrow (*Passer montanus*) by Clancey (1948).

By collecting in late fall we have minimized variation in bill length caused by differences in degree of wear, but, owing to regional variation in relative abundance of various types of foods, intersample variation of this type cannot be entirely eliminated (Kleinschmidt, *in* Steinbacher, 1952:23–24). Steinbacher (1952:28) suggests that House Sparrows from southern regions may experience less bill wear than those from northern regions because of a greater relative abundance of insects and soft seeds in their diets.

Tomial flanges. Davis (1954:147) noted unilateral or bilateral flanges on the

TABLE 3

MEASUREMENTS OF TWO SAMPLES OF HOUSE SPARROWS FROM PROGRESO, TEXAS

Sample	Date	Number of specimens	Wing length, mm		Tail length, mm		Bill length, mm		Weight, g		Adjusted weight, g	
			Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Adult males												
19b	17, 20 Nov.	30	77.66	1.65	58.22	1.36	9.51	0.36	29.00	1.37	29.70	1.29
19a	14–15 Dec.	22	77.57	1.78	57.97	1.91	9.27	0.32	30.24	2.16	30.34	1.96
Significance of difference[a]:			$t = 0.188$		$t = 0.553$		$t = 2.505^*$		$t = 2.535^*$		$t = 1.424$	
First-year males												
19b	17, 20 Nov.	24	77.53	1.53	57.87	1.23	9.40	0.25	28.45	1.23	29.01	1.17
19a	14–15 Dec.	92	77.24	1.55	57.00	1.52	9.25	0.33	30.44	1.61	30.62	1.62
Significance of difference[a]:			$t = 0.818$		$t = 2.588^*$		$t = 2.069^*$		$t = 5.633^{**}$		$t = 4.563^{**}$	

[a] The difference is significant at the 5% level ($P \leqslant 0.05$), indicated by *; or at the 1% level ($P \leqslant 0.01$), indicated by **.

central part of the upper tomia in 6 of 52 House Sparrows collected near Pasadena, California, from March to July. We presume that these flanges result from tomial malocclusion and are most likely to develop in birds feeding on soft foods, such as insects or "chicken mash." Grossly anomalous flanges caused by the almost complete absence of the mandible were reported by Poland (1940) and Dow and Hesse (1965).

Tomial flanges are shown by 0.5% of our specimens, all of which are adult. The highest frequency is in the sample from Oahu, in which three males (5% of adults) and one female (4% of adults) have unilateral flanges. That no first-year birds show this aberrancy probably reflects the limited time they had to grow such flanges between hatching and time of collection. Selection against this character presumably is relatively light, for the probability that an affected bird will reproduce at least once would seem to be largely independent of the anomaly.

Effects of wear on color of plumage. Because slight degrees of abrasion of the feathers may significantly alter the color of the plumage, only specimens showing no evidence of wear were used for color determinations. As a result, approximately a quarter of the adult specimens and half the first-year specimens were excluded from consideration in our analysis of color variation.

VARIATION IN SIZE

The significance of variation owing to age, sex, and sample locality was determined for each size character by a mixed-model, three-way analysis of variance, with age and sex as fixed effects and locality as a random effect. The analyses involved 24 North American samples for linear dimensions and 22 samples for weight and adjusted weight. Appropriate F-ratios were computed, as shown in table 4. For all characters the effect of locality is highly significant. Unbiased estimates of intrapopulation differences between age and sex groups (tables 5 and 7) were obtained from weighted mean intrasample differences where interaction involving locality was absent and from unweighted mean differences where significant interaction was indicated (see Steel and Torrie, 1960:270).

TABLE 4

ANALYSIS OF VARIANCE OF SIZE CHARACTERS IN NORTH AMERICAN HOUSE SPARROWS[a]

Source of variation	Degrees of freedom	F-ratio[b]					Degrees of freedom	F-ratio[b]	
		Wing length	Tail length	Bill length	Bill width	Tarsus length		Weight	Adjusted weight
Sex	1, 23	1115.315**	674.037**	0.109	0.576	17.997**	1, 21	16.912**	34.131**
Age	1, 23	16.564**	34.192**	33.470**	16.421**	0.793	1, 21	0.501	0.007
Locality	23, 1911	9.103**	6.748**	10.192**	9.752**	10.716**	21, 1828	28.604**	30.123**
Sex-age	1, 23	1.458	0.079	2.861	0.368	0.122	1, 21	7.301*	6.563*
Sex-locality	23, 1911	1.282	0.865	0.802	0.995	0.822	21, 1828	1.084	1.172
Age-locality	23, 1911	2.160**	2.719**	0.791	0.852	0.947	21, 1828	1.423	1.196
Sex-age-locality	23, 1911	1.005	1.320	0.629	0.574	1.041	21, 1828	1.442	1.391

[a] Mixed-model, three-way analysis, with sex and age fixed, locality random; 24 samples (total $n = 2007$ specimens) for linear dimensions, 22 samples (total $n = 1916$ specimens) for weight and adjusted weight.
[b] The effect is statistically significant at the 5% level ($P \leqslant 0.05$), indicated by *; or at the 1% level ($P \leqslant 0.01$), indicated by **.

AGE VARIATION

The postjuvenal molt of the House Sparrow involves complete replacement of the juvenal plumage (Dwight, 1900; Witherby *et al.*, 1940:159; Weaver, 1942:190), but first-year primaries and rectrices grown at the postjuvenal molt average slightly shorter than those grown by adult birds at the postnuptial molt (table 5). For both wing length and tail length there is a significant interaction between age and locality (table 4); this appears to be in large part because of the sample from Death Valley, in which first-year birds of either sex average larger than adults in wing length and tail length.

In both sexes mean bill dimensions are greater in adults than in first-year birds, but neither sex shows a significant age difference in tarsus length.

The *F*-ratios for the effect of age on weight and on adjusted weight are not

TABLE 5

AGE VARIATION IN SIZE IN NORTH AMERICAN HOUSE SPARROWS
(Unbiased estimates of intrapopulation differences between adult and first-year birds)

Character	Males[a]		Females[b]	
	Mean difference: Absolute	Percentage	Mean difference: Absolute	Percentage
Wing length	0.53 mm	0.68	0.35 mm	0.47
Tail length	0.75 mm	1.29	0.80 mm	1.41
Bill length	0.13 mm	1.35	0.06 mm	0.62
Bill width	0.05 mm	0.65	0.05 mm	0.74
Tarsus length	0.04 mm	0.20	0.02 mm	0.08
Weight	−0.29 g	−0.97	0.23 g	0.80
Adjusted weight	−0.20 g	−0.65	0.27 g	0.93

[a] 24 samples (493 adults, 639 first-year birds) for linear dimensions; 22 samples (463 adults, 616 first-year birds) for weight and adjusted weight.
[b] 24 samples (287 adults, 588 first-year birds) for linear dimensions; 22 samples (270 adults, 567 first-year birds) for weight and adjusted weight.

TABLE 6

AGE VARIATION IN FAT CONDITION IN HOUSE SPARROWS

(Unbiased estimate of intrapopulation difference in fat-category scores between adult and first-year birds)

Period of collection	Sex	Number of samples	Number of specimens Adult : first-year	Mean difference in fat-category scores
Oct.–early Nov.	Male	21	441 : 534	–0.13
	Female	21	199 : 505	–0.04
Late Nov.–Feb.	Male	5	54 : 134	–0.05
	Female	5	34 : 80	–0.02
Combined: Oct.–Feb.	Male	26	495 : 668	–0.12
	Female	26	233 : 585	–0.04

significant (table 4) owing to a cancelling of age effects in the two sexes, which is reflected in the significant interaction between age and sex. In the female, first-year birds average 0.80% lighter in body weight than adults, but first-year males are 0.97% heavier than adult males (table 5).

Studies of the annual cycle in Kansas and Texas (Selander and Johnston, unpublished data) explain this sexual difference. In October, after the annual molt, males experience testicular recrudescence, which is more marked in adult than in first-year individuals. Associated with this autumnal gonadal activity is a reduction in body fat, owing, presumably, in part to increased physical activity involved in courtship and territorial behavior (Summers-Smith, 1963); and the greater activity of the adult males is accompanied by a larger decrease in fat deposits. This is demonstrated in table 6 for our material and in the annual cycle of weight variation in males at Austin, Texas (fig. 1). Note that in November, following the period of autumnal activity of the testes, adult males weigh 1.7% more than first-year males. Vernal testicular recrudescence is also accompanied by a loss in weight (fig. 1). Average weight of adult males, which are more advanced in testis development than first-year males, decreases in January, but weight loss is not apparent in first-year males until February.

Females experience no conspicuous autumnal gonadal recrudescence (Summers-Smith, 1963:98; Selander and Johnston, unpublished data) and, correspondingly, no decrease in body weight. Body weights and average levels of subcutaneous fat are similar in the two age groups (tables 5 and 6).

In specimens from the "Filderpopulation" collected in four villages near Stuttgart, Germany (Löhrl and Böhringer, 1957), age differences in wing length (1.28% for 248 adult [skull completely ossified] and 490 first-year [skull not completely ossified] males, and 0.93% for 225 adult and 447 first-year females) are greater than the mean values for our samples. Adults of the "Filderpopulation" sample, which was taken in November and December following the period of autumnal gonadal recrudescence, are 1.77% (males) and 1.93% (females) heavier than first-year birds. This difference presumably is attributable partly to age variation in average level of fat deposition but may also reflect an age difference in nonfat body mass.

Graber and Graber (1965) found that the brain averages 109 mg heavier ($P < 0.01$) in House Sparrows from 100 to 180 days old than in adult individuals, primarily as a result of greater absolute water content.

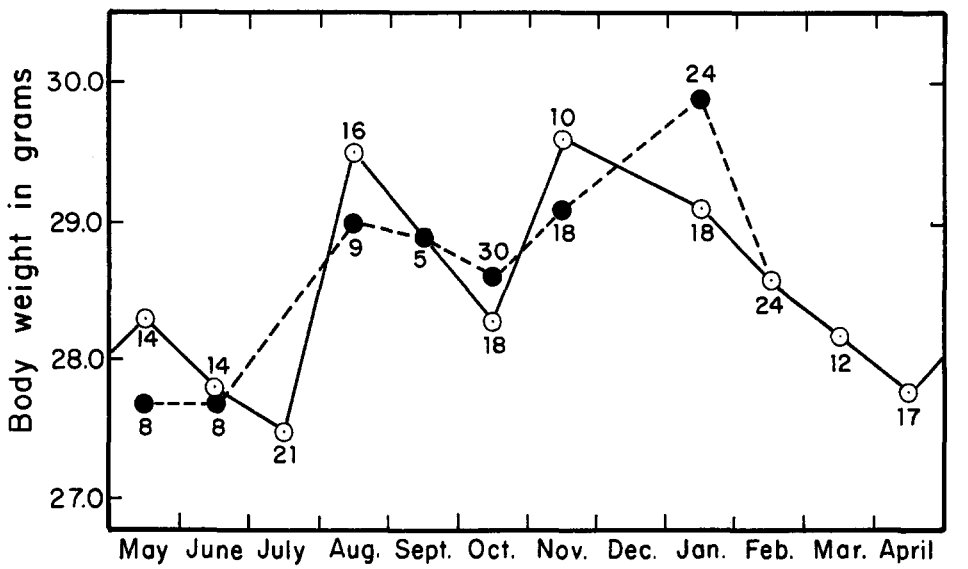

Figure 1. Seasonal variation in mean body weight of adult (circles) and first-year (dots) male House Sparrows at Austin, Texas. Numerals indicate sample sizes.

Sexual Dimorphism

Sexual dimorphism is evident in all mensural characters except bill length and width (tables 5 and 7). Relative to body mass, as reflected by tarsus length or cube root of body weight, the wing and tail are disproportionately longer in males than in females.

