SEASONAL VARIATION IN PLUMAGE COLOR IN HOUSE SPARROWS

BY RICHARD F. JOHNSTON

The buffy and brown feathers of female House Sparrows (*Passer do-mesticus*) approximate a match to environmental background or soil color (Johnston 1966, 1972). Analyses supporting these color matches were done on data from specimens taken in autumn and early winter, when the birds were in fresh and nearly unworn feather. In the course of an annual cycle, wear and exposure to sunlight result in progressive feather color change; feathers tend to become paler or, sometimes, darker, depending on locality. The extent to which such wear and fading can influence a seeming match between feather color and environment has not been studied quantitatively, although it is clear that qualitative changes can be appreciable. The studies reported here look at seasonal variation at 5 localities (identified in Table 1) in mid-continental North America and examine interpopulation variation at 4 times of the year.

MATERIALS AND METHODS

Reflectance spectrophotometry was carried out with a Bausch and Lomb Spectronic 505 recording spectrophotometer fitted with a reflectance bulb and with beam condensers in the transmittance sample chamber. Size of the scanning port was unmodified. Reflectance profiles spanning 400 to 700 m μ were taken for nape (pileum), flank, and rump feathers and converted to CIE "brightness" (Y) in accord with standard practice (Selander and Johnston 1967, Johnson and Brush 1972). This report largely concerns female specimens; thus, the feather colors are various shades of buff and brown. The paler colors have high scores on CIE "brightness" scales, and the darker colors have low scores.

RESULTS

Intralocality variation.—Color of the 3 variables at each locality for the 4 seasonal samples was examined by analysis of variance (ANOVA). Color varied significantly at all localities except Salida, and tended to proceed from medium brown in fall and winter to paler brown in spring and summer; this is indicated for nape feathers in Table 1. The degree of variation was essentially the same at any season of the year at all localities. ANOVA statistics for flank and rump color are similar to those

Locality	Color (=brightness "Y")			
sample (n)	Mean	\$	CV	
Lawrence, Kansas				
November (23)	69.04	11.53	16.60	
February (20)	75.45	13.65	18.09	
May (21)	92.24	9.10	9.87	
Julý (20)	102.20	14.12	13.82	
Hays, Kansas				
November (21)	72.29	14.20	18.84	
February (22)	90.54	11.20	12.38	
May (25)	70.00	13.80	19.65	
Julý (19)	81.30	16.40	20.15	
Kit Carson, Colorado				
November (22)	78.77	13.03	16.54	
February (20)	86.65	15.10	17.03	
May (18)	88.00	16.20	18.41	
Julý (25)	104.64	15.79	15.09	
Salida, Colorado				
November (11)	73.09	13.57	18.56	
February (12)	75.50	16.48	21.83	
May (4)	86.00	9.38	10.91	
July (13)	76.46	17.95	23.47	
Gunnison, Colorado				
November (6)	92.83	16.94	18.25	
February (10)	90.80	10.53	11.60	
May (8)	91.25	9.79	17.33	
Julý (10)	107.40	9.97	9.28	

TABLE 1. Interlocality temporal variation in brightness "Y" of nape feathers in female House Sparrows from the central United States.

for nape, but at Gunnison flank color becomes darker from fall to summer.

Interlocality variation.—Geographic variation in nape color is found in all 4 seasonal samples. In November, geographic variation proceeds from medium brown at Lawrence to pale beige at Gunnison; this is an east-to-west line of variation that has been noted earlier for breast color in specimen sets from slightly different localities (Johnston 1966). Clinally gradient geographic variation in nape color of November samples can be inferred from data in Table 1. However, the samples from February, May, and July, though they show significant variation, lack any east–west trends in color. The patterns of variation in color of flank and rump feathers are similar to those of the nape.

Even though east-west, or high altitude-low altitude, variation in color is absent in samples taken in February, May, and July, the relative color at a locality tends to be the same throughout the year—e.g., birds tend to be pale at any time of the year at Gunnison and dark at any time at Hays. Moreover, males and females show similar relative color at a locality (Table 2). The scores in Table 2 were arrived at as follows: specimens from a time sample were ranked by locality mean values for rump, nape, and flank color; rank-order scores from 1, palest, to 5, darkest, were then assigned to each locality sample for each time period. A sample that received a "1" for each feather area (such as females from Gunnison in November or February) would total "3" for the time sample, whereas a sample receiving a "5" for each feather area (such as males from Hays in November) would total "15." If a locality had samples that were consistently the palest it would total "12" for the 4 time samples; if consistently the darkest the total would be "60."

None of the samples is as consistent as that, however, and the two relatively pale series from Gunnison receive a total of "20," while the relatively dark birds from Hays score "47" for females and "49" for males. Finally, when the annual total scores are compared between sexes, the rank-order correlation coefficient is $r_s = 0.975$ ($P \le 0.05$). Areas of male plumage apart from the high-contrast patches for visual display seem to be under controls similar to those for females, a point to be considered below.

