House Sparrows: Rapid Evolution of Races in North America

Abstract. *Conspicuous adaptive differentiation in color and size has occurred in the house sparrow* (Passer domesticus) *in North America and the Hawaiian Islands since its introduction in the middle of the 19th century. Patterns of geographic variation in North America parallel those shown by native polytypic species, in conformity with Gloger's and Bergmann's ecogeographic rules. Racial differentiation of house sparrow populations may require no more than 50 years.*

A number of workers have attempted to demonstrate evolutionary changes in the house (English) sparrow (*Passer domesticus*) in North America since its introduction from England and Germany in 1852 (*1*). Several early studies based on small samples of specimens produced results (*2*) which were negative or statistically unreliable. In an investigation which has been widely cited (*3*) as evidence for slow rates of evolution of avian races, Lack (*4*) found no unequivocal evidence of divergence in bill and wing dimensions of the North American and Hawaiian populations from the Old World stock. However, Calhoun (*5*), using larger samples and employing refined methods of analysis, was able to show that average wing length in populations of the eastern and central United States increased slightly more than 1 mm between the time of introduction and 1930. He also demonstrated geographic variation in average length of wing, femur, and humerus correlated with regional differences in duration and severity of freezing temperatures in the United States. Recently, the possibility that New World populations exhibit regional color differences has been suggested by Keve (*6*).

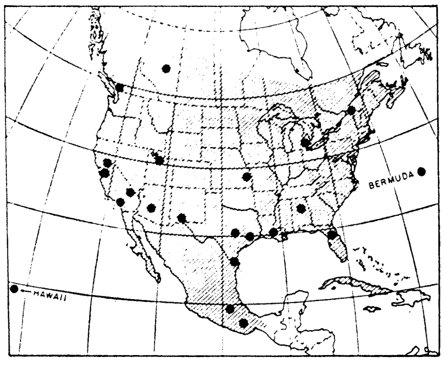

Fig. 1. Map of North America showing distribution of house sparrow (shaded area) and localities where specimens were taken (dots).

To assess the full extent of variation in characters of color and size, series of 100 to 250 specimens of house sparrows in fresh plumage were taken by us in October and November, 1962 and 1963, at various localities in North America and in the Hawaiian Islands, Bermuda, England, and Germany (Fig. 1). This extensive material clearly demonstrates the existence of pervasive geographic variation in a large number of characters in the North American and Hawaiian populations. Each New World population sampled has differentiated to greater or lesser degree from any other and from the Old World stock. Preparation and analysis of this material is still in process, but the preliminary findings presented here provide a general indication of the surprising extent to which selection has produced morphologic differentiation in a small number of generations. We have not as yet undertaken studies of the developmental basis of the morphologic characters of the house sparrow populations, but, in view of extensive evidence for comparable racial characters in other species of birds and in mammals (*7*), we are safe in assuming that the geographically variable characters of color, pattern, size, and body proportions are in fact genetically controlled and are either directly adaptive in themselves or represent selectively neutral or weakly non-adaptive correlates of other adaptive characters.

In analyzing individual and geographic variation in color, as well as in size, we have found it useful to segregate our specimens into adult and first-year age groups, since many of the characters studied exhibit significantly different means and variances in the two age groups.

In general, geographic variation is more pronounced in characters of color than in those of size. Specimens from northern and Pacific coastal localities and from the Valley of Mexico (Mexico City) are darkly pigmented, and those from Vancouver, British Columbia, are especially dark. Sparrows from collecting stations in the arid southwestern United States from southern California east to southern and central Texas are relatively pale in color, with extremes of pallor being achieved in samples from Death Valley, California, and Phoenix, Arizona. Samples from Salt Lake City, Utah, Lawrence, Kansas, and other localities in North America can be categorized broadly as intermediate in color. Specimens from Zachary, Louisiana, and Oaxaca City, Mexico, have a conspicuous yellow wash on the posterior under parts which is absent or only weakly indicated in birds from other North American localities.