Wing-length measurements from samples of German populations of the House Sparrow show sexual differences similar to those in our material: 3.51% (650 males, 626 females; Niethammer, 1953); 3.22% (392, 312; Grimm, 1954); 3.40% (240, 279; Geiler, 1959); adult birds, 3.75% (248 males, 225 females), first-year birds, 3.40% (490, 447; Löhrl and Böhringer, 1957). Grimm's study (1954) shows a 4.97% sexual difference in mean tail length (374 males, 302 females), which is unaccountably large.

Largely as a result of reduction in body fat in males in periods of testicular activity, the degree of sexual dimorphism in body weight varies seasonally. In our samples, most of which were taken in the period of autumnal recrudescence of the testes, adult males are only 0.35% heavier than adult females (table 7), but, because autumnal weight loss is less marked in first-year males, sexual difference in weight in first-year birds is greater, amounting to 2.25%. In the German "Filderpopulation" sample collected in November and December, sexual differences in weight are 2.74% for adults and 2.90% for first-year birds (Löhrl and Böhringer, 1957). Grimm's data (1954) from a sample of 672 males and 581 females taken in central Germany from December through February show a 3.08% sexual difference in body weight, and Geiler (1959) demonstrated a 2.26% difference in 241 males and 279 females collected in February at Grosspösna, Germany. Finally, Niethammer's data (1953) for a sample of 650 males and 626 females collected in March show a 1.01% sexual difference in body weight.

TABLE 7

SEXUAL DIMORPHISM IN SIZE IN NORTH AMERICAN HOUSE SPARROWS
(Unbiased estimates of intrapopulation differences between males and females)

Character	First-year[a]		Adult[b]	
	Mean difference: Absolute	Percentage	Mean difference: Absolute	Percentage
Wing length	2.88 mm	3.71	2.70 mm	3.50
Tail length	1.84 mm	3.28	1.96 mm	3.42
Bill length	−0.01 mm	−0.06	0.05 mm	0.55
Bill width	0.01 mm	0.10	−0.01 mm	−0.18
Tarsus length	0.15 mm	0.83	0.16 mm	0.89
Weight	0.66 g	2.25	0.10 g	0.35
Adjusted weight	0.81 g	2.73	0.28 g	0.96

[a] 24 samples (639 males, 588 females) for linear dimensions; 22 samples (616 males, 567 females) for weight and adjusted weight.
[b] 24 samples (493 males, 287 females) for linear dimensions; 22 samples (463 males, 270 females) for weight and adjusted weight.

Considering all available data, we estimate that the actual sexual difference in body mass in the House Sparrow is approximately 2.8%. This is equivalent to a difference in cube root of body weight of 0.9%, which is similar to the percentage difference calculated for tarsus length (table 7).

Quiring and Bade (1943) reported that mean weights of the brain and liver are greater in males and eye weight is greater in females, but the observed sexual differences in brain weight and eye weight are actually not significant ($t = 1.78$, 99 *d.f.* and $t = 1.95$, 98 *d.f.*), and the difference in liver weight is not highly significant ($t = 2.41^*$, 99 *d.f.*). In a recent study, Graber and Graber (1965:310) found no significant sexual variation in brain weight, and corroboratory evidence of a lack of sexual difference in eye weight is provided by Payne (1961). Confirming a report by Quiring and Bade (1943), Hartman (1946) found no sexual differences in mean weights of the adrenals and thyroids.

Adaptive significance of sexual dimorphism in size. The slightly larger body size of the male may be attributed to Darwinian sexual selection. We presume that sexual differences in wing length and tail length relative to body mass are adaptively related to behavioral differences. It is likely that male House Sparrows fly more often, for longer distances, or at a different average speed than females, as Banks (1964:43) has suggested for the White-crowned Sparrow (*Zonotrichia leucophrys*), another species in which sexual dimorphism in wing length exceeds that in tarsus length or other linear dimensions. Annan's (1965) alternative suggestion that dimorphism in wing length in the White-crowned Sparrow is related to sexual differences in distance or duration of migratory flight obviously cannot apply to the nonmigratory House Sparrow or to the resident races of the White-crowned Sparrow.

The close similarity in bill size in male and female House Sparrows may be adaptive in relation to niche utilization. We suggest that selection maintains bill size in both sexes at the optimum for utilization of food resources, with the result that, relative to body mass, the bill is disproportionally small in the male and large in the female. As noted by Selander (1966), small degrees of sexual dimorphism in bill size occur in omnivorous species of birds, which, like the House Sparrow

TABLE 8

INTRAPOPULATION VARIABILITY IN SIZE IN HOUSE SPARROWS FROM NORTH AMERICA, HAWAIIAN ISLANDS, AND BERMUDA

Character	Males			Females			F[a]
	No. of samples	Mean sample size	Unweighted mean coefficient of variation (%)	No. of samples	Mean sample size	Unweighted mean coefficient of variation (%)	
Wing length	29	42	1.876	27	32	1.879	1.00
Tail length	30	41	2.604	27	33	2.799	1.16
Bill length	30	42	3.794	27	35	3.870	1.04
Bill width	30	43	3.434	27	35	3.470	1.02
Tarsus length	30	43	3.618	27	35	3.675	1.03
Weight	24	64	5.821	22	35	5.956	1.05

[a] $F = \frac{0.4343 \log [1 + (\text{C. V.}_{F})^2]}{0.4343 \log [1 + (\text{C. V.}_{M})^2]}$, where C. V. is in the form $s/\bar{x}$ (Wright, 1952; Bader and Lehmann, 1965; Lewontin, 1966); for all characters, $P > 0.05$.

(Kalmbach, 1940; Southern, 1945; Hammer, 1948; Mansfeld, 1950), exploit food supplies that are sufficiently abundant to permit extensive sexual overlap in utilization, whereas marked sexual divergence in bill size, with an accompanying sexual difference in niche utilization functioning to alleviate intersexual competition for food, is characteristic of food specialists. A parallel relationship exists between food abundance and interspecific difference in bill size among sympatric congeneric species of birds (Schoener, 1965).

INTRAPOPULATION VARIABILITY

Mean coefficients of variation for linear dimensions and body weight are shown in table 8. In order of increasing variability, the characters are wing length, tail length, bill width, tarsus length, bill length, and body weight. The sequence is "standard" for birds in that wing length is the least variable linear dimension and bill length is the most variable.

In each of the six characters studied, the mean coefficient of variation for females is slightly larger than that for males ($P = 0.03$ by two-tailed Sign Test), although for no single character is the difference significant. Because mean sample size is smaller for females than for males, application of Haldane's (1955) correction for bias would increase rather than reduce the sexual difference. Females are also slightly more variable than males in eight German samples studied by Niethammer (1953). The probable cause of this minor sexual difference in variability relative to the mean is the fact that, while females average slightly smaller than males, variances are equal in the sexes, there being no correlation between variance and mean, as demonstrated for bill width in figure 2.

In the absence of scaling of variance and mean, direct comparison of the untransformed sample variances is possible, employing Bartlett's test of homogeneity (table 9). Since only 3 of 27 chi-square values are significant at the level of $P \leq 0.05$, the data provide strong evidence for an absence of geographic variation in intrapopulation variability of size characters in North America.

Finding no greater variability in wing length and bill length in North American House Sparrow populations than in those of England and Germany, Lack (1940)

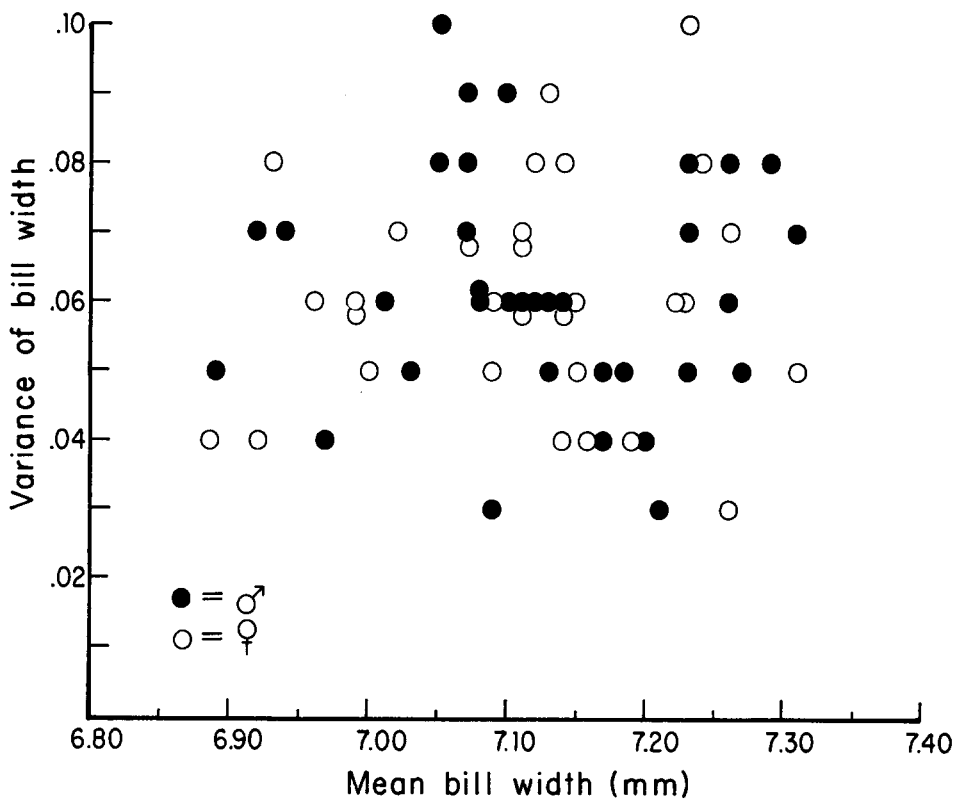

Figure 2. Absence of scaling of mean and variance in bill width in samples from North America, Oahu, and Bermuda.

concluded that, if there was a phase of increased variability following introduction, it was confined to a brief period when the populations were rapidly expanding and adapting to new environmental conditions. Calhoun (1947a) also found no increased variability in wing length in North American populations, and, similarly, a comparison of our samples of New World populations with those from England and Germany (table 10) reveals no difference in average level of variability. As expected, samples from single localities are generally less variable than those collected over wider geographic areas, and, for this reason, coefficients of variation for Lack's samples for "England" and "Germany" are not strictly comparable with those for our samples and the German samples shown in table 10.

Correlations and Regressions

Intrasexual correlations and regressions. Linear product-moment correlations between all paired combinations of body dimensions and weight were computed for 18 samples of males and 18 samples of females, with the age groups combined. Coefficients of correlation between weight and adjusted weight are heterogeneous ($\chi^2_{(17)} = 75.81^{**}$ for males and 36.61^{**} for females), but those for other pairs of characters are homogeneous ($\chi^2_{(17)} < 33.4$, $P > 0.01$).

TABLE 9

BARTLETT'S TEST OF HOMOGENEITY OF VARIANCE IN SIZE IN NORTH AMERICAN HOUSE SPARROWS

Character	Adult males[a]		First-year males[b]	
	Number of samples	Corrected chi-square	Number of samples	Corrected chi-square
Wing length	29	21.92	29	24.10
Tail length	29	40.53	29	30.56
Bill length	29	21.64	29	38.50
Bill width	29	34.56	29	26.72
Tarsus length	29	37.80	29	48.16*
Weight	25	24.38	25	49.09**
Adjusted weight	25	28.91	25	47.77**
Character	Adult females[c]		First-year females[d]	
	Number of samples	Corrected chi-square	Number of samples	Corrected chi-square
Wing length	28	17.31	29	36.54
Tail length	28	28.59	29	24.75
Bill length	28	24.44	29	29.41
Bill width	28	22.87	29	36.03
Tarsus length	28	18.36	29	19.82
Weight	24	14.09	25	25.17
Adjusted weight	24	14.21	25	27.96

[a] $n = 540$ for linear dimensions; 500 for weight and adjusted weight.
[b] $n = 761$; 705.
[c] $n = 315$; 293.
[d] $n = 651$; 586.