Possible cause for organized variation in feather color.—At first glance it may seem unsatisfactory that the variation in feather color shows clinal variation only at the time feathers are newly-grown and not subsequently through their period of use. Yet fall and winter are demanding times for House Sparrows. They can experience difficulty in finding food under the snow (Hamilton and Johnston 1978), and they may experience an increase in predation pressure. Specifically, House Sparrows are subject to predation by hawks and other visually-orienting predators, and in fall and winter some predators become specialists on flocks of House Sparrows (Tinbergen 1946). Therefore, I propose that feather color in House Sparrows is adjusted by selection, as a result of visuallyorienting predators, in accord with wintertime background color. The proposition is involved with the following considerations:

First, the color of newly-grown feathers can be more nearly what genetic coding dictates than can color of feathers subjected to unpredictable degrees of wear and fading. (In Table 1, note that color becomes ever paler only at Lawrence and Kit Carson. At Hays color is paler in February and is intermediate in July. Color is nearly invariant at Salida and Gunnison, except for May (Salida) and July (Gunnison).)

Second, visually-orienting predators should tend to catch birds departing from average coloration when the birds assort themselves in flocks in autumn and winter. Potentially strong stabilizing selection can be implicated in accord with the studies of Mueller (1968) on hunting behavior of American Kestrels (*Falco sparverius*) under controlled experimental conditions.

Third, wintertime cold stress and any snowcover that obscures food decreased the ability of individuals in bird flocks to detect possible pred-

	Sample				
	Nov	Feb	May	Jul	Total
Females ²					
Gunnison	3	3	8	6	20
Salida	12	11	9	13	45
Kit Carson	7	8	10	9	34
Hays	13	11	13	10	47
Lawrence	10	12	5	7	34
Males					
Gunnison	$6 (7)^3$	3 (12)	5 (10)	6 (12)	20
Salida	9 (6)	12 (10)	12 (4)	11 (3)	44
Kit Carson	7 (30)	7 (25)	12 (22)	10(21)	36
Hays	15 (17)	13 (21)	10 (24)	11 (19)	49
Lawrence	8 (22)	10 (21)	6 (21)	7 (19)	31

TABLE 2.	Quarterly and annual locality totals of combined rank-order brightness scores
	for mid-continental House Sparrows. ¹

¹ Each entry is the sum of locality rank-order standings (palest = 1, darkest = 5) in brightness values for flank, rump, and nape feathers.

² Sample sizes as in Table 1.

³ Minimum sample size; n higher for some variables.

ators. In House Sparrows the incidence of fighting and of threat postures increases significantly when snow covers foraging arenas (Cink 1977), which should reduce time spent looking for predators.

If this is so, there should be some evidence of a color match between House Sparrow plumages and measures of winter snowcover. Of the data available in standard climatic summaries, significant regression relationships were found between mean maximum January wetbulb temperature and each of the 3 plumage variables of females for the November samples (Fig. 1).

The regression relationships are ones that would be expected to be discernable if winter climate and feather color are covariant. The climatic variables used to test the a posteriori hypothesis of relationship were values for January means, as follows: maximum, average, and minimum drybulb temperatures; maximum wetbulb temperature; 01:00 and 13:00 relative humidity; absolute humidity; and the value for annual temperature range (mean summer maximum minus mean winter minimum drybulb temperatures). I have assumed that January WBT varies positively with amount and duration of snowfall. Additionally, the fact that feather color data from 5 localities for November from 3 distinct regions of plumage all bear the same regression relationship to winter WBT makes it difficult to dismiss the relationship as coincidental or otherwise spurious.

Feather color variation for February (with one exception, noted in Fig. 1), May, and July bears no statistically significant relationship to winter WBT. However, that variation likewise shows no relationship to



JAN MAX WBT°F



FIGURE 1. Regressions of brightness of color of (A) nape (pileum), (B) rump, and (C) flank of female House Sparrows on January maximum wetbulb temperatures at 5 localities in Kansas and Colorado. The relationships for all 3 variables for November samples, "N," as well as that for February ("F") rump, are statistically significant and are depicted by means of thick lines. In each instance, more than 90% of the variation in brightness can be "explained" by variation in wetbulb temperatures. The relationships shown by means of thin lines failed to achieve statistical significance, but they are included in the Figure to suggest the nature of the color changes in the 3 regions of plumage.

measures of summertime climate. I take this to mean that feather color for spring and summer may be related to some other feature of the environment, such as soil color. Contrariwise, there may well be no great selective pressure on feather color in spring and summer, for sparrows characteristically dust-bathe, which leaves their feathers coated with soil the color of their habitats; the birds cannot readily do this at the montane localities throughout winter, and at the downstream localities during times of the winter snows.

SUMMARY

Feather color of House Sparrows was studied from specimens taken in December, February, May, and July from Kansas (Lawrence and Hays) and Colorado (Kit Carson, Salida, and Gunnison). A color gradient along the transect varies from dark (Lawrence) to pale (Gunnison), and has a statistically significant relationship to measures of wintertime snowcover at the 5 localities for the specimens taken in November. Color of the specimens taken in February, May, and July cannot be related to any environmental variable. An hypothesis that color of freshly-grown feathers is adjusted by natural selection by visually-orienting predators in accord with wintertime background color is proposed.

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Museum of Natural History and Department of Systematics and Ecology, The University of Kansas, Lawrence 66045. Received 20 Oct. 1980; accepted 6 Mar. 1981.