

DIFFERENCES IN SEXUAL SIZE DIMORPHISM AND BODY PROPORTIONS BETWEEN ADULT AND SUBADULT HOUSE SPARROWS IN NORTH AMERICA

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ABSTRACT.—North American samples of House Sparrows (*Passer domesticus*) collected by R. F. Johnston and R. K. Selander (see Johnston and Selander 1971, Johnston 1973) were separated into adult (19 localities) and subadult (21 localities) groups. Significant clines were generated for all age and sex combinations through regression of locality means for body size against environmental seasonality. The strong body-size clines for subadult House Sparrows suggest a large genetic component to geographic variation in House Sparrow body size. There were no significant differences between the male and female clines for either age group. Therefore, there was no consistent relationship between sexual size dimorphism (SSD) in adult House Sparrow populations and environmental factors. Adult levels of SSD were higher than subadult levels at localities with distinct seasonalities. This resulted from selection against relatively large subadult females in areas with cold winters. Adult males were larger than subadult males, but whether this represented growth or selection is equivocal.

The ratio of body core to limb variables was correlated poorly with the winter temperatures of the collecting localities. The relationship improved if samples from coastal areas were excluded. Adult levels of this ratio were higher than subadult levels at localities with low January temperatures. Overwinter changes in both House Sparrow size and shape can be correlated with environmental variables. Although selection for efficient thermoregulatory design is implied, it is difficult to account for the mortality of large subadult females over cold winters and to completely discount the effects of growth. Received 15 October 1986, accepted 30 April 1987.

SEXUAL size dimorphism (SSD) is the difference between male and female size. In theory, it excludes shape differences between the sexes, but in practice it is difficult to separate shape from overall size (Reyment et al. 1984, McGillivray 1985, Somers 1986). SSD therefore is related to, but clearly a subset of, sexual dimorphism. It is conceptually important to recognize that selection cannot act directly on SSD. To explain high SSD, it is necessary to determine why a selective advantage for large size exists in one sex but is not evident (or as strong) in the other sex.

Selander and Johnston (1967) postulated that SSD in House Sparrows (*Passer domesticus*) resulted from selection for relatively large size in males. Larger males are presumed dominant to smaller males in disputes over nest sites and access to females for mating. Johnston and Fleischer (1981) suggested that House Sparrow SSD is large at high latitudes and small at low latitudes. This presumably is not a result of more intense sexual selection at high latitudes but a

consequence of the increasing severity of winter conditions (Johnston and Fleischer 1981, Fleischer and Johnston 1984) or possibly of reduced interspecific competition (Hamilton and Johnston 1978).

The empirical evidence for the existence of a latitudinal cline in SSD came from the work of Johnston and Selander (1973a) and Hamilton and Johnston (1978). However, currently accepted measures of SSD [such as the difference between male and female locality mean scores on the first principal component (PC) obtained from skeletal characters (Johnston and Fleischer 1981)] were not used in their studies. Johnston and Selander (1973a) compared male and female scores on a discriminant axis derived from five external characters. This axis represented a contrast between wing length and the other four characters; it was not a simple size axis. In effect, Johnston and Selander showed that sexual dimorphism of external characters increased from south to north, but they did not address the question of sexual size dimorphism directly.

Hamilton and Johnston (1978) used the variance of combined male and female PC scores as a measure of SSD. Because this statistic includes within-sex variation as well as between-sex differences, it will measure SSD directly only if within-sex variation is identical for all localities.

By defining SSD as the difference between male and female size and noting that body-size clines are well described for House Sparrows (Johnston and Selander 1971, Murphy 1985), it should be easy to compare male and female size clines to determine if SSD varies with latitude or climate. In North America Johnston and Selander (1971) found a strong relationship between both male and female House Sparrow body size and the January wet-bulb temperature of the collecting locality. They suggested that males showed a greater increase in size in association with low January temperatures than did females as the slope of the body size vs. temperature regression was slightly higher for males [males: $PC\ 1\ (size) = 4.75 - 0.04T$, $P < 0.004$, where T is the mean January temperature; females: $PC\ 1 = 4.36 - 0.03T$, $P < 0.005$]. Murphy (1985) found a similar relationship between seasonality (d , the difference between the mean July and mean January temperatures of a locality) and body size in North American House Sparrows (males: $PC\ 1 = 120.5 + 0.128d$, $r = 0.76$, $P < 0.01$; females: $PC\ 1 = 119.0 + 0.120d$, $r = 0.76$, $P < 0.01$). If SSD increased in association with greater climatic severity, then the male and female body-size clines generated by regressions on size and climate would differ significantly. Neither Johnston and Selander (1971) nor Murphy (1985) provided a test of the equality of male and female regression slopes, thus preventing a clear assessment of SSD variation in relation to climate.