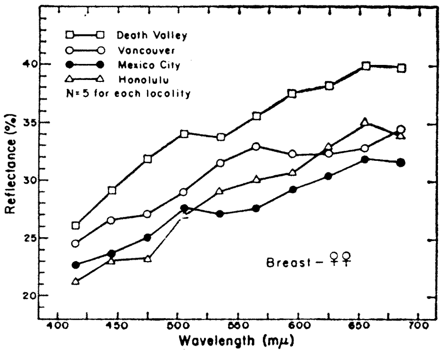

Fig. 2. Spectral reflectance curves for the breast of female house sparrows from Honolulu, Hawaii, and several North American localities.

Geographic variation in color of the breast in female house sparrows from Honolulu, Hawaii, and several localities in North America is shown in Fig. 2, which presents spectral reflectance curves (*8*) for five specimens from each locality.

The overall geographic pattern of color variation in North American house sparrows conforms with Gloger's ecogeographic rule, which relates color to regional variation in temperature and humidity (*9*). Students of geo-

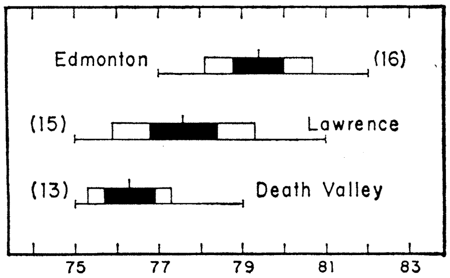

Fig. 3. Individual and geographic variation in wing length in adult male house sparrows from three localities. Vertical line: mean; horizontal line: observed range; solid rectangle: 2 standard errors on either side of mean; open rectangle: one standard deviation on either side of mean.

graphic variation in warm-blooded vertebrates a priori expect native North American species to be darker along the northwestern coast and paler in the arid southwest. The fact that house sparrows manifest this pattern of variation is evidence for the selective action of the same environmental factors that are assumed to be significant for native species.

Sparrows from Oahu, Hawaiian Islands, are very distinctive in color, being unlike specimens from English, German, and North American localities. They are characterized by a reduced value of the dark markings of the plumage, a general absence of fine streaks on the under parts, and an overall rufous-buff color which is especially intense on the breast and flanks. The legs and feet tend strongly to be pale buff in color rather than dark brown as in continental birds. The unusually strong differentiation of the sparrows of the Hawaiian Islands is not surprising in view of their geographic isolation and the fact that they have had an evolutionary history apart from North American populations. Sparrows were introduced to the islands in 1870 or 1871 from a New Zealand stock, which in turn had been brought to New Zealand from England in the years 1866–1868 (*10*).

We emphasize the fact that geographic variation in color in New World house sparrows does not consist merely of subtle average differences among the samples, with broadly overlapping ranges of variation. On the contrary, in many cases the color differences between samples are both marked and consistent, permitting 100 percent separation of specimens from the two localities. For example, we have observed no overlap in color of the pileum (top of the head) in females between samples from Oakland, California, and Progreso, Texas, or between those from Death Valley, California, and Vancouver, British Columbia. Again, specimens of either sex from the Hawaiian Islands and any of the North American localities are consistently separable on the basis of color.

Geographic variation occurs as regularly in size as in color, and for the most part parallels trends which are generally characteristic of indigenous species. The pattern of variation in size is largely clinal: in the United States and Canada the largest individuals are from the more northerly localities sampled, the smallest are from the desert southwest, and birds from other stations are of intermediate sizes. Some indication of the degree of geographic variation in wing length in North America is provided by data for adult males of three populations shown in Fig. 3. Variation in bill length in four representative populations is shown in Fig. 4. Note that the bill averages longer in the sample from Honolulu than in the continental populations. This was previously suggested by Lack's data (*4*), which had been considered equivocal because of uncertainties concerning seasonal variation in his material (*11*).

