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COMPARISONS BETWEEN MORPHOMETRIC AND GENETIC DIFFERENTIATION AMONG POPULATIONS OF THE EURASIAN TREE SPARROW (*PASSER MONTANUS*)

VINCENT L. ST. LOUIS[1] AND JON C. BARLOW[2]

ABSTRACT.—Eurasian Tree Sparrow (*Passer montanus*) populations, established by introductions outside of the native range, provide a unique opportunity to assess the relationship of morphometric and genetic change in a new environment. No statistically significant morphometric-genetic relationships were found among six populations of *P. montanus* when we (1) correlated morphometric size with heterozygosity; and (2) estimated degree of population differentiation using morphometric and genetic distance measures. Factors influencing both genetic and morphometric differentiation include the founding events and the ecological changes associated with them. *Received 21 Oct. 1986, accepted 1 May 1987.*

The relationship between genetically and ecophenotypically influenced morphometric variation is unknown in most studies. The degree of genetic-morphometric relationship may be clarified in part by examining the association or correlation of genetic characters, such as heterozygosity, with phenotypic states such as size (e.g., Wheat et al. 1974, bass [*Micropterus* sp.]; Singh and Zouros 1978, American oysters [*Crassostrea virginica*]; King 1985, herring [*Clupea harengus*]; Wooten and Smith 1985, mammals; see also Mitton and Grant 1984) or variation (e.g., Eanes 1978, monarch butterflies [*Danaus plexipus*]; Mitton 1978, killifish [*Fundulus heteroclitus*]; King 1985, herring; Fleischer et al. 1983, House Sparrows [*Passer domesticus*]). Other investigators (e.g., Zink 1982, Lindenfelser 1984, Van Wagner and Baker 1986) used multivariate methods (e.g., distance measures between populations) to examine the extent to which the genome and phenotype are similarly influenced. Two hypotheses attempt to explain observed genetic-morphometric relationships: (1) heterozygous lineages show superior growth rates, obtain greater size, and have buffered developmental processes, resulting in little morphological variation (heterosis [Lerner 1954]); and (2) increased environmental heterogeneity causes maintenance of high levels of genetic variation (e.g., Mayr 1954).

The Eurasian Tree Sparrow (*Passer montanus*) has been introduced

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[1] Dept. Zoology, Univ. Toronto, Toronto, Ontario M5S 1A1, Canada.
[2] Dept. Ornithology, Royal Ontario Museum, Toronto, Ontario M5S 2C6, Canada and Dept. Zoology, Univ. Toronto, Toronto, Ontario M5S 1A1, Canada.

extralimitally several times, for example, from West Germany to North America in 1870, and from China to Australia in 1863 (Long 1981). As a consequence of these introductions, this species has encountered a variety of new genetic (St. Louis and Barlow, in press) and environmental (Barlow 1973, 1980) influences. Factors influencing the genetic structure of the introduced North American population of *P. montanus* have included the general impact of the founding event, mutation, and stochastic processes such as genetic drift (St. Louis and Barlow, in press). Possible selective pressures on the genotypes, however, cannot be excluded as forces controlling the population's genetic structure. Differences in mensural characters between North American and ancestral German populations were attributed to the founding event and differential ecological conditions (Barlow 1973, 1980; Thompson 1983).

We studied relationships between genetic and morphometric variation and covariation among six populations of *P. montanus* by: (1) relating heterozygosity measures with morphometric "size" and (2) assessing the degree of population differentiation using morphometric and genetic distance measures to delineate causal factors influencing genotypic and, in particular, phenotypic structure of *P. montanus* populations.