Both Johnston and Selander (1971) and Murphy (1985) combined measurements from subadult (collected before their first winter) and adult birds (here defined as having survived at least one winter) to arrive at locality estimates of House Sparrow size. It is not clear what effect this would have on body-size clines, but it is of concern simply because of the selective role winter conditions are thought to play in determining adult House Sparrow body size (Bumpus 1899, Calhoun 1947, Lowther 1977, Johnston and Fleischer 1981, Fleischer and Johnston 1982) and shape (Fleischer and Johnston 1984).

For North American House Sparrows, the ra-

tio of body core to limb variables is high where January temperatures are low, and low where July temperatures are high (Johnston and Selander 1973b). This provided strong empirical support for Allen's ecogeographic rule. As in previous studies, however, subadults and adults were combined. Because Fleischer and Johnston (1982) demonstrated overwinter selection for the body core to limb ratio in House Sparrows at Lawrence, Kansas, the inclusion of birds that had not experienced a winter probably reduced the strength of the cline described by Johnston and Selander (1973b).

We constructed separate body-size clines for subadult and adult House Sparrows and tested for a relationship between SSD and climate. The correlation between body core to limb ratios and climate for both adults and subadults was examined to assess the significance of the effect of winter conditions on body proportions.

METHODS

Data collection.—A suite of 14 skeletal measures obtained from approximately 3,000 skeletons of adult and subadult House Sparrows from 56 North American localities was used (see primarily Johnston and Selander 1971, Johnston 1973). The localities and the sample sizes for each age and sex combination are listed in the Appendix. Subadult birds were used only if collected in October, November, or December. Weather data for the localities were provided by E. C. Murphy (see Murphy 1985). Because some birds were prepared with the rhamphotheca removed and others with it attached, bill measures were adjusted so that skull length became total skull length minus premaxilla length and mandible length became total mandible length minus dentary length.

Data analysis.—House Sparrow size was estimated by summing the 12 skeletal measures $\sum_i X_i$. This estimate was used because $\sum_i X_i$ is a standard size axis

(terminology of Mosimann 1970), and it provides a close parallel to first PC scores derived from a correlation matrix of raw data (Somers 1986). Principal components analysis based on either a covariance matrix of log-transformed data or a correlation matrix of raw data is a standard procedure in morphometrics (Reyment et al. 1984). The relative merits of covariance- and correlation-based methods depend on the researcher's interest in interpreting variance (Pimentel 1979, McGillivray 1985, Somers 1986). The first principal component is considered a "size" axis if the coefficients of the eigenvector are equal to a constant; the vector then is termed an isometric size vector (Somers 1986) or ideal size axis (McGillivray 1985). The sum of all variables is equivalent to a PC score

TABLE 1. Coefficients (loadings) obtained from analysis of 2 samples of House Sparrows from Alberta for first PC scores compared with the isometric-size axis, and second PC scores compared with the Allen axis. Because all loadings on PC 1 are not equal, aspects of shape are represented as well as size (Somers 1986). For PC 2 the loadings produce only an approximation to a core : limb ratio.