Average intrapopulation correlation coefficients for the 18 samples, weighted and corrected for bias, are shown in table 11. All coefficients are positive, and, with the exceptions of those for tarsus length–tail length in both sexes and tail length–bill width in males, all are significant at the 1% level. The strongest correlations are between wing length and tail length and between weight and adjusted weight.

For 14 of the 21 pairs of characters, correlation coefficients are slightly larger for females than for males ($P = 0.03$ by two-tailed Sign Test). The fact that correlations involving body weight tend to be weaker in males may be attributed, at least in part, to greater intrapopulation variation in body weight resulting from age and individual variation in degree of loss of body fat in the autumnal period of activity of the testes.

Partial correlation and regression coefficients for three sets of size characters are presented in table 12. The strong total correlation between wing length and tail length is independent of body weight, and the total correlation between bill width and tarsus length results mainly from partial correlations of these characters with body weight.

Correlation coefficients for certain size characters in the House Sparrow were previously presented by other authors. For sparrows collected at Hohenthurm, central Germany, in December, Grimm (1954) obtained the following coefficients: wing length–tail length, $r = 0.408$ (374 males); wing length–weight, 0.614 (247 males); bill length–weight, 0.251 (93 males); tail length–weight, 0.290 (374 males) and 0.408 (302 females). In a sample from Stuttgart, Germany, studied by Löhrl and Böhringer (1957), wing length and body weight were significantly correlated

TABLE 10

INTRAPOPULATION VARIABILITY IN SIZE IN HOUSE SPARROWS FROM ENGLAND AND GERMANY

Locality	Males		Females	
	Number of samples	Unweighted mean coefficient of variation (%)	Number of samples	Unweighted mean coefficient of variation (%)
		Wing length		
"England"[a]	1	2.44		
Oxford, England[b]	1	2.28	1	1.90
"Germany"[a]	1	2.45		
North Rhine-Westphalia, Germany[c]	8	2.050	8	2.066
Central and western Germany[d]	3	2.163	2	2.060
Filderpopulation, Stuttgart, Germany[e]	1 (adult)	1.89	1 (adult)	1.95
	1 (first-year)	2.02	1 (first-year)	1.87
		Tail length		
Oxford, England	1	2.54	1	2.44
Central and western Germany	1	4.32	1	3.38
Ludwigsburg, Germany[b]	1	2.45	1	2.34
		Bill length		
"England"	1	3.99		
Oxford, England	1	3.62	1	4.41
"Germany"	1	3.81		
Ludwigsburg, Germany	1	3.82	1	4.76
		Bill width		
Oxford, England	1	3.98	1	4.11
Ludwigsburg, Germany	1	3.68	1	3.49
		Tarsus length		
Oxford, England	1	4.51	1	3.94
Ludwigsburg, Germany	1	3.61	1	4.03
		Weight		
Oxford, England	1	6.01	1	5.92
North Rhine-Westphalia, Germany	8	4.704	8	5.385
Central and western Germany	4	5.795	3	6.590
Filderpopulation, Stuttgart, Germany	1 (adult)	4.82	1 (adult)	5.50
	1 (first-year)	5.45	1 (first-year)	5.09
Ludwigsburg, Germany	1	5.30	1	6.23

[a] Lack (1940).
[b] Present study.
[c] Niethammer (1953).
[d] Grimm (1954).
[e] Löhrl and Böhringer (1957).

in all sex and age groups: 248 adult males, $r = 0.38$; 490 first-year males, 0.31; 225 adult females, 0.21; and 447 first-year females, 0.38. In males from Berkeley, California, Lack (1940:241) found no significant correlation between wing length and bill depth or length and between bill length and bill depth, presumably because the specimens were collected in a variety of seasons. As noted by Grimm (1954:316), existing correlations involving bill length or wing length may be obscured by individual and seasonal variation in amount of wear.

TABLE 11

INTRAPOPULATION CORRELATIONS OF SIZE CHARACTERS IN HOUSE SPARROWS
(Unbiased estimates[a] of linear product-moment correlation coefficients based on samples from 18 localities)

	Wing length	Tail length	Bill length	Bill width	Tarsus length	Weight	Adjusted weight
Wing length	x	0.623	0.140	0.186	0.257	0.285	0.286
Tail length	0.580	x	0.122	**0.074**	**0.006**	0.099	0.122
Bill length	0.242	0.135	x	0.204	0.245	0.197	0.214
Bill width	0.186	0.129	0.207	x	0.265	0.380	0.367
Tarsus length	0.250	**0.089**	0.263	0.263	x	0.389	0.399
Weight	0.285	0.200	0.263	0.428	0.407	x	0.963
Adjusted weight	0.285	0.201	0.263	0.425	0.399	0.965	x

Explanation: Coefficients above diagonal, males; below diagonal, females. All coefficients significant at the 1% level are in roman type; those below this level are in **boldface**. Degrees of freedom = 892 for males, 596 for females.

[a] Snedecor (1956:178–180).

Significant correlations between body weight and heart weight ($r = 0.805$) and body weight and liver weight ($r = 0.451$) were reported by Quiring and Bade (1943).

Intersexual correlations and regressions. From data for 18 samples, we computed unweighted intersexual correlation and regression coefficients for means of linear dimensions and adjusted body weight (fig. 3), all of which are highly significant ($P < 0.001$). The apparent variation in strength of correlation among the six characters is not confirmed by a test of homogeneity ($\chi^2_{(5)} = 7.092$).

Interpopulation correlations. Interpopulation correlations (table 13) are strong for wing length–tail length and weight–adjusted weight and moderate for bill length–tarsus length, bill width–tarsus length, and tarsus length–weight, but coefficients for other pairs of characters are not significant, indicating that the linear dimensions and body weight tend to vary geographically in more or less independent fashion.

TABLE 12

PARTIAL INTRAPOPULATION CORRELATIONS AND REGRESSIONS OF SELECTED SIZE CHARACTERS
(Unbiased estimates of coefficients based on samples from 18 localities)

Dependent variable	Independent variables	Partial correlation coefficient		Partial regression coefficient (b)	
		Males	Females	Males	Females
Tail length	Wing length[a]	0.628	0.545	0.692	0.649
	Adjusted weight	−0.109	0.049	0.069	0.035
Bill length	Tarsus length	0.176	0.184	0.100	0.109
	Adjusted weight	0.119	0.166	0.024	0.037
Bill width	Tarsus length	0.119	0.113	0.045	0.045
	Adjusted weight[b]	0.310	0.361	0.048	0.058

[a] For each coefficient, $P < 0.01$.
[b] For each coefficient, $P < 0.05$.

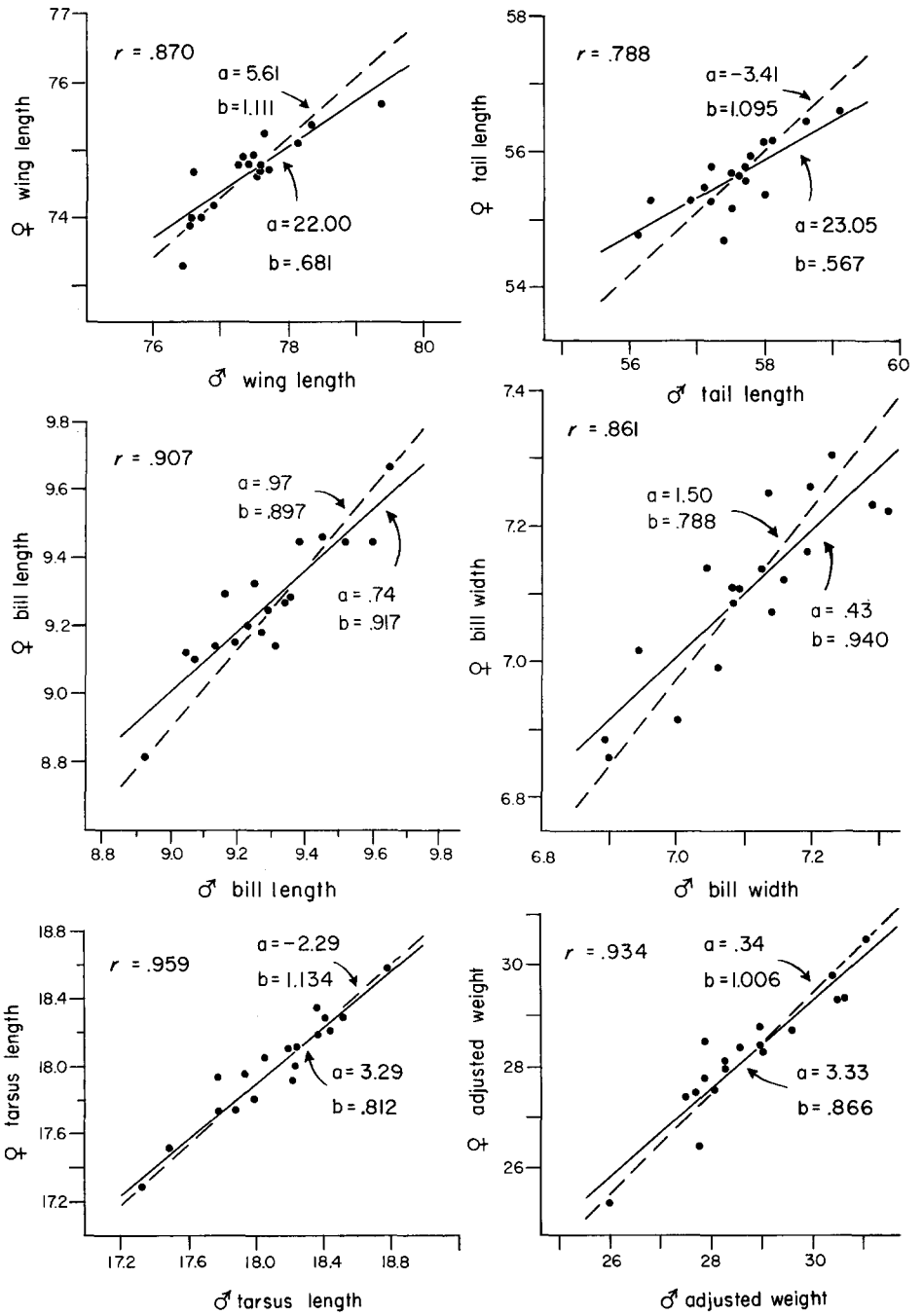

Figure 3. Linear correlation and regression of mean measurements of male and female House Sparrows from 18 localities in North America. Solid line, regression of female on male; dashed line, regression of male on female.

TABLE 13

INTERPOPULATION CORRELATIONS OF SIZE CHARACTERS IN HOUSE SPARROWS
(Unweighted linear product-moment correlation coefficients of means for samples from 18 localities)

	Wing length	Tail length	Bill length	Bill width	Tarsus length	Weight	Adjusted weight
Wing length	x	0.871	**0.468**	**0.118**	**0.381**	**0.476**	**0.476**
Tail length	0.869	x	**0.315**	**–0.104**	**0.100**	**0.271**	**0.258**
Bill length	**0.504**	**0.477**	x	**0.184**	0.603	**0.079**	**0.094**
Bill width	**0.343**	**0.112**	**0.351**	x	**0.588**	**0.442**	**0.479**
Tarsus length	**0.393**	**0.237**	0.680	0.683	x	**0.570**	0.591
Weight	**0.404**	**0.373**	**0.166**	**0.491**	**0.589**	x	0.996
Adjusted weight	**0.410**	**0.356**	**0.183**	**0.512**	0.631	0.990	x

Explanation: Coefficients above diagonal, males; below diagonal, females. All coefficients significant at the 1% level are in roman type; those below this level are in **boldface**.