METHODS

Samples from the North American population of *Passer montanus* were obtained between 1983 and 1985 at three locales in west-central Illinois (Woodson, Morgan County: N = 24, adult males [am] = 5, adult females [af] = 7; Naples, Scott County: N = 17, am = 4, af = 5; and White Hall, Greene County: N = 52, am = 15, af = 24) ca 40–50 km apart. Specimens of the ancestral European population came from Karlshrule, West Germany (N = 30, am = 10, af = 8), ca 50 km from Ludwigsburg where earlier samples studied by Barlow (1980) were obtained. The above samples were compared with each other and with Australian (N = 15, am = 8, af = 5) and Swedish (N = 25, am = 5, af = 9) specimens. Birds were collected from winter flocks with mist nets. Specimens were preserved in dry ice to minimize degradation of tissue enzymes. Skin-skeleton specimens were subsequently prepared at the Royal Ontario Museum in Toronto. Birds with skulls completely ossified were classified as adults (Nero 1951).

Horizontal starch gel electrophoresis of all *P. montanus* collected, used to measure the genetic structure of the populations, is described in St. Louis and Barlow (in press). Thirty-nine presumptive gene loci were resolved. Sixteen skeletal measurements (see Table 1) used by Johnston and Selander (1971) in studies of House Sparrow variation and by Barlow (1980) and Thompson (1983) on *P. montanus* were taken on the adult *P. montanus* using dial calipers accurate to 0.05 mm. A 17th variable (premaxilla length 2, measured from the posterior edge of the nasal to the anterior tip of the premaxilla) corresponding to Barlow's (1980) premaxilla length, was used for comparative purposes.

Principal component analysis (PCA) (Cooley and Lohnes 1971), based on a correlation matrix, was performed on the standardized means (mean = 0, SD = 1) of the raw data for the morphometric characters of each population for each sex to identify sets of characters that best described the variation among populations.

Taxonomic distances (Sneath and Sokal 1973) were computed from the standardized

TABLE 1

THE FIRST THREE PRINCIPAL COMPONENTS EXTRACTED FROM THE CORRELATION MATRIX AMONG MEANS OF SIX POPULATIONS OF *PASSER MONTANUS* FOR THE MALE AND FEMALE MORPHOMETRICS

	Males			Females		
Character	PC 1	PC 2	PC 3	PC 1	PC 2	PC 3
Premaxilla length 1	0.286	0.243	−0.009	0.191	0.304	0.094
Narial width	0.110	0.341	−0.081	−0.128	0.306	−0.390
Skull width	0.320	−0.062	0.170	0.305	−0.152	0.045
Skull length	0.236	0.252	0.299	0.170	0.317	0.279
Dentary length	0.156	0.354	−0.088	0.003	0.404	−0.087
Mandible length	0.311	0.199	−0.069	0.105	0.326	−0.280
Coracoid length	0.289	−0.245	−0.025	0.336	0.055	0.042
Sternum length	0.228	−0.282	−0.084	0.296	−0.199	0.043
Keel length	0.246	−0.214	−0.061	0.314	−0.514	0.073
Sternum length	0.036	−0.221	0.592	0.087	−0.057	0.685
Humerus length	0.315	−0.178	0.085	0.330	0.034	−0.159
Ulna length	0.290	0.113	0.360	0.306	0.170	−0.100
Femur length	0.215	−0.233	−0.337	0.307	−0.128	−0.218
Femur width	0.233	0.232	−0.327	−0.008	0.395	0.159
Tibiotarsus length	0.246	−0.222	−0.346	0.317	0.015	−0.216
Tarsometatarsus length	0.196	−0.279	0.121	0.324	−0.069	−0.111
Premaxilla length 2	0.217	0.279	0.095	0.074	0.379	−0.167
Eigenvalue	7.47	6.25	1.70	8.60	6.00	1.82
% Variation	44.0	36.8	10.0	50.6	35.3	10.7
Cumulative	44.0	80.8	90.8	50.6	85.7	96.6

means of the skeletal characters between populations for each sex using TAXON from the numerical taxonomic system of multivariate statistical programs, NTSYS (Rohlf et al. 1982). Through use of the unweighted pair-group method with arithmetic averages (UPGMA) (Sneath and Sokal 1973), a phenogram was obtained using TAXON from the taxonomic distances. Cophenetic correlation values were calculated for each phenogram to measure distortion between the original distance matrix and the phenogram.