Variable	PC 1		Isometric size	PC 2		Allen
	Calgary (n = 147)	Peace River (n = 71)		Calgary (n = 147)	Peace River (n = 71)	
Skull width	0.12	0.15	1.0	-0.09	0.02	0.0
Mandible	0.11	0.14	1.0	-0.20	-0.09	0.0
Skull length	0.14	0.20	1.0	-0.11	-0.03	0.0
Coracoid	0.28	0.36	1.0	-0.09	0.03	0.0
Sternum length	0.38	0.25	1.0	0.32	0.38	1.0
Keel	0.52	0.30	1.0	0.60	0.63	1.0
Sternum depth	0.27	0.30	1.0	-0.07	0.34	1.0
Humerus	0.28	0.32	1.0	-0.15	-0.12	0.0
Ulna	0.31	0.32	1.0	-0.10	-0.07	0.0
Femur	0.26	0.33	1.0	-0.37	-0.25	-1.0
Tibiotarsus	0.25	0.32	1.0	-0.36	-0.35	-1.0
Tarsometatarsus	0.29	0.35	1.0	-0.40	-0.35	-1.0

obtained through multiplication of the raw data by an eigenvector where all elements are 1.0. Size, as measured by $\sum X_i$, will be highly correlated with PC 1 scores unless the first PC contains significant negative as well as positive elements (McGillivray 1985).

An assumption of this method is that all variables should be weighted equally; therefore, large characters contribute more to the estimate of overall size than do small characters. Skeletal characters have often been standardized or log-transformed to remove scale effects. If the characters define OTU's in a taxonomic study or assess growth or patterns of variation, then standardization is critical (Sneath and Sokal 1973) to prevent minor variations in large characters from obscuring relatively large variation in small characters. We are interested here in an estimate of absolute size, however, so neither standardization nor transformation is appropriate.

In previous House Sparrow morphometric studies, a PC axis has generally approximated a body core to limb ratio axis and allowed an examination of Allen's rule (Johnston and Selander 1971, Fleischer and Johnston 1984). Because a PC axis contains contributions from all variables, variation in scores linked to variables other than limb or body-core characters cannot be eliminated. Therefore, for a direct test of the limb or body-core variation, we generated an "Allen" axis by summing standardized lengths (Z-scores) for femur, tibiotarsus, and tarsometatarsus length and subtracting the total from the summed standardized values for sternum length, keel length, and sternum depth. Standardization was necessary because our interest was in relative size.

An advantage to the use of "ideal" axes is their consistency across localities. Principal components computed separately for each locality are not directly comparable even though they may be interpreted

similarly. Raw data from different localities can be combined and a single set of principal components generated, but these components are weakened to the extent that interlocality differences contribute to the overall size and shape variation.

The difference between the first two eigenvectors obtained through a PC analysis of House Sparrow skeletons and the two derived axes used in this study is shown for two samples from Alberta (Table 1). Even in this two-sample case (e.g. PC 2 loadings for sternum depth), combining the raw data from two localities and generating principal components will produce "average" axes (and loadings) that only approximate significant sources of variation within a locality and provide only weak tests of the inter-character relationships of interest.

Historically, principal components have been used in morphometric studies because they represent important patterns of covariation in the data that often

TABLE 2. Pearson product-moment correlations among geographic and environmental variables used to demonstrate clines in House Sparrow body size. The sample consists of 40 localities (Appendix) for which long-term weather data are available. ** = $P < 0.01$.

	January temperature	July temperature	Seasonality	Latitude
January temperature	—	0.56**	-0.91**	-0.88**
July temperature		—	-0.16	-0.66**
Seasonality			—	0.71**
Latitude				—

are related to geographic or environmental factors. Our interest was not in assessing important sources of variation but in the amount of geographic variation in absolute size and a specific ratio (i.e. limb to body core). The statistical importance of a derived axis can be calculated, however, by computing the percentage of total variation for which it accounts. This is determined in the same way as for principal components (percentage explained = $\sum_i S_i^2 R_i^2 / \sum_i S_i^2$, where S_i^2 is

the variance associated with variable i and R_i^2 is the square of the correlation between variable i and the derived axis).

All multivariate analyses were run on the SAS statistical package (SAS Inst. 1985) and univariate analyses on SAS or a pocket calculator.