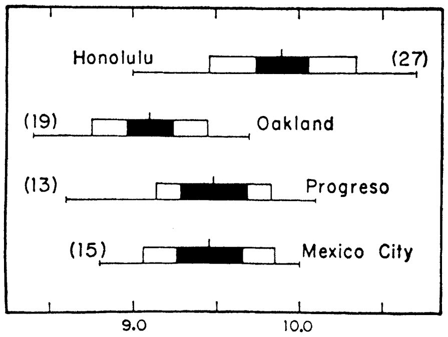

Fig. 4. Individual and geographic variation in bill length (from nostril) in adult male house sparrows from four localities. See Fig. 3 for an explanation of the graph.

For reasons not important to the exposition here, wing length in house sparrows tends to vary independently of body size. Body weight is a good index of size, provided weights are taken from specimens having similar relative amounts of body fat, a character known to vary seasonally with the gonadal condition of the individual (*12*). Our samples are strictly comparable, since all were taken when the birds had just completed the annual molt and were in the same condition gonadally and physiologically; all specimens show uniformly moderate degrees of subcutaneous lipid deposition.

In Fig. 5, mean body weights of adult males from 17 localities in North America are plotted against isophanes of the localities. Isophanes are calculated from latitude, longitude, and altitude of the localities and hence reflect gross climatic features (*13*). For localities north of southern Texas a simple relationship is evident, and a straight line fitted to the points by the method of least squares has the equation $Y = 24.1 + 0.12X$. The regression coefficient is highly significant (99.9 percent confidence interval = 0.02 to 0.21), and 93 percent of the variability is attributable to the linear regression effect. The observed relationship, which was predictable on the basis of Calhoun's geographically more restricted study (*5*) of linear dimensions, exemplifies the ecogeographic rule of Bergmann, which describes adaptive trends in body size as they relate to problems of heat flow and temperature regulation (*9*). Birds of larger body size occur at localities hav-

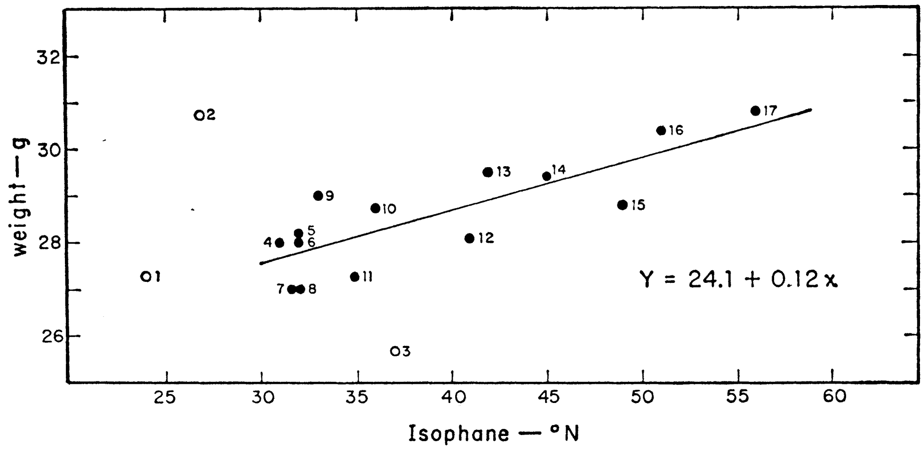

Fig. 5. Mean body weights of adult male house sparrows plotted against isophanes (see text for explanation). Localities: 1, Oaxaca City, Mexico; 2, Progreso, Tex.; 3, Mexico City, Mexico; 4, Houston, Tex.; 5, Los Angeles, Calif.; 6, Austin, Tex.; 7, Death Valley, Calif.; 8, Phoenix, Ariz.; 9, Baton Rouge, La.; 10, Sacramento, Calif.; 11, Oakland, Calif.; 12, Las Cruces, N.M.; 13, Lawrence, Kan.; 14, Vancouver, B.C.; 15, Salt Lake City, Utah; 16, Montreal, Quebec; 17, Edmonton, Alb. The regression line is based on data from localities 4 to 17.

ing high isophane numbers, reflecting boreal climates with severe winter cold; and those of smaller body size are from stations with low isophane numbers, reflecting mild or austral climates, occasionally with severe summer heat. A similar relationship between body size and climate is found in many native species of birds.