VARIATION IN PLUMAGE

Effects of soiling. The effects of soiling on breast color in females are indicated in table 14, which presents color values for specimens before and after washing. For birds from rural areas (*e.g.*, Bastrop), which were discolored with light soil, washing produced sizable decreases in both brightness and purity. This finding is consistent with Johnston's report (1966) that feather pigments of the breast of females are darker than the soil washed from the plumage with white gasoline. But in specimens from downtown Detroit (Wayne State University campus), which were discolored with black soot, brightness increased 11.0% after washing. On a percentage basis, changes in brightness of pileum color in males produced by washing are even greater (table 15).

Xanthophyll pigments. The plumage of the House Sparrow has a pale yellow "wash," which is most conspicuous on the belly, where the feathers are otherwise white. The color is more apparent in washed than in soiled specimens and varies geographically in degree of saturation, being most intense in birds from Detroit and Pittsburgh and least in those from Oakland (table 16). First evidence that the yellow pigment is not a melanin was provided by reflectance spectra. As shown in figure 4, the diffuse reflectance curves of belly feathers have alternating peaks of reflectance (443 and 477 mμ) and absorbance (433, 457, and 488 mμ), whereas melanins show no maxima or minima in the visible wavelength range (Fox, 1953:69). The presence of this yellow pigment on the breast and other areas of the plumage heavily pigmented with melanin is indicated by the same pattern of peaks, weakly expressed (fig. 4).

The yellow pigment was extracted from the belly feathers of females by heating them for 20 minutes in ethanol containing 5% of potassium hydroxide solution (10% by weight in water). The pigment proved to be hypophasic xanthophyll with absorption maxima in petroleum ether at 419, 442, and 471 mμ. Apparently identical pigment was extracted from the base of the bill and from the subcutaneous fat. When chromatographed on an Eastman silica gel plate with a solvent of 80% ethyl acetate and 20% methylene dichloride, the pigment extracted from the belly feathers separated into an intense slow zone (maxima in petroleum ether at 419, 442, and 470 mμ) (fig. 5) and a pale fast zone. The component of the fast zone has yet to

TABLE 14

EFFECT OF SOILING ON BREAST COLOR IN FEMALE HOUSE SPARROWS

Locality and age	Number of specimens	Condition of plumage	Brightness		Dominant wavelength		Purity	
			Mean	SD	Mean	SD	Mean	SD
Bastrop								
Adult	11	Unwashed	28.33	2.21	579.2	0.6	24.45	2.32
		Washed	25.88	3.10	579.3	1.1	20.41	2.93
First-year	13	Unwashed	26.75	2.99	578.8	0.7	23.84	2.33
		Washed	24.52	4.01	579.2	0.7	20.30	2.50
Age difference		Unwashed	5.6% ($t = 0.998$)		0.4 mμ ($t = 1.260$)		2.5% ($t = 0.638$)	
		Washed	5.3% ($t = 0.916$)		0.1 mμ ($t = 0.322$)		0.5% ($t = 0.959$)	
Mean change with washing[a]								
Adult			8.6% ($t = 3.324^{**}$)		−0.1 mμ ($t = -0.289$)		16.5% ($t = 5.746^{**}$)	
First-year			8.3% ($t = 3.880^{**}$)		−0.4 mμ ($t = -1.477$)		14.8% ($t = 10.239^{**}$)	
Las Cruces								
Adult	10	Unwashed	26.32	2.18	579.4	0.5	23.27	1.62
		Washed	25.06	2.17	579.2	0.8	21.83	1.23
First-year	14	Unwashed	26.37	3.15	579.1	0.5	23.01	1.96
		Washed	23.84	3.07	579.1	0.7	19.95	2.63
Age difference		Unwashed	−0.2% ($t = -0.004$)		0.3 mμ ($t = 1.614$)		1.1% ($t = 0.347$)	
		Washed	4.9% ($t = 1.093$)		0.1 mμ ($t = 0.413$)		8.6% ($t = 2.095^{*}$)	
Mean change with washing[a]								
Adult			4.8% ($t = 2.973^{**}$)		0.2 mμ ($t = 0.612$)		6.2% ($t = 2.387^{*}$)	
First-year			9.6% ($t = 2.599^{**}$)		0.0 mμ		13.3% ($t = 7.986^{**}$)	
Oahu								
Adult	13	Unwashed	25.40	2.81	579.3	0.6	28.27	2.07
		Washed	21.55	2.48	579.2	0.8	24.70	3.55
First-year	11	Unwashed	24.35	2.31	579.2	0.7	29.03	2.31
		Washed	22.64	2.35	579.4	0.7	24.99	2.24
Age difference		Unwashed	4.1% ($t = 0.991$)		0.1 mμ ($t = 0.141$)		−2.6% ($t = -0.848$)	
		Washed	−4.8% ($t = -1.101$)		−0.2 mμ ($t = -0.134$)		−1.2% ($t = -0.236$)	
Mean change with washing[a]								
Adult			15.2% ($t = 4.376^{**}$)		0.1 mμ ($t = 0.291$)		12.6% ($t = 4.207^{**}$)	
First-year			7.0% ($t = 3.615^{**}$)		−0.2 mμ ($t = -0.690$)		13.9% ($t = 5.250^{**}$)	

TABLE 14. *Continued*

Locality and age	Number of specimens	Condition of plumage	Brightness		Dominant wavelength		Purity	
			Mean	SD	Mean	SD	Mean	SD
Detroit 1963								
Adult	3	Unwashed	21.70	—	579.3	—	19.57	—
		Washed	21.87	—	578.3	—	18.13	—
First-year	15	Unwashed	19.84	4.61	579.0	0.9	22.65	5.96
		Washed	22.29	9.33	579.2	0.6	22.48	8.38
Age difference		Unwashed	8.6%		0.3 mμ		−13.6%	
		Washed	−1.9%		−0.9 mμ		−19.3%	
Mean change with washing[a]								
Adult			−0.7%		1.0 mμ		7.4%	
First-year			−11.0% ($t = -4.326^{**}$)		−0.2 mμ ($t = -0.676$)		0.8% ($t = 0.314$)	

[a] Significance judged by *t*-test of difference between correlated means (Steel and Torrie, 1960:78–79). Significant differences are noted at the 5% level (*) or at the 1% level (**).

be identified, but that of the slow zone is similar to if not identical with canary-xanthophyll (maxima at 418, 443, and 472 mμ) described by Brockmann and Völker (1934). Among other species of the Ploceidae, xanthophyll (lutein) or its transformation product canary-xanthophyll has been identified in feathers of *Ploceus cucullatus* and several forms of *Euplectes* (Brockmann and Völker, 1934; Kritzler, 1943).

ADULT PLUMAGE

In adult plumages of the House Sparrow (described by Witherby *et al.*, 1940:159), the major sexually dimorphic characters are on the anterior part of the body (table 17). Sexual dimorphism in pattern of the head and breast is best appreciated when birds are viewed head-on (fig. 6), as they are by recipients of threat displays (Daanje, 1941; Summers-Smith, 1963). In general, areas that are darkly colored in the male are lightly colored in the female. The bill of the male, which becomes black in the breeding season under the influence of androgen (Keck, 1934; Witschi, 1936; Witschi and Woods, 1936), is surrounded by black feathers of the frontal, loral, lateral postmandibular, and chin regions. Dorsally, this black face "mask" contrasts with the gray pileum and is further accentuated by the white supraloral-frontal line, which is continued posteriorly by the white postocular region. Laterally, the mask contrasts with the gray cheeks, which are bounded posteriorly by the chestnut lateral nape crescents. The pattern in the female is reversed, the mask being light grayish brown and the cheeks and the pileum darker brown. The bill of the female is light grayish brown in the nonbreeding season but darkens slightly at the time of gonadal activity, occasionally becoming almost black (Nichols, 1935: 12; Witschi, 1961:144). Whether this change is effected by estrogen or reflects a low titer of androgen in the female remains to be determined experimentally.

In the threat display, given by both sexes, the partially spread wings of the male reveal chestnut epaulets contrasting with white wing bars, while there is less bright color and contrast in the brown or chestnut-brown epaulets and buff wing bars of the female.

TABLE 15

AGE VARIATION IN PILEUM COLOR IN MALE HOUSE SPARROWS

Locality and age	Number of specimens	Condition of plumage	Brightness		Dominant wavelength		Purity	
			Mean	SD	Mean	SD	Mean	SD
Los Angeles								
Adult	16	Unwashed	9.26	1.08	578.6	1.7	20.48	2.77
		Washed	7.99	0.84	579.0	1.8	20.03	3.78
First-year	26	Unwashed	8.65	0.87	579.6	1.6	24.46	3.71
		Washed	7.68	0.85	579.8	1.7	24.24	3.89
Age difference[a]		Unwashed	6.6% ($t = 2.013$)		−1.0 mμ ($t = 1.894$)		−16.3% ($t = 3.875^{**}$)	
		Washed	3.9% ($t = 1.158$)		−0.8 mμ ($t = 1.459$)		−17.4% ($t = 3.444^{**}$)	
Mean change with washing[a]								
Adult			13.7% ($t = 9.142^{**}$)		−0.4 mμ ($t = -0.659$)		2.2% ($t = 0.734$)	
First-year			11.2% ($t = 9.693^{**}$)		−0.2 mμ ($t = -0.481$)		0.9% ($t = 0.362$)	
Oahu								
Adult	23	Unwashed	8.57	0.95	580.0	1.3	26.17	2.98
		Washed	7.32	0.97	579.7	1.6	26.26	3.85
First-year	26	Unwashed	8.43	0.77	580.3	1.5	28.66	4.03
		Washed	7.06	0.83	580.3	1.4	29.48	5.79
Age difference[a]		Unwashed	1.6% ($t = 0.560$)		−0.3 mμ ($t = 0.725$)		−8.7% ($t = 2.456^{*}$)	
		Washed	3.5% ($t = 1.012$)		−0.6 mμ ($t = 1.422$)		−10.9% ($t = 2.260^{*}$)	
Mean change with washing[a]								
Adult			14.6% ($t = 7.067^{**}$)		0.3 mμ ($t = 0.536$)		−0.3% ($t = 0.258$)	
First-year			16.2% ($t = 14.906^{**}$)		0.0 mμ —		−2.8% ($t = -1.558$)	

[a] Significance judged by *t*-test of difference between correlated means (Steel and Torrie, 1960:78–79). Significant differences are noted at the 5% level (*) or at the 1% level (**).

FIRST-YEAR PLUMAGE

Female. First-year and adult females cannot be consistently distinguished on the basis of plumage. Harrison's report (1961:81) that first-year females "show the broad [chestnut] edges to the secondaries which are lacking in adults" is puzzling, for in our material these "edges" are as fully developed in adults as in first-year birds.

Unwashed first-year and adult females are closely similar in breast color and pileum color (tables 18 and 19). There is no significant age difference in dominant wavelength, but small average differences in brightness and purity are apparent. In washed specimens, age variation in brightness and dominant wavelength of breast color is insignificant, but there is a significant age difference in purity (tables 20 and 21).