Ordinations of the populations were obtained using nonmetric multidimensional scaling (Kruskal 1964a, b) (with MDSCALE from NTSYS [Rohlf et al. 1982]) on the taxonomic distances for each sex to establish interrelationships of the populations not indicated in a cluster diagram, and to compare with the ordination obtained from the genetic data (see St. Louis and Barlow, in press). A transformation on the taxonomic distances (using GOWER [Gower 1968] from NTSYS [Rohlf et al. 1982]) yielded a Q matrix (Gower 1968) of the populations which was used as initial input to multidimensional scaling. Goodness-of-fit of distances in the ordination to the monotonic function of the original distances was measured by calculation of stress values. A minimum spanning tree demonstrated proximity of populations in multidimensional space (Sneath and Sokal 1973).

Rogers' (1972) genetic distances, calculated from the electrophoretic data in St. Louis and

Barlow (in press), and taxonomic distances were compared using permutation tests (Dietz 1983) to determine covariation of genetic and morphometric data. Kendall's tau statistic was calculated from permutation tests using a Fortran program provided by Dietz (1983).

Spearman correlation coefficients on ranked means (Sokal and Rohlf 1969) were computed to assess the relationship (termed developmental homeostasis by Lerner [1954]; see also Zink et al. [1985] for review) between individual heterozygosity and individual size. Individual heterozygosity was calculated as the number of heterozygous loci per individual. The mean PC 1 or size value for individuals, determined a posteriori to PCA, was calculated for each heterozygosity value. PC 1 values were obtained from PCA for individual adults for each sex. Spearman coefficients on ranked means were also computed to assess the relationship between (termed genetic homeostasis [Lerner 1954; see also Zink et al. 1985]) population heterozygosity and mean morphometric size in the population. Population heterozygosity (direct count) values were obtained from St. Louis and Barlow (in press). Because there was no difference in allelic frequencies, age classes and the sexes were not separated. Size was determined a posteriori from scores of each population for each sex on PC 1, a size-related factor.

Spearman correlation coefficients on ranked means were computed to evaluate the relationship between mean morphometric size in the population (PC 1 scores) for each sex and average monthly and annual temperature (°C) and precipitation (mm). Temperature and precipitation data were obtained from Wernstedt (1972). Climatic variables for the periods July–December and January–June for North America and Europe were compared with corresponding January–June and July–December values for Australia.

Using climatic data obtained from U.S. Department of Commerce records, we calculated average monthly temperatures (°C) and precipitation (mm) for Jacksonville, Illinois (ca 10 to 50 km from the various Illinois collecting sites) to determine if any differences in local weather among North American sites occurred between 1982 and 1983 (two years prior to specimen acquisition at Woodson and Naples) and 1983 and 1984 (two years prior to sampling at White Hall).

RESULTS

The first three factors obtained from PCA accounted for 90.8% and 96.6% of the variation in male and female mensural characters respectively (Table 1). PC 1 accounted for 44% of the variation in males and was interpreted as representing overall size because all characters except sternal depth had positive loadings of similar value. No patterns of variation emerged that separated the introduced from the ancestral populations (Fig. 1). PC 2 in males was interpreted as reflecting shape because most body and appendage characters had negative loadings relative to head characters, with loadings, other than in skull width, showing similar values. PC 2 accounted for 36.8% of the variation. Along PC 2 for males, Australian specimens were distinct from other populations (Fig. 1). PC 3, which accounted for 10% of the variation, is more difficult to explain in general terms than PC 1 and PC 2. Sternal depth loaded highest, followed by leg characters. Skull length also loaded high on PC 3. PC 3 separated the German and Swedish populations from the others (Fig. 1). PC 1 in females, which accounted for 50.6% of the variation, was also

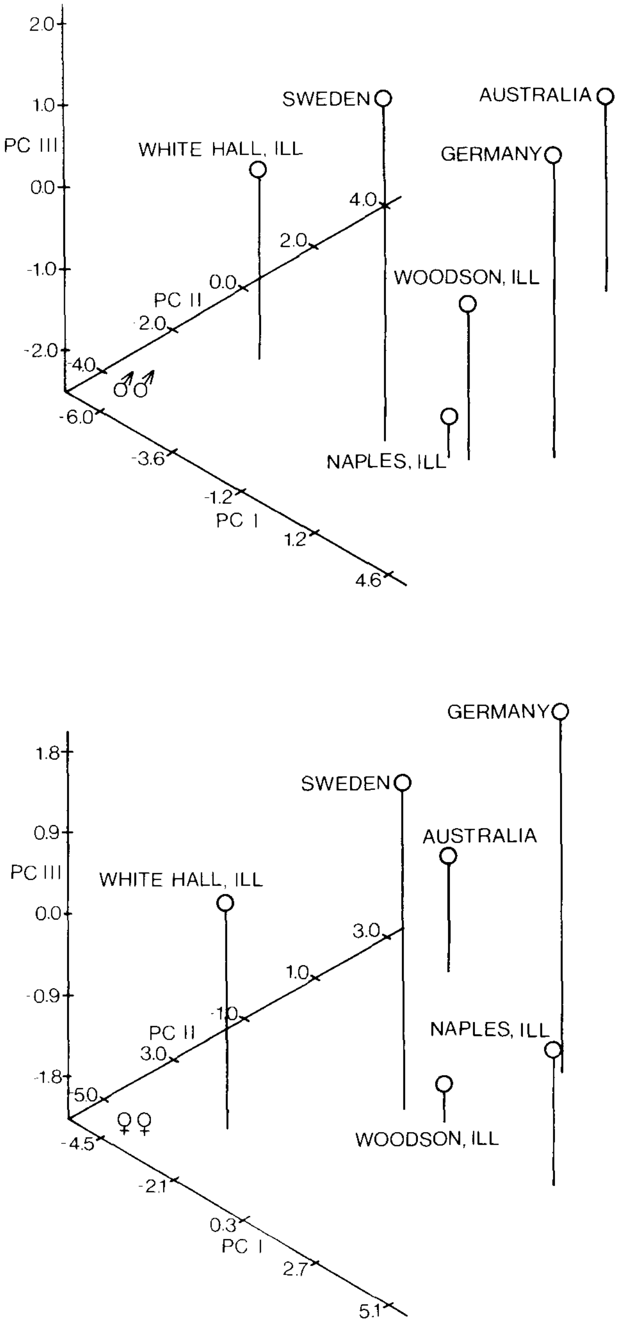

FIG. 1. Three dimensional principal component ordinations of skeletal characters of six populations of *Passer montanus* for males and females.

TABLE 2

TAXONOMIC DISTANCES BETWEEN POPULATIONS OF *PASSER MONTANUS* CALCULATED FOR MALE (ABOVE DIAGONAL) AND FEMALE (BELOW DIAGONAL) SKELETAL CHARACTERS

Population	1	2	3	4	5	6
Australia (1)		1.582	1.662	1.662	1.829	1.614
Germany (2)	1.418		0.985	1.101	1.956	0.887
Naples (3)	2.142	1.207		1.039	1.591	0.717
Sweden (4)	1.392	0.935	1.255		1.272	0.877
White Hall (5)	1.688	1.811	1.921	0.987		1.648
Woodson (6)	1.473	1.140	0.995	0.818	1.277	

size related. Length of sternum, keel and appendages had the highest loadings. Sternal depth, however, had a low positive value. As in the males, no patterns of variation in female characters were found that separated introduced from ancestral populations (Fig. 1). Head and bill characters (other than skull width) and femur width had high positive loadings on PC 2. PC 2 accounted for 35.3% of the variation in females. Sternal length and depth, keel length, femur length, and tarsometatarsus length had negative loadings that were lower than the values for head characters. Again, no pattern of variation emerged that distinguished the introduced from the ancestral populations (Fig. 1). PC 3 accounted for 10.7% of the variation. In males, PC 3 was more difficult to interpret than PC 1 and PC 2; sternal depth loaded highest. PC 3 for females separated the German and Swedish birds form the other samples.

Phenograms constructed from the taxonomic distances for each sex (Table 2) differed from each other in that the Woodson population clustered closest to the Naples and Swedish population in male and female clusters, respectively (Fig. 2).

A minimum stress of 0.005 or less ("excellent fit" [Kruskal 1964a]) was achieved with two dimensions for each sex and therefore was used to interpret the relationships of the populations (Fig. 3). The Australian males and females were most distant from other samples in their respective ordination figures. Swedish birds fell between White Hall and Woodson, with Naples closest to Woodson. The German and Australian populations had different positions in male and female ordinations. The German population was closest to Woodson and to Sweden in the ordinations of males and females respectively. The Australian population was closest to German and Swedish populations in the male and female ordinations respectively.

No significant similarity in distances between the populations was found

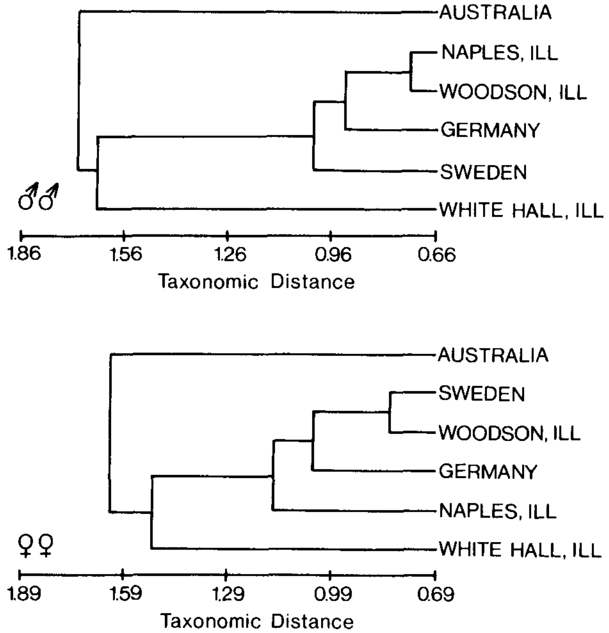

FIG. 2. UPGMA phenograms derived from the taxonomic distances among six populations of *Passer montanus* for the male and female skeletal morphometrics. The cophenetic correlation values were 0.928 and 0.710 for the male and female cluster analyses, respectively.

for male morphometric-genetic or female morphometric-genetic comparisons using the Kendall's tau statistic at the $P \leq 0.05$ level.

There was no significant relationship between mean individual size and individual heterozygosity in males ($r_s = 0.286$, $P = 0.53$) or females ($r_s = -0.107$, $P = 0.82$) (Fig. 4). There was also no significant relationship between population heterozygosity and population size in both males ($r_s = 0.714$, $P = 0.111$) and females ($r_s = 0.714$, $P = 0.111$) (Fig. 5).

No climatic variables were significantly correlated with PC 1 scores in males or females.

DISCUSSION

Genetic-morphometric relationships.—Phenotypic skeletal characters are influenced by both genetic structure of individuals and the ecological factors imposed upon the individuals during postembryonic development (Atchley et al. 1981, James 1983). Although size is partially heritable and controlled by many loci, both nutritional intake (e.g., Ricklefs 1968) and temperature (Gould and Johnston 1972) may affect the maximum po-

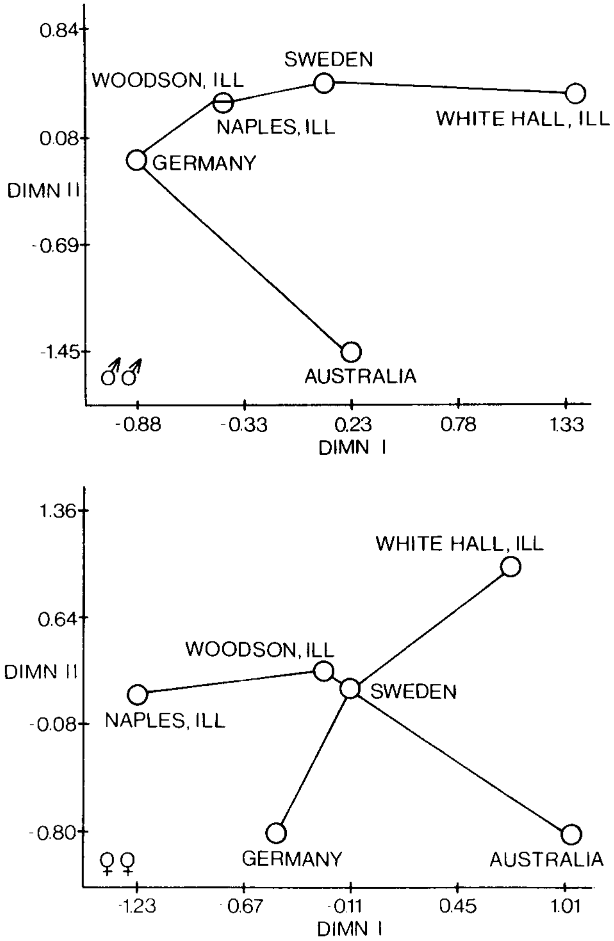

FIG. 3. Two dimensional ordinations from multidimensional scaling on the taxonomic distances among six populations of *Passer montanus* for the male and female skeletal morphometrics. Populations were joined using a minimum spanning tree (see text).

tential size reached by an individual. For the enzymes examined in electrophoretic studies, the proportion of heterozygous loci observed is assumed to be representative of the total genome (Barrowclough 1983). Morphometric differences between two populations, however, might not be reflected in allozyme loci that comprise only a portion of the genome (Wilson et al. 1977, Lewontin 1984). In the present study we found no significant relationship between either male or female genetic and morphometric comparison to support hypotheses regarding genetic-morpho-

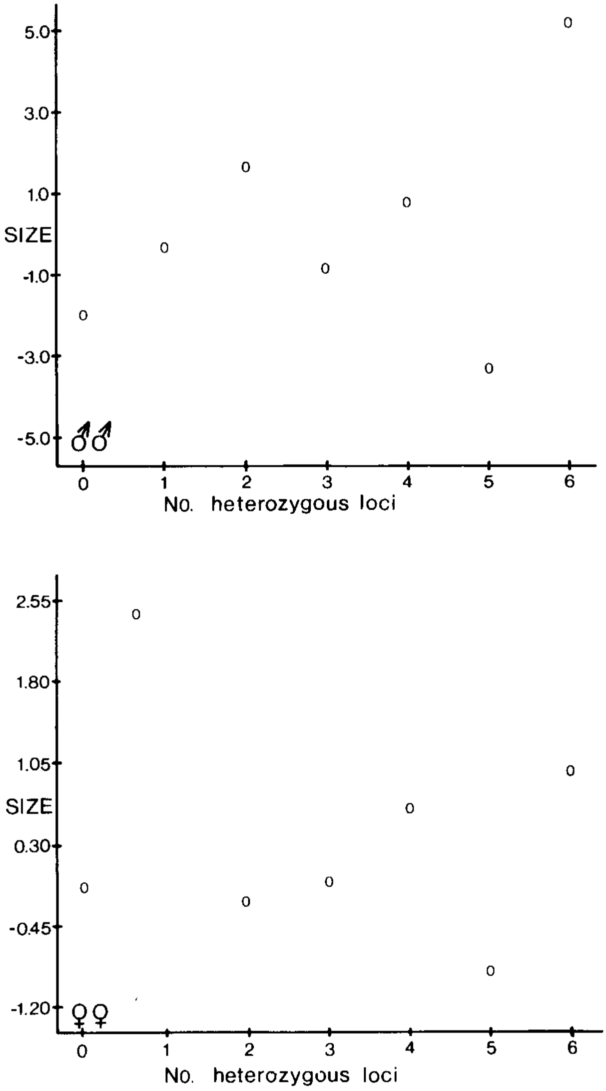

FIG. 4. Plot of number of heterozygous loci vs mean individual size for male and female *Passer montanus.*

metric covariation. St. Louis and Barlow (in press) previously attributed factors influencing genetic makeup of populations of *P. montanus* examined here to mutation, genetic drift, effective population size, and possibly unknown selective factors.

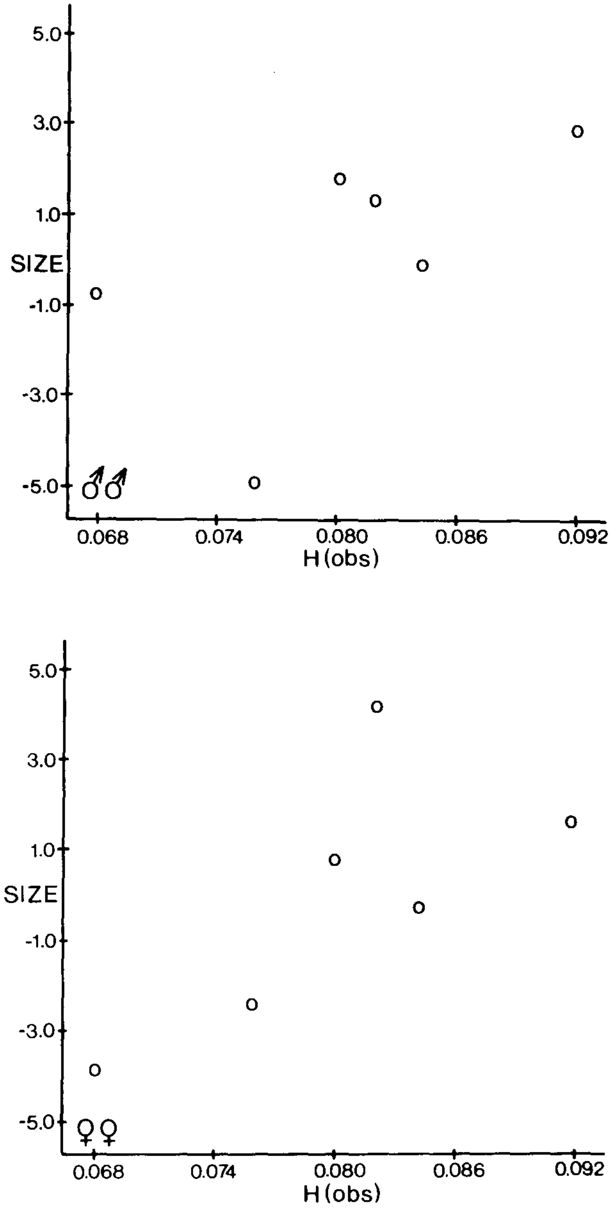

FIG. 5. Plot of observed heterozygosity vs mean population size of male and female *Passer montanus*.

Morphometric differentiation.—Differences in both sexes in bill and head characters between the German and North American populations of *P. montanus* were attributed to resource use by Barlow (1980) and Thompson (1983). Because a portion of the variation among populations of *P. montanus* is related to head and bill characters (PC 2) in males and females, it is thought that foraging-related differences occur across all the populations. PC 2 in males separated the Australian population from other samples. In the present study, variation in leg characters in male *P. montanus* only separated the Australian populations from the other five. Australian males had shorter and thicker legs than did males from the other populations. Because the Australian population inhabits the warmest climate of those encountered in this study, short legs with a large core area would not be expected in terms of thermoregulatory adaptations. Perhaps leg size difference of the Australian birds reflects difference in perching habits (Barlow 1980) or an unknown ancestral character state in the Chinese population. The shape component of female morphology (PC 2) indicated higher variation in head characters than in leg characters, and thus trends in females did not closely resemble those in Australian males. The differences in sternal depth between the North American and Australian and the German populations described by PC 3 may be a result of differential annual migration patterns and muscle developement (Barlow 1980).

Overall size, as explained by PC 1, showed no pattern of divergence among the populations corresponding to the known history of *P. montanus*. Variation in size, as reflected in the ordination of the North American populations in both PCA and two dimensional scaling, is partially accounted for by the differences seen between the smaller White Hall specimens and the other two North American populations, Woodson and Naples. Woodson and Naples were sampled a year earlier than White