South of latitude 28°N in North America, other selective factors tend to override the effects of selection for body size as described by Bergmann's ecogeographic rule. Although mean body weight in the sample from Oaxaca City does not fall far from an expected position along the regression line based on data from samples taken in the United States and Canada, birds from Mexico City are surprisingly light in weight and those from Progreso, Texas, are unexpectedly heavy. That these differences reflect real variation in body size and not merely nongenetic variation in level of fat deposition is indicated not only by examination of the fat condition of the specimens but also by data on the length of the tarsus, which in house sparrows is closely correlated with body weight.

Current taxonomic practice gives formal nomenclatural recognition, at the subspecific level, to morphologically definable geographic segments of species populations. And it is obvious that the levels of differentiation achieved by the introduced house sparrow in the Hawaiian Islands and in a number of areas in North America are fully equivalent to those shown by many polytypic native species. Although application of subspecific trinomials to certain New World populations of sparrows would be fully warranted, we are not convinced that nomenclatural stasis is desirable for a patently dynamic system. Nomenclatural considerations aside, the evolutionary implications of our findings are apparent. Current estimates of the minimum time normally required for the evolution of races in birds range upward from about 4000 years (*14*), and nowhere is there a suggestion that such conspicuous and consistent patterns of adaptive evolutionary response to environments as we have found in New World house sparrows are to be expected within a period covering not more than 111 generations. Actually, much of the differentiation in North American populations must have occurred in the present century, since sparrows did not reach Mexico City until 1933 (*15*), and they were not present in Death Valley before 1914, or in Vancouver before 1900. Our findings are consistent with recent evidence of evolutionary changes in some other groups of animals, including mammals and insects (*16*), within historical times. Clearly, our thinking must not exclude the possibility of animals attaining to extremely rapid rates of evolution at the racial level.

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Labeled Oxygen: Transport through Growing Corn Roots

Abstract. *Oxygen, labeled with oxygen-18, is transported across wax membranes penetrated by growing corn roots. The rate of transport is a linear function of the number of penetrating roots. Other factors also influence the rate of transport.*

In a previous report, Jensen and Kirkham (*1*) observed that diffusion of O^{18}-labeled oxygen through cores of moist soil increased as growing corn roots penetrated the cores. The increased diffusion could not be accounted for by changes in soil porosity, and Jensen and Kirkham assumed that the oxygen was moving through the intercellular spaces of the root for at least part of its path. However, when a nonporous layer (for example, paraffin, 6 mm thick) was placed below the soil core, transport of oxygen was barely detectable when corn roots pierced the layer. Results obtained by Ebert and Howard (*2*) suggested that tissue near the root tip may offer more resistance to the diffusion of oxygen than tissue farther back.

We repeated the wax layer experiment of Jensen and Kirkham with modifications intended to test the effect of proximity of the root tips. Our experimental container was similar to that used previously (Fig. 1). The lower wax membrane was near the root tips; however, we increased the length of the soil column to 17.8 cm and added a 1.4-cm gap, 5.6 cm from the top of the column, which contained a second wax membrane. Roots growing through the upper membrane continued downward for 12.2 cm before reaching the lower membrane. Growth generally ceased when the root tips were 1 to 2 cm below the lower membrane. In this way, the mean distance of the membrane from the root tips that had penetrated it was greater for the upper membrane than for the lower. In addition, the upper membrane was nearer the foliage than the lower one.

The soil in the container was Yolo