Intrapopulation variability in color of the breast and pileum is indicated for unwashed material by the following unweighted mean coefficients of variation (in %) derived from 26 samples from North America, Oahu, Bermuda, and England (mean

TABLE 16

VARIATION IN BELLY COLOR IN ADULT MALE HOUSE SPARROWS

Sample locality	Number of specimens	Brightness		Dominant wavelength		Purity	
		Mean	SD	Mean	SD	Mean	SD
Oakland	10	68.49	4.22	574.6	0.5	10.33	1.74
Detroit 1965	10	64.98	3.04	574.6	0.5	21.13	3.83
Significance of difference[a]:		$t = 2.132$				$t = 8.120^{**}$	

[a] Cochran's approximation to Behrens-Fisher test for samples with unequal variance (Snedecor, 1956:97).

sample size: 21 for breast, 22 for pileum): breast Y = 10.81; breast $P_e = 10.55$; pileum Y = 10.85; pileum $P_e = 7.01$. Color is equally variable in samples from England and Germany and those from the New World.

Coefficients of linear product-moment correlation of brightness and purity of breast and pileum colors were computed for each of 25 samples from North America, Oahu, and Bermuda (total $n = 476$). Finding no heterogeneity among the coefficients, we computed average coefficients (weighted and corrected for bias) for the 25 samples, as follows: breast Y–breast P_e, $r = -0.119$; pileum Y–pileum P_e, $r = -0.164$; breast Y–pileum Y, $r = 0.356$; and breast P_e–pileum P_e, $r = 0.227$. With 426 degrees of freedom, all coefficients except that for breast Y–breast P_e are significant at the 1% level.

Interpopulation correlation coefficients based on 25 sample means of brightness and purity are: breast Y–breast P_e, $r = -0.137$; pileum Y–pileum P_e, $r = -0.212$; breast Y–pileum Y, $r = 0.745$; and breast P_e–pileum P_e, $r = 0.233$. With 23 degrees of freedom, only the coefficient for breast Y–pileum Y is significant.

First-year females tend to have a darker ground color and more conspicuous dark shaft-streaks on the belly. Variation in the latter character was analyzed by assigning females to six categories from 0 (conspicuously streaked) to 5 (unstreaked). The distribution of scores is shown in table 22, and the observed age difference is highly significant. For each size character studied, first-year females in belly-streaking categories 0 to 1 average slightly smaller than those in categories 2 to 5, but for no single character is the effect of belly-streaking class significant (table 23). Our samples are too small to permit a similar analysis for adult females.

The degree of belly streaking varies geographically, and, for 16 localities from which large samples of first-year and adult females are available, the coefficient of correlation between mean scores for the two age groups is 0.776 ($P < 0.001$). Geographic variation in belly streaking of males parallels that of females.

Male. In gross appearance the first-year male plumage is similar to the adult plumage, but we have detected important average differences in the head region, and other authors have noted other, relatively minor, differences. As noted by Keck (1934:318), in both sexes the first-year plumage differs from the adult in having buff feather edgings more evident, so that black, chestnut, and gray colors of the male are less prominent. The only distinction noted by Witherby *et al.* (1940:159) is that the first-year male has "more white on tips of feathers of chin." Harrison (1961:81) correctly reports that first-year males can often be recognized by the less pure gray pileum, but we find no basis for his assertion that first-year males have broader chestnut edges on the secondaries.

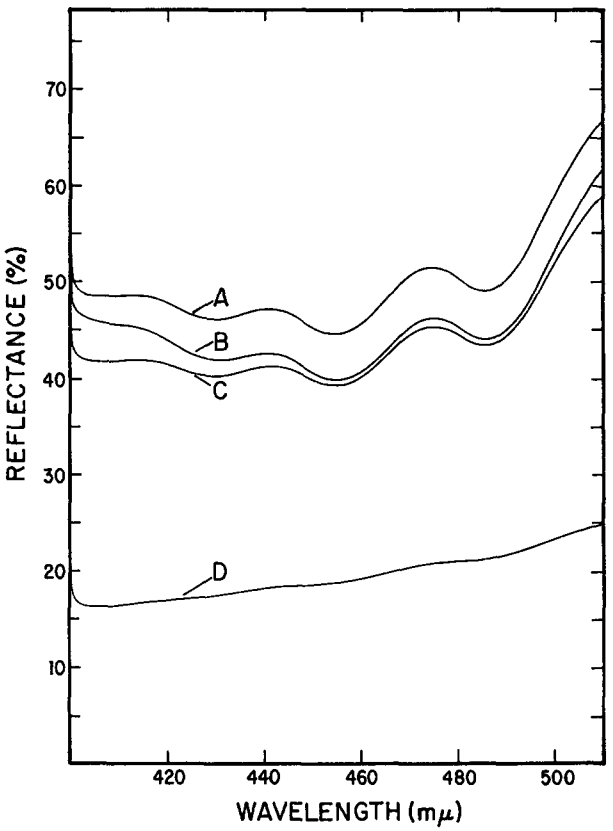

Figure 4. Diffuse reflectance spectra of belly plumage (A, B, C) and breast plumage (D), showing peaks characteristic of xanthophyll pigments. A, adult male, Zachary, Louisiana; B, adult male, Detroit, Michigan; C, adult male, Birmingham, Alabama; D, first-year female, Bastrop, Texas.

First-year males vary greatly in the degree to which the plumage of the head departs from the female-juvenile pattern and approaches the adult male pattern, characterized principally by the black face "mask" (frontispiece). To measure this variation, males were assigned to nine categories of color of the loral region, ranging from 0 (gray) to 8 (black), and the resulting data are shown in table 24. The lore-pattern score assigned to a specimen is a good index to the general degree of "masculinity" of the entire head pattern, for the degree of darkness of the loral region is strongly correlated with that of the frontal, postmandibular, subocular, and postocular triangle regions. Moreover, it is correlated with the degree of development of the supraloral-frontal white stripe and with the degree of grayness of the pileum. In low loral categories the buff edgings of the broad, chestnut lateral stripe are larger and the gray margins of the bib feathers and the brown margins of the pileum are wider.

First-year males have lighter loral areas, on the average, than do adults and are more variable individually (table 24 and frontispiece). Viewed frontally, the dark-gray mask of the average first-year bird is intermediate in pattern between

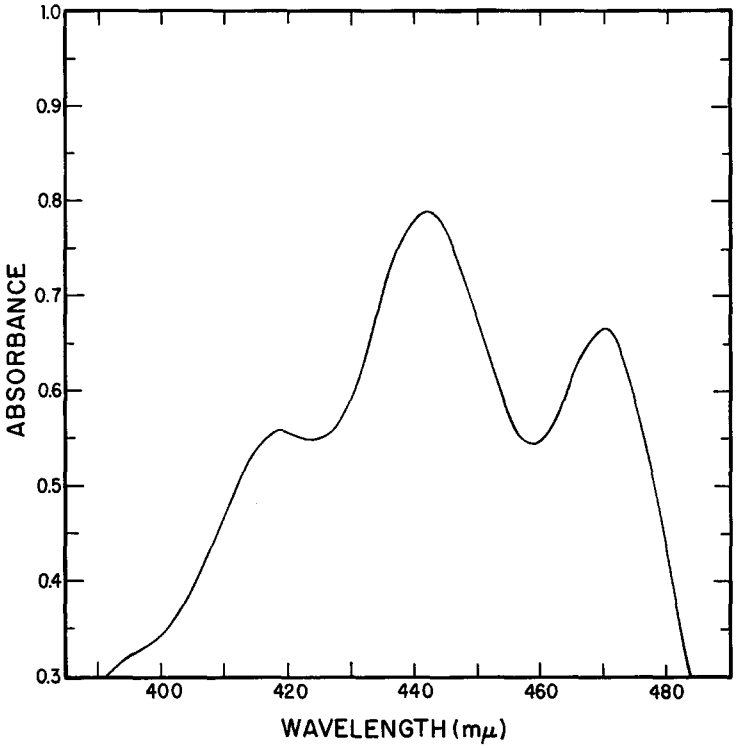

Figure 5. Absorption spectrum of xanthophyll (in petroleum ether) extracted from belly plumage of the House Sparrow.

the typical adult male and female (fig. 6). In the 12.4% of first-year males falling in categories 6, 7, and 8, the loral region is black or nearly so, as in the majority of adult males. Note also that 35% of males classified as adult on the basis of complete cranial ossification fall in categories 2 to 5, in which the lore is decidedly gray, as it is in most known first-year birds.

There is conspicuous geographic variation in North America in the average lore-pattern scores of adults and of first-year birds and in the degree of difference between average scores for the two age groups. Perhaps this variation is in part genetically determined, but interpretation is difficult because of the uncertainty that cranial ossification is a completely reliable criterion for age determination. Variation in scores for samples of "adult" birds could result from the inclusion of a geographically variable proportion of advanced first-year individuals that had achieved complete cranial ossification. When the percentages of "adult" males in our samples in the grayer lore categories are plotted against the isophanes (Hopkins, 1938) of the sample localities (fig. 7), a significant relationship is apparent, the percentage decreasing with isophane. At southern and coastal localities, where mild climates permit relatively long breeding seasons and there is greater opportunity for first-year birds to achieve cranial ossification by October or November, samples contain relatively large proportions of "adult" birds with gray lores. We suspect that many of these birds are in fact advanced first-year individuals.

TABLE 17

COLOR OF SEXUALLY DIMORPHIC PLUMAGE REGIONS IN HOUSE SPARROWS

Region	Female	First-year male	Adult male
Pileum (crown of head)	Uniform brown (feathers with narrow brownish-gray subbasal region and broad brown terminal region)	Grayish brown	Light brownish gray (feathers with gray subbasal region which becomes black distally; and narrow, pale-brown terminal region)
Supraloral-frontal	Brown	Light grayish brown	Light gray or dull white
Frontal	Light grayish brown	Dark brownish gray	Black
Loral	Light grayish brown	Dark brownish gray	Black
Lateral postmandibular	Light brown	Dark brownish gray	Black
Postocular triangle	Dark gray	Black or dull black	Black
Subocular	Light grayish brown	Black or dull black	Black
Superior postocular	Buff	Buffy white	White
Lateral stripe	Buff	Chestnut with large buff flecks (feathers chestnut, with buff terminal regions)	Chestnut with small buff flecks (feathers chestnut, with buff terminal regions)
Superior lateral stripe margin	Dark brown	Chestnut	Chestnut
Inferior lateral stripe margin	Dark brown	Chestnut	Chestnut
Cheek	Light brown	Light brownish gray	Gray
Chin, throat, and breast	Light brown (paler on chin and throat) with dark gray "ghost" bib usually present on chin and throat; highly variable individually	Black; feathers broadly margined with light brownish gray	Black; feathers narrowly margined with gray
Epaulet	Brown	Chestnut	Chestnut
Wing bar	Buff	Buffy white	White

In known first-year males it is possible to show relationships between lore pattern and certain size characters (table 25). Tail length increases with darkness of the lore, and wing length shows a similar trend, although the observed effect is not significant at conventional levels. Body weight decreases as the lore darkens, presumably because the darker-lored males are older (see below) and, hence, more responsive to environmental factors that stimulate autumnal gonadal development and the associated decrease in subcutaneous fat. When body weights are adjusted for fat condition, the effect of lore pattern on weight is lost. Surprisingly, our data demonstrate an inverse relationship between lore-pattern category and tarsus length.