RESULTS

Geographic patterns of House Sparrow body size and sexual size dimorphism have been demonstrated through regression against latitude, mean January temperature, mean July temperature, and seasonality of the collecting localities (Johnston and Selander 1973a, Murphy 1985). The geographic and climatic variables were weakly to highly correlated for 40 North American localities where House Sparrows have been collected (Table 2). In these localities winter conditions contributed more strongly to seasonality differences among localities than did summer conditions. The variance around mean January temperatures was significantly greater than that around mean July temperatures [$F = 104.65/18.75 = 5.58$, $df = (39, 39)$, $P < 0.001$]. Therefore, the demonstrated effect of climate on North American patterns of House Sparrow body size is most likely mediated by midwinter conditions.

Body size ($\sum_i X_i$) for adult and subadult

House Sparrows at 19 and 21 North American localities increased with seasonality (Fig. 1). The standard errors were sufficiently large that no pair of regression lines differed significantly. The size of subadults showed a stronger correlation with average seasonality values than did the average size of adults, but these differences were not statistically meaningful. Because there were no significant differences between the body-size clines for males and females, it is not surprising that no relationship between environmental variables and both adult and subadult levels of SSD emerged (Table 3). The only significant correlation was between adult SSD and male size, but these are expected to be re-

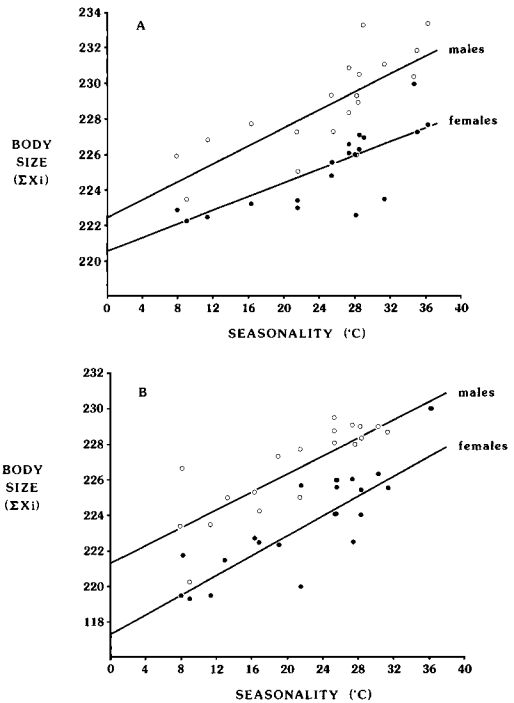


Fig. 1. Body size ($\sum_i X_i$) of House Sparrows vs.

seasonality (annual temperature range). (A) Adult males (O): size = $222.49 + 0.25(\text{seasonality})$, $r = 0.78$, $n = 19$, $P < 0.01$, $SE\ b_1 = 0.05$; adult females (●): size = $220.58 + 0.19(\text{seasonality})$, $r = 0.73$, $n = 19$, $P < 0.01$, $SE\ b_1 = 0.04$. (B) Subadult males (O): size = $221.35 + 0.25(\text{seasonality})$, $r = 0.85$, $n = 21$, $P < 0.01$, $SE\ b_1 = 0.04$; subadult females (●): size = $217.36 + 0.28(\text{seasonality})$, $r = 0.85$, $n = 21$, $P < 0.01$, $SE\ b_1 = 0.04$.

lated statistically because SSD was calculated from male size.

Thirteen localities allowed direct comparison of subadult and adult body sizes (Appendix). On average adult males were larger than subadults ($\bar{x}_m = 1.08$, $S_m = 1.87$, $n = 13$, $t = 3.6$, $P < 0.01$), but adult and subadult females did not differ in size ($\bar{x}_f = 0.64$, $S_f = 2.16$, $n = 13$, $t = 1.06$, $P > 0.05$). There was geographic variation in the degree of difference between adult and subadult body size (Table 4). The difference in size between subadult and adult females was positively correlated with January temperature and negatively correlated with the seasonality of the collecting locality. If average January temperatures were sufficiently low (approximately -4.2°C), the female size change became negative (i.e. subadults larger than adults). Adult

TABLE 3. Pearson product-moment correlations between levels of sexual size dimorphism (SSD) in adult and subadult House Sparrows and characteristics of the localities where they were collected. The mean numbers of localities used are given in parentheses. ** = $P < 0.01$.

	Male size	Female size	January temperature	Seasonality	Subadult SSD
Adult SSD	0.65** (19)	0.22 (19)	-0.27 (19)	0.31 (19)	-0.02 (13)
Subadult SSD	0.12 (21)	0.03 (21)	0.33 (21)	-0.18 (21)	

males were on average larger than subadult males, and in cold environments adult females were the same size as (or slightly smaller than) subadult females; thus, in these areas the level of SSD was higher for adults than for subadults. This was confirmed by positive correlations between the change (subadult to adult) in SSD and adult male size ($r = 0.65$, $n = 13$, $P < 0.05$) and locality seasonality ($r = 0.52$, $n = 13$, $0.05 < P < 0.1$).

There was a weak correlation between the scores of adult males on the Allen axis and the mean January temperature at the collecting localities ($r = -0.45$, $n = 18$, $0.05 < P < 0.1$). Hence, in areas with cold winters male House Sparrows have relatively large body cores relative to leg lengths. No significant correlation between these variables was found for adult females ($r = -0.14$, $n = 18$, $P > 0.05$). Also, no significant correlations were found between Allen scores and January temperatures for either sex of subadult House Sparrows.

The differences for both sexes between subadult and adult scores on this axis were correlated negatively with the mean January temperature at the collecting localities and positively with locality seasonality (Table 4). Hence, core to limb ratios were increased more from subadults to adults where winter temperatures were low.

DISCUSSION

To detect a cline in House Sparrow SSD related to climatic factors, the body-size clines of males and females would have to be divergent. Although the adult body-size clines were not parallel, the differences between the slopes were not significant, and we conclude that there is

TABLE 4. Pearson product-moment correlations between subadult and adult differences in size and core to limb ratio and three characteristics of the collecting localities ($n = 13$). * = $P < 0.05$, ** = $P < 0.01$.

	Male size	January temperature	Seasonality
Subadult vs. adult differences in size			
Males	0.29	0.24	-0.26
Females	-0.47	0.78**	-0.73**
Core to limb ratio			
Males	0.31	-0.62*	0.59*
Females	0.39	-0.63*	0.57*

no cline in adult SSD. Confirmation was obtained from the nonsignificant correlations between adult SSD and both January temperature and seasonality of the collecting localities.

The strong relationships between body size of subadult male and female House Sparrows and average seasonality values were surprising. This implies that a cohort of juvenile sparrows need not necessarily experience selection over winter to show clinal variation similar to adult members of the species. If we accept that most selection on House Sparrow body size occurs during winter (Lowther 1977; Fleischer and Johnston 1982, 1984), then the clinal pattern of prewinter size of subadults suggests a large genetic component to the pattern of geographic variation in size exhibited by House Sparrows. This is not to deny the potential role of the nest environment (e.g. James 1983) in morphological differentiation. However, in-nest effects would have to be consistently different among localities yet remarkably constant among breeding seasons at a locality to generate the clinal patterns observed here. In addition, to date no direct environmental effects on avian skeletal morphology have been demonstrated.

Size differences between subadult and adult birds could reflect growth, selection for certain size classes of birds over winter, or sampling error. There is considerable potential for sampling error in comparisons of subadult with adult morphologies. In particular, one must assume that all specimens are typical for a particular locality. Although there will be some intralocality temporal variation, the existence of significant body-size clines for both sexes and age groups suggests that this assumption is reasonable.

The relative contributions of growth and selection to subadult vs. adult size differences are

difficult to separate. The difference overall in size between adult and subadult males suggests growth effects, yet for 4 of the 13 localities adults were smaller than subadults. All but one of the reported skeletal measures describes a bone length, and adult bone lengths are thought to be reached before complete skull ossification (J. D. Rising MS), which occurs at about 200 days (Nero 1951). Most subadults collected in late autumn would be 5–7 months old, implying complete growth; considerable annual variation is expected, however, because House Sparrows are multibrooded.

To measure growth accurately, the same individuals would have to be measured at various ages (cf. Smith et al. 1986). This precludes the use of skeletal measures on collected specimens. Traditional measures such as wing length or mass can be taken on live birds, but both vary seasonally in House Sparrows, which prevents their use as unbiased indicators of size (Rising 1973, McGillivray 1981). Because adult females are not significantly larger than subadult females and were smaller in 4 of 13 localities (as was found for males), significant growth probably does not occur during the winter months.

In localities with cold winters, large subadult females probably are selected against (Table 4). This is counter to the expectations of Bergmann's rule, but it supports conclusions obtained from single-locality studies using Bumpus's (1899) data (Johnston et al. 1972). Similarly, Johnston and Fleischer (1981) demonstrated selection against large females and increased SSD during a cold winter at Lawrence, Kansas. Our data show that the change in SSD from subadults to adults that results from selection against large subadult females is positively correlated with seasonality. This change, however, is insufficient to generate a cline in adult SSD associated with seasonality.

In male and female House Sparrows the ratio of body core to leg variables was higher for adults than for subadults. The lower the mean January temperature (or the higher the annual seasonality), the greater the difference between adult and subadult ratios. A similar pattern of overwinter shape change occurred over a cold winter at Lawrence (Fleischer and Johnston 1982). There is little doubt that the thermoregulatory advantage of large body core to limb ratios (i.e. Allen's rule) in cold climates explains the observed overwinter changes both at Lawrence and at the localities with high seasonalities in this study.

The increase in body core to limb ratio that occurs over winter suggests that a cline should exist between adult levels of this ratio and January temperatures at collecting localities. We found only a weak cline for males, however, and none for females. House Sparrows from coastal areas (see Appendix) have high body core to limb ratios despite relatively high January temperatures. If these samples are removed, the relationships between adult body core to limb ratio and January temperature become significant for both sexes (males: $r = -0.67$, $n = 15$, $P < 0.01$; females: $r = -0.41$, $n = 16$, $0.05 < P < 0.1$). Therefore, the proportioning of House Sparrow body core to limb ratios was related to winter temperatures but only in continental populations.

Lowther (1977) indicated that the adaptation of House Sparrows to local conditions was essentially complete for overall size but still ongoing in the proportioning of body parts. Our observations differ to the extent that there also appears to be selection against large subadult females at localities with high seasonalities. On average there were significant differences between the mean size of subadult and adult males, yet these differences did not covary with climatic factors. Growth may account for these differences in males, but it is unclear why continued growth does not occur in females. It will be important to experiment in future studies to separate growth effects from those due to selection.

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APPENDIX. Localities and sample sizes used in the geographic comparisons.*

Locality	Subadult		Adult	
	Male	Female	Male	Female
Edmonton, Alberta	40	20	5	17
Regina, Saskatchewan	31	19	10	13
Montreal, Quebec	29	12	—	—
Manhattan, Kansas	81	71	45	29
Lawrence, Kansas	123	87	183	133
Hays, Kansas	20	17	69	66
Topeka, Kansas	—	—	43	51
Gove, Kansas	—	—	15	16
Fargo, North Dakota	11	16	—	—
Jamestown, North Dakota	11	7	—	—
Bancroft, North Dakota	—	—	15	6
Sisseton, South Dakota	—	—	32	15
Burlington, Iowa	—	—	7	13
Kit Carson, Colorado	20	18	73	63
Salida, Colorado	5	11	35	40
Gunnison, Colorado	—	—	35	25
Pt. Reyes, California	41	19	62	39
Oakland, California	18	11	7	20
Sacramento, California	27	15	—	—
Los Angeles, California	50	25	—	—
Salt Lake City, Utah	12	18	—	—
Las Cruces, New Mexico	13	15	9	14
Houston, Texas	52	21	11	9
Bastrop, Texas	38	22	—	—
Gainesville, Florida	35	7	—	—
Tampa, Florida	14	6	24	16
Ithaca, New York	10	7	27	11

* Climatic data were also used from the following localities: Peace River, Alberta; Vancouver, British Columbia; Udal and Elkhorn, Kansas; Bishop, Austin, and Progresso, Texas; Eagle Lake, New Mexico; Duluth, Minnesota; Baton Rouge, Louisiana; San Jose, California; Phoenix, Arizona; Mexico City, Mexico.