Assuming that some or all gray-lored males with complete cranial ossification are first-year in age, we might expect them to average slightly smaller in size than adults with black lores. However, we are unable to demonstrate a relationship between lore category and any size character (table 26). If the gray-lored males

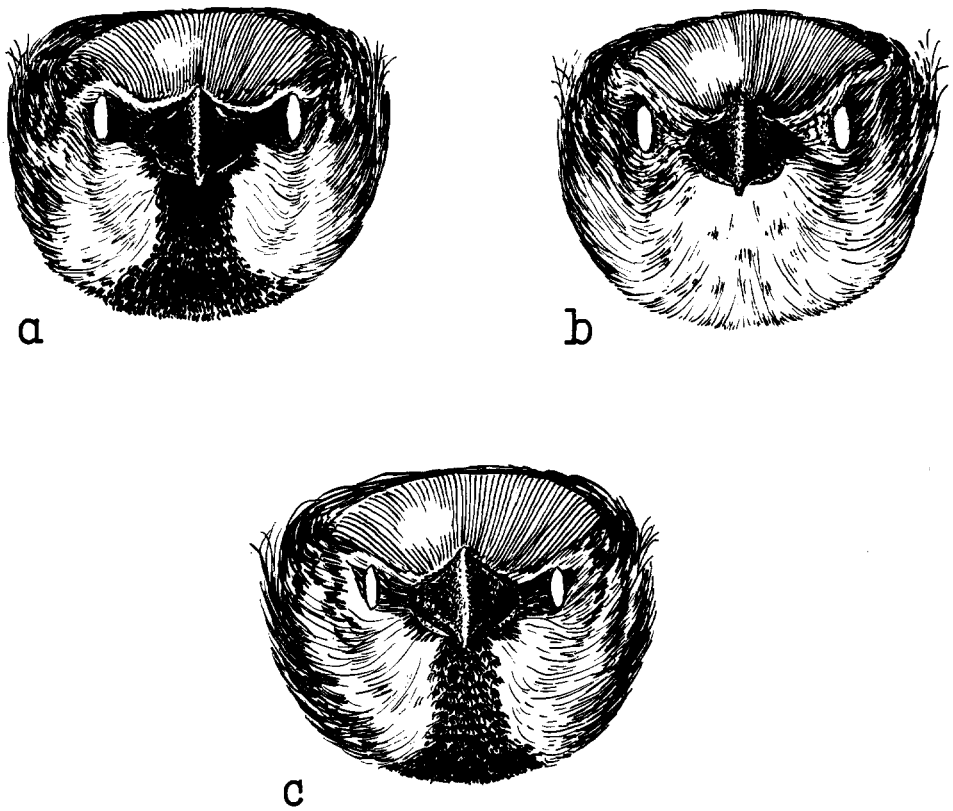

Figure 6. Frontal view of (a) adult male, (b) adult or first-year female, and (c) first-year male. Drawn from study skins by Pauline West.

with complete cranial ossification are in fact first-year birds, they are fully as large as true adults.

Individual and age variation in color of the pileum in males from Oahu and Los Angeles is shown in table 15. In both samples pileum color of first-year birds is significantly purer, on the average, than that of adults, and, although the data suggest that first-year birds are less bright in color than adults, the observed differences are not statistically significant.

Juvenal Plumage

Male and female juvenal plumages are similar to that of the first-year or adult female, but the colors are generally paler and the crown and rump are mottled with brown (Witherby *et al.*, 1940:159). Some sexual dimorphism is evident in the juvenal plumage, with juvenal males showing weak expression of several secondary sexual characters that are more fully developed in first-year and adult males (Nichols, 1935; Weaver, 1942; Harrison, 1961).

Atypical Plumage Variation

Rare plumage variants of the House Sparrow have been described by Nichols

TABLE 18

AGE VARIATION IN COLOR OF BREAST AND PILEUM IN UNWASHED FEMALE HOUSE SPARROWS FROM NORTH AMERICA
(Unbiased estimates of intrapopulation differences between adult and first-year birds)

Parameter	Mean difference: Absolute	Mean difference: Percentage
Breast[a]		
Brightness	0.77	2.98
Dominant wavelength	−0.12 mμ	−0.02
Purity	−0.67	−2.86
Pileum[b]		
Brightness	0.04	0.57
Dominant wavelength	0.12 mμ	0.02
Purity	−0.99	−2.96

[a] 25 samples (201 adults, 323 first-year birds).
[b] 24 samples (191 adults, 333 first-year birds).

(1935), Calhoun (1947b), and Harrison (1963a), and intersexes are described by Mayr (1949), Harrison (1961), and Selander, Johnston, and Cantu (unpublished data). Here we are concerned only with several relatively frequent plumage variants.

Chestnut on bib, rump, and pileum of males. In males chestnut color (erythromelanin; see Harrison, 1965) is often present on the normally black feathers of the bib, particularly on the lower breast (Piechocki, 1954:302). The rarity of occurrence of chestnut on the chin or throat may result from selection against variation in the appearance of the male as it is viewed from the front while displaying. From one to all feathers of the bib may be partly or wholly chestnut, but individuals in which more than half the bib is chestnut are rare (Witherby *et al.*, 1940:159; Calhoun, 1947b:305; Summers-Smith, 1963:99). The degree to which this and other variant plumage characters are genetically determined is unknown.

TABLE 19

ANALYSIS OF VARIANCE IN BREAST COLOR AND PILEUM COLOR IN UNWASHED FEMALE HOUSE SPARROWS FROM NORTH AMERICA

Source of variation	Degrees of freedom	*F*-ratios: Brightness	*F*-ratios: Dominant wavelength	*F*-ratios: Purity
Breast color[a]				
Age	1, 24	12.025**	3.232	5.693*
Locality	24, 474	8.086**	2.627**	9.639**
Age-locality	24, 474	0.680	0.919	1.522
Pileum color[b]				
Age	1, 23	0.192	3.116	35.096**
Locality	23, 476	10.238**	4.565**	3.980**
Age-locality	23, 476	0.857	1.032	0.526

[a] Mixed-model, two-way analysis, with age fixed, locality random. 25 samples (total $n = 524$ specimens). Significance of variation is noted at the 5% level (*) or at the 1% level (**).
[b] 24 samples (total $n = 524$ specimens).

TABLE 20

AGE VARIATION IN BREAST COLOR IN WASHED FEMALE HOUSE SPARROWS FROM NORTH AMERICA[a]
(Unbiased estimates of intrapopulation differences between adult and first-year birds)

Parameter	Mean difference: Absolute	Percentage
Brightness	0.32	1.25
Dominant wavelength	0.09 mμ	0.02
Purity	−1.01	−4.55

[a] 23 samples (233 adults, 258 first-year birds).

Male skins were assigned to five categories representing progressive degrees of expression of chestnut on the bib (table 27). Category 0 represents the usual condition in which all bib feathers are grossly black, but most males assigned to this category actually had one or more feathers showing a faint chestnut cast when viewed under strong illumination.

Chestnut is present on the bib of 25.49% of adult males but only 12.43% of first-year males (table 27). In a sample of 122 males from Echterdingen, Germany, studied by Löhrl and Böhringer (1957:238), approximately 25% of adults and 10% of first-year birds showed the character, and, for the entire sample, the percentage was 13.9. In central Germany, Piechocki (1954:301) found 3.5% of 5992 males with chestnut feathers on the black bib, and Calhoun (1947b:305) noted that 8.2% of 974 males from the United States showed chestnut on the bib.

Our samples show significant differences in frequency of the chestnut bib character, but the pattern of variation bears no apparent relationship to climatic or other environmental variables. Marked regional differences in frequency of this character were also noted by Piechocki (1954) in local populations in the Saale district, central Germany.

The normally buff feathers of the rump and the gray or grayish buff feathers of the pileum of males are occasionally tinged or conspicuously marked with chestnut (table 28). Chestnut occurs with approximately equal frequency in the two plumage regions, and the character apparently is more common in adult than in first-year birds. Variant males of *Passer d. domesticus* in Europe having chestnut on the pileum have been reported by Meise (1936), Daanje (1941), Piechocki (1954:302),

TABLE 21

ANALYSIS OF VARIANCE IN BREAST COLOR IN WASHED FEMALE HOUSE SPARROWS FROM NORTH AMERICA[a]

Source of variation	Degrees of freedom	*F*-ratios: Brightness	Dominant wavelength	Purity
Age	1, 22	0.713	0.681	14.814**
Locality	22, 445	5.689**	5.655**	9.208**
Age-locality	22, 445	0.821	1.623*	0.866

[a] Mixed-model, two-way analysis, with age fixed, locality random. 23 samples (total $n = 491$ specimens). Significance of variation is noted at the 5% level (*) or at the 1% level (**).

TABLE 22

INDIVIDUAL AND AGE VARIATION IN BELLY STREAKING IN FEMALE HOUSE SPARROWS

Age group	Number of specimens[a]	% in indicated belly-streaking category					
		0	1	2	3	4	5
Adult	266	2.3	18.8	40.6	20.3	13.9	3.8
First-year	694	6.3	36.0	40.5	13.7	3.3	0.1

[a] 30 samples.
Comparison: adult vs. first-year, $\chi^2_{(2)} = 75.09^{**}$, lumping categories 0–1, 2–3, and 4–5.

and Harrison (1961); and Calhoun (1947b) examined a male from Louisiana with the crown "completely chestnut."

From the frequencies of occurrence of chestnut on the bib, pileum, and rump in our samples, it is possible to predict the numbers of specimens that would be expected to exhibit chestnut in two plumage regions or in all three, assuming independence of the characters. For all associations, deviations from expected numbers are positive and highly significant (table 29).

"Hispaniolensis" breast pattern in males. In 15 adult and 16 first-year males, the lower breast posterior to the bib shows a black streaked pattern resembling that normally found in males of *Passer hispaniolensis*. This plumage variation has been noted by Harrison (1961:100) in males of *P. domesticus* from England.

Albinism. Many albino House Sparrows have been reported (Bumpus, 1898; Ross, 1963; Sage, 1963; Gross, 1965), but few data are available on the incidence of albinism in populations. Only partial albinism is represented in our material (table 30), varying in extent from a single feather to a condition in which approximately one-third of the plumage is white. The value of 1.89% for "conspicuous" albinism in males and females of both age groups is similar to those reported by Ilyenko (1960; *fide* Sage, 1963) for Moscow, Russia, and by Calhoun (1947b) for museum specimens from the United States, but it is greater than the 0.11% recorded in 20,931 birds from Germany by Piechocki (1954). Allowing for variation among workers in degree of thoroughness of examination, we conclude that the average frequency of readily detectable albinism in House Sparrow populations is from

TABLE 23

VARIATION IN SIZE IN RELATION TO BELLY STREAKING IN FIRST-YEAR FEMALE HOUSE SPARROWS

Size character	Mean for indicated belly-streaking class		Effect of belly-streaking class[a]
	0–1	2–5	F-ratio ($d.f.$ = 1, 11)
Wing length	74.743	74.961	1.9923
Tail length	55.678	55.691	0.0057
Bill length	9.223	9.278	1.9796
Bill width	7.055	7.112	2.9577
Tarsus length	17.931	17.985	0.4292
Weight (g)	28.356	28.502	0.4514
Adjusted weight (g)	28.322	28.448	0.4595

[a] Two-way, mixed-model analysis of variance, with belly-streaking class fixed, locality random; 12 samples (total n = 339).

TABLE 24

LORE PATTERN IN MALE HOUSE SPARROWS

Sample	Number of specimens in indicated lore-pattern category[a]									First-year		Adult	
	0	1	2	3	4	5	6	7	8	*n*	Mean	*n*	Mean
Edmonton			1	2	4(2)	1(6)	3(17)	2(10)	(1)	13	4.7	36	6.1
Montreal			1	3	3	2(2)	1(12)	(9)		10	3.9	23	6.3
Middlebury	1	3	3	6			(4)	(2)		13	2.1	6	6.3
Pittsburgh area	1	1	10	13(2)	7(3)	4(12)	3(19)	1(11)	(1)	40	3.3	48	5.8
Detroit area		4	20	25	10(4)	7(6)	10(12)	2(8)	(2)	78	3.4	32	5.9
Roodhouse		1	1	5		2	1	(1)		10	3.4	1	7.0
Salt Lake City		10	24	25	21	6(3)	3(7)	(7)		89	3.0	17	6.2
Lawrence	1	6	6	11(2)	8(2)	8(4)	3(9)	(7)		43	3.3	24	5.7
Vancouver		2	8	6	5	4(2)	3(3)	(6)		28	3.4	11	6.4
Oakland		3	5	1	4(2)	1(3)	4(12)	2(6)	(1)	20	3.8	24	6.0
Sacramento		4	8	11	10	3(2)	3(6)	(5)		39	3.2	13	6.2
Stockton			1		6(1)	2(1)	2(5)	(3)	(1)	11	4.3	11	6.2
Los Angeles		1	5	8	15(2)	11(4)	7(5)	1(8)	(1)	48	4.1	20	6.1
Death Valley		2	1	1	2(2)	1(3)	1(5)	(3)		8	3.2	13	5.7
Phoenix			1(1)	5	2(1)	1(3)	2(6)	(3)	(1)	11	3.8	15	5.7
Las Cruces		3	3	9(1)	8(7)	3(7)	2(4)	(7)	(1)	28	3.4	27	5.4
Bastrop	1	8	9	15	8(3)	4(6)	1(10)	(3)		46	2.8	22	5.6
Devine		2	2	3	2(1)	(2)	(1)	1(1)		10	3.0	5	5.4
Del Rio		4	8	10(1)	7(3)	9	5(4)	2(1)		45	3.7	9	5.1
Houston		2	3	7(2)	6(8)	3(10)	4(5)	(2)		25	3.7	27	4.9
Progreso 1963	4	14	23	31(2)	11(5)	9(5)	2(6)	(2)		94	2.7	20	5.0
Progreso 1965		1	4	5	3(5)	3(11)	6(8)	2(4)	(2)	24	4.2	30	5.6
Baton Rouge			2(1)	1(1)	3	(1)	1(1)			7	3.6	4	4.0
Zachary		2	(1)		1(2)	1(4)	(4)	(3)		4	2.8	14	5.4
Birmingham		1	2	4	2(1)	1(4)	2(5)	(3)		12	3.5	13	5.8
Camilla			1	2	(1)	(3)	(3)	(1)		3	2.7	8	5.5
Gainesville	1	1		5(1)	11	4(4)	(5)	(6)		22	3.6	16	5.9
Mexico City			4	5	1(2)	1(5)	2(5)	1(14)	(3)	14	3.6	29	6.4
Oaxaca		2	1	5	4(6)	1(6)	2(7)	2(12)	(2)	17	3.9	33	5.9
Oahu		7	5	2(6)	3(8)	3(10)	7(20)	(12)	(1)	27	3.4	57	5.5
Hawaii			1		3	(1)	(1)	(1)		4	3.5	3	6.0
Bermuda		4	4	8	4(1)	3(1)	3(2)			26	3.3	4	5.2
Oxford		3	3	9	5(2)	4(2)	2(11)	2(7)		28	3.6	22	6.1
Ludwigsburg		1	5	4	4	1(1)		(2)	(1)	15	2.9	4	6.7
First-year[b]													
Totals	5	78	152	216	172	94	83	18	0	818			
Per cent	0.6	9.5	18.6	26.4	21.0	11.5	10.2	2.2	0.0	100.0			
Weighted mean											3.43		
Adult[b]													
Totals	0	0	3	16	69	129	218	168	18			621	
Per cent	0.0	0.0	0.5	2.6	11.1	20.8	35.1	27.0	2.9			100.0	
Weighted mean													5.80

[a] Numbers of adults in parentheses.
[b] Excluding Progreso 1963.

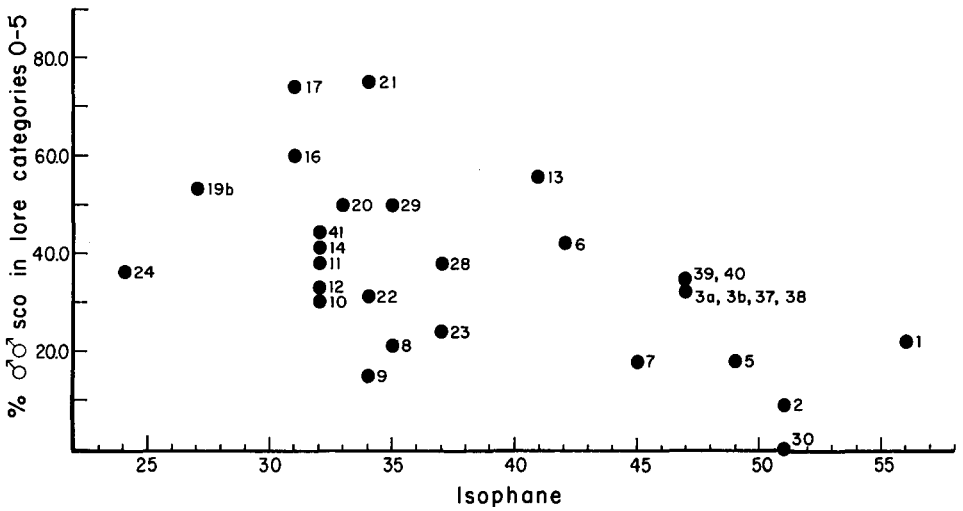

Figure 7. Relationship between sample locality isophane and proportion of males with complete cranial ossification ("SCO") having gray lores. Numerals indicate sample localities (see table 1). The linear regression equation is $Y = 83.25 - 1.24X$; $F = 10.75$.**

1 to 2%. There is no evidence that albinism is more frequent in New World than in Old World populations.

Ilyenko (1960; *fide* Sage, 1963) reported that albinism was two and one-half times as frequent in females as in males in Moscow. In our samples there is no significant sexual difference in frequency, but albinism is more extensive in females (table 31). Albinism is more than twice as frequent in adult as in first-year birds (table 30).

As noted by Michener and Michener (1936:107), Davis (1947), Sick (1959), and Ilyenko (1960; *fide* Sage, 1963), there is marked interpopulation variation in the frequency of albinism. In our material the frequency of partial albinos varies from 0.6% at Salt Lake City (n = 173 specimens) to 13.0% on Oahu, Hawaii

TABLE 25

VARIATION IN SIZE IN RELATION TO LORE PATTERN IN MALE HOUSE SPARROWS WITH INCOMPLETE CRANIAL OSSIFICATION (KNOWN FIRST-YEAR BIRDS)

Size character	Mean for indicated lore-pattern class			Effect of lore pattern[a]
	0–2	3–4	5–8	F-ratio ($d.f.$ = 2, 34)
Wing length	76.923	77.013	77.404	2.9342
Tail length	57.043	57.320	57.933	8.2818**
Bill length	9.232	9.233	9.302	1.8113
Bill width	7.072	7.058	7.063	0.0652
Tarsus length	18.244	18.190	17.983	3.6815*
Weight (g)	28.804	28.819	28.176	3.6787*
Adjusted weight (g)	28.936	29.009	28.474	2.8688

[a] Two-way, mixed-model analysis of variance, with lore-pattern class fixed, locality random; 18 samples (total n = 540). Significance of effect is noted at the 5% level (*) or at the 1% level (**).

TABLE 26

VARIATION IN SIZE IN RELATION TO LORE PATTERN IN MALE HOUSE SPARROWS WITH COMPLETE CRANIAL OSSIFICATION

Size character	Mean for indicated lore-pattern class			Effect of lore pattern[a]
	0–4	5–6	7–8	F-ratio ($d.f. = 2, 30$)
Wing length	77.601	77.767	77.721	0.2342
Tail length	58.084	58.135	58.257	0.3333
Bill length	9.354	9.398	9.378	0.3008
Bill width	7.100	7.123	7.121	0.1446
Tarsus length	18.315	18.166	18.216	1.1738
Weight (g)	28.586	28.633	28.629	0.0176
Adjusted weight (g)	28.852	28.878	28.816	0.0289

[a] Two-way, mixed-model analysis of variance, with lore-pattern class fixed, locality random; 16 samples (total $n = 394$).

($n = 123$), and 13.7% at Lawrence, Kansas ($n = 117$). Probably only a small proportion of the cases of albinism recorded for the House Sparrow is genetically determined, for albinism in birds results from a variety of other causes, including disease, physiological abnormalities, injury, and diet (Miller, 1935:306–307; Rollin, 1959; Sage, 1962). Therefore, geographic variation in frequency of albinism is of relatively little interest in evolutionary studies.

PHYSIOLOGICAL CONTROL AND ADAPTIVENESS OF PLUMAGE VARIATION

Referring to the work of Miller (1935), Witschi (1935:187) asserts that thyroxine administration causes regenerating feathers of male House Sparrows to "revert to the juvenal [pattern], which is close to the hen type." Taken at face value, this statement suggests that thyroxine may be involved in the normal control of sexual dimorphism in plumage and also raises the possibility that age variation in degree of "masculinity" of the plumage in males is influenced by thyroxine titers.

To determine for ourselves the effect of thyroxine on plumage, we repeated one of Miller's (1935) experiments. On 8 January 1963 feathers were plucked from

TABLE 27

CHESTNUT ON BLACK BIB OF MALE HOUSE SPARROWS

Age group	Number of specimens[a]	Per cent in indicated category[b]					Per cent in categories 1–4
		0	1	2	3	4	
Adult	557	74.5	11.3	12.6	1.1	0.5	25.49
First-year	756	87.6	5.5	6.5	0.4	0.0	12.43
Adult and first-year	1313	82.0	8.0	9.1	0.7	0.2	17.97

[a] 29 samples.

[b] Bib category — Description

0	All feathers black
1	1 to 3 feathers partly chestnut
2	4 to 10 feathers partly chestnut
3	Bib ½ chestnut
4	Bib more than ½ chestnut

Comparison: Adult vs. first year, $\chi^2_{(2)} = 37.14^{**}$, lumping categories 2–4.

TABLE 28

CHESTNUT ON PILEUM AND RUMP OF MALE HOUSE SPARROWS

Age group	Number of specimens[a]	Per cent with chestnut: On pileum	On rump
Adult	558	8.42	8.24
First-year	769	5.07	5.46
Adult and first-year	1327	6.48	6.63

[a] 31 samples.
Comparisons: Pileum: Adult vs. first-year, $\chi^2_{(1)} = 5.96^*$.
Rump: Adult vs. first-year, $\chi^2_{(1)} = 4.09^*$.

various plumage regions of 20 males and 5 females captured in Austin, Texas. The feathers were allowed to regenerate, and all birds, except a few controls, were given intramuscular injections of 1 mg thyroxine on 12, 16, and 21 January. When feather growth was completed, the birds were sacrificed and prepared as study skins.

Results of the experiment confirm those reported by Miller (1935). Thyroxine induces markedly abnormal changes in feather structure and in amount and pattern of deposition of melanin in males and females, but experimental hyperthyroidism in males obviously does not produce a reversion to the plumage pattern of the juvenile and female. As already noted by Miller (1935:307), feathers regenerated by males under experimental hyperthyroidism are only superficially if at all like those of the female, and superphysiological doses of thyroxine are required to produce discernible effects.

Keck (1934) demonstrated that sexual dimorphism in the first-year and adult plumages of the House Sparrow is not controlled by sex hormones, and there is no evidence that pituitary or other hormones are involved in the normal physiological control of patterns of these plumages. At least from the time of completion of growth of the juvenal plumage, maturation of the feather papillae is apparently under "direct" genetic control, being independent of hormonal influence. Corroboratory evidence is provided by the existence of gynandromorphs exhibiting male plumage on the right side of the body and female plumage on the left (Selander, Johnston, and Cantu, unpublished data).

Failure of most first-year males to attain the plumage pattern of the adult male, characterized primarily by a black face "mask," must result from the postjuvenal molt occurring while the feather papillae are changing from a condition in which

TABLE 29

ASSOCIATION OF CHARACTERS IN 1327 MALE HOUSE SPARROWS

Characters	Expected Number	Expected Per cent	Observed Number	Observed Per cent	Index of association[a]
Chestnut on pileum and rump	5.7	0.43	18	1.36	2.2
Chestnut on pileum and bib	15.4	1.16	42	3.16	1.6
Chestnut on rump and bib	15.8	1.19	44	3.32	1.8
Chestnut on rump, pileum, and bib	1.1	0.08	12	0.90	9.9

[a] Deviation/expected; $P < 0.001$ for each association.

TABLE 30

PARTIAL ALBINISM IN NORTH AMERICAN HOUSE SPARROWS

Sex and age	Number of specimens	Per cent exhibiting: Albinism[a]	Per cent exhibiting: "Conspicuous" albinism[b]
Males (31 samples)			
Adult	558	6.63	2.69
First-year	769	2.21	0.91
Subtotal	1327	4.07	1.66
Females (30 samples)			
Adult	257	9.73	4.67
First-year	687	3.78	1.31
Subtotal	944	5.40	2.22
Totals: Adult male and female	815	7.61	3.31
First-year male and female	1456	2.95	1.10
Grand total (all specimens)	2271	4.62	1.89

[a] One contour feather white.
[b] One or more remiges or rectrices, or two or more contour feathers, white.
Comparisons:
Albinism: Adult vs. first-year male, $\chi^2_{(1)} = 16.26^{**}$; adult vs. first-year female, $\chi^2_{(1)} = 12.93^{**}$; adult male vs. adult female, $\chi^2_{(1)} = 2.40$; first-year male vs. first-year female, $\chi^2_{(1)} = 3.10$.
"Conspicuous" albinism: Adult vs. first-year male, $\chi^2_{(1)} = 5.10^{*}$; adult vs. first-year female, $\chi^2_{(1)} = 8.32^{**}$; adult male vs. adult female, $\chi^2_{(1)} = 2.17$; first-year male vs. first-year female, $\chi^2_{(1)} = 0.23$.

they produce feathers of the juvenile-female type. The marked variability in degree of "masculinity" of first-year male plumages reflects comparable individual variation in degree of "maturation" of papillae at the time of the postjuvenal molt, which we assume to be related, at least in part, to variation in elapsed time between hatching and molting. In the House Sparrow, as in certain icterids (Selander and Giller, 1960), the House Finch, *Carpodacus mexicanus* (Michener and Michener, 1940; Gill and Lanyon, 1965), and the Bullfinch, *Pyrrhula pyrrhula* (Newton, 1966), it is likely that males hatching early in the breeding season are older than later-hatching individuals at the time of the postjuvenal molt in August and September (Weaver, 1942) and may, therefore, acquire feathers more nearly adult-like in color. That the maturation of feather papillae of first-year males continues after the postjuvenal molt is shown experimentally by the fact that feathers of the head regenerated by first-year birds in December and early January are more nearly like those of the adult than are those grown by the same birds at the postjuvenal molt in September (table 32).

On the assumption that age variation in color of male plumages has no adaptive significance, it might be suggested that first-year males differ from adults simply because of an intrinsic limitation in rate of maturation of the feather papillae. However, this hypothesis does not account for the fact that it is only the papillae of the head, and particularly those of the facial mask, that are not fully mature at the time of the postjuvenal molt. We suggest that rates of maturation are adjusted by selection and that the failure of a sizable proportion of males to acquire the full plumage color and pattern of the adult at the postjuvenal molt is in some way adaptive. In attempting to interpret this age variation, we have followed a line of reasoning developed in studies of blackbirds and other icterids (Selander and Giller,

TABLE 31

OCCURRENCE OF ALBINOTIC FEATHERS BY PLUMAGE REGION IN PARTIAL ALBINO HOUSE SPARROWS (54 MALES AND 51 FEMALES)

Plumage region	Per cent individuals with one or more white feathers in indicated region	
	Male	Female
Frontal	15	49
Pileum	43	31
Nape	22	25
Auricular	2	2
Postauricular	0	4
Cheek	0	2
Chin	4	0
Throat	6	6
Breast	4	2
Flank	0	4
Back	0	5
Scapular	0	2
Rump	0	4
Upper tail coverts	4	8
Under tail coverts	0	2
Primaries	2	6
Secondaries	2	4
Secondary coverts	0	2
Rectrices	9	2

1960; Selander, 1965) and have relied extensively on ecological investigations of the House Sparrow reported by Summers-Smith (1963).

As young House Sparrows fledge, they gather in flocks that forage in areas where food is plentiful and roost communally at night. When gonadal regression of adult birds occurs at the end of the breeding season in August, they join the foraging flocks of young birds, and molt occurs in August and September while the birds are flocked. However, many of the flocking adults, especially males, remain attached to their nest sites in this period, regularly returning to roost at night in their nests.

At the time of autumnal recrudescence of the gonads in October, adult pairs return to their breeding areas and spend a considerable part of their time at their nests. Some nest-building occurs and adult pairs are territorial, threatening or chasing first-year birds that later in the month visit the nesting areas "prospecting" for nest sites (Summers-Smith, 1963). Replacement of pair members that have died may occur in this period but rarely involves first-year birds; Summers-Smith (1963) suggests that any first-year birds mating in this period are individuals from the early broods of the year. Thus while many adults remain paired and attached to their nest sites through the late fall and winter, first-year birds are unmated and flocked.

Many first-year birds mate and breed in the spring, but their reproductive success is generally inferior to that of adults, and some first-year birds, presumably those from late-summer broods, fail to breed (Niethammer, 1937; Weaver, 1939). Summers-Smith (1963) reports that first-year males have difficulty securing nest sites in competition with adult males and may not obtain sites until after the breeding season is well under way. Flocks of unmated males, presumably first-year birds,

TABLE 32

CHANGE IN COLOR OF FEATHERS OF LORAL REGION OF FIRST-YEAR MALE HOUSE SPARROWS REGENERATED AFTER PLUCKING

Specimen number (K. U.)	Categories of loral-region pattern: Left side	Right side (regenerated)[a]	Mean units of change
45377	1	5	
45361	1	5	4.5
45368	2	4	
45364	2	5	
45370	2	6	3.0
45369	3	4	
45366	3	4	
45365	3	5	
45367	3	5	
45374	3	5	
45376	3	6	
45371	3	7	
45373	3	7	2.4
45363	4	6	
45375	4	6	2.0
45362	5	7	2.0
45372	6	7	
45360	6	7	1.0
Means ($n = 18$)	3.17	5.67	2.50

[a] Feathers plucked from right side of head 3 December 1963; birds sacrificed 13 January 1964, following regeneration of feathers.

are reported in England as late as April, a month after the nesting period begins, and, in New York, Weaver (1939) noted small flocks of unmated birds throughout the breeding season. Moreover, mated pairs of first-year birds usually do not breed until May or June, thus producing fewer clutches per season than do adult birds, and fledging success per nest presumably is poorer for first-year birds than for pairs of older birds.

We suggest that, because young, inexperienced males have little chance of acquiring good nesting sites and mating in the fall in competition with established, older males, the more or less "neutral" and relatively inconspicuous first-year head pattern is selected for its value in facilitating flocking by reducing the frequency of agonistic behavioral interactions and in increasing chances of survival through the fall and winter by rendering the birds less conspicuous to predators. By early spring, wear of the brown edges of the feathers of the pileum and the gray edges of the loral region and bib has diminished the distinction between the adult and first-year male head patterns, but an average difference remains throughout the year. We presume that it is the older (early-hatching) males that have the best chance of obtaining nest sites, attracting females, and reproducing, and it is these birds that show adult-like development of the secondary sexual plumage characters used in agonistic and epigamic display. For many younger individuals the probability of

reproducing may be sufficiently low that maximum total reproduction is achieved by delaying breeding until the second year of life, thus avoiding the physiological strain and other risks to survival involved in an attempted breeding effort in the first year (Lack, 1954). We suggest that the physiological mechanism controlling plumage color in the first-year male House Sparrow is adjusted by selection so that the degree of development of the masculine head pattern is directly related to the probability of successful reproduction in the first year. At the postjuvenal molt, first-year males of early broods acquire a plumage equivalent, or nearly so, to that of adult males, while the young of late broods become to varying degrees adaptively "handicapped" in plumage characters in competition with older males and, therefore, presumably fail to maintain nesting sites and to reproduce except, possibly, in years when adult mortality is unusually heavy or for other reasons there is a surplus of nesting sites.

Perhaps late-fledging female House Sparrows fail to reproduce in their first year for adaptive "reasons" similar to those suggested for males. But, because the female plumage is cryptic in color and pattern, with relatively few features functioning in display, age variation is much less marked in females than in males.

SUMMARY

Individual, age, and sexual variation in external morphology of the House Sparrow (*Passer domesticus*) was analyzed in preparation for studies of evolution in populations of North America and other regions in which the species has been introduced since 1850. The analysis was based on 2877 first-year and adult specimens collected in 1962, 1963, and 1965 at 37 localities in North America, the Hawaiian Islands, Bermuda, England, and Germany.

Listed in order of increasing intrapopulation variability, the size characters measured are wing length, tail length, bill width, tarsus length, bill length, and body weight. In both sexes all linear dimensions except tarsus length average slightly larger in adults than in first-year birds. Because of seasonal variation in level of subcutaneous and other body fat, body weight is probably an unreliable character for systematic study. Regional and seasonal variation in amount of wear of the bill tip is likely to obscure any genetically determined geographic variation in bill length.

Within local populations, linear correlations of size characters are generally weak, but there is a strong correlation between wing length and tail length, which is independent of body size. Coefficients of intrapopulation correlation derived from samples of 18 populations were homogeneous.

Males average larger than females in wing length, tail length, tarsus length, and body weight, but bill size is similar in the sexes, suggesting equality in foraging behavior and utilization of food resources. A sexual difference in flight behavior is suggested by the fact that, relative to body mass, the wing and tail are disproportionately longer in males than in females.

Variation in color of the pileum (crown) and breast was analyzed objectively in terms of values of dominant wavelength, brightness, and excitation purity derived from spectral reflectance curves obtained with a recording spectrophotometer. Thorough cleaning of the plumage by washing with detergent and white gasoline is essential to a reliable evaluation of color, since all House Sparrows, even those collected just after the annual molt, from both rural and industrial areas are discolored with soil or soot.

The yellow plumage pigment of the House Sparrow is a xanthophyll, similar to if not identical with canary-xanthophyll.

First-year and adult females differ slightly in average brightness and purity of color and in average expression of dark streaks on the belly. In both pileum color and breast color of females, brightness and purity exhibit a weak, negative intrapopulation correlation. Within populations, breast color and pileum color are weakly correlated with respect to either brightness or purity, but the interpopulation correlation between mean values of brightness of breast color and brightness of pileum color is moderately strong.

First-year males are highly variable in the degree to which the plumage departs in color from the cryptic juvenile–female pattern and approaches that of the adult male, which is characterized by a black facial "mask" and other secondary sexual characters functioning in epigamic and agonistic display. The possible adaptive significance of plumage variation in males is considered, and it is suggested that the physiological mechanism controlling plumage color in the first-year male is adjusted by selection so that, for the individual, the degree of development of the masculine plumage pattern is directly related to the probability of successful reproduction in the first year of life, with males of early broods of the season acquiring, on the average, more nearly adult-like plumage than those of later broods.

New World House Sparrows derived from introductions do not differ from those of the original stock in England and Germany in average levels of intrapopulation variability of characters of size and plumage color, degrees of age difference and sexual dimorphism in size and color, or incidence of partial albinism and other plumage variants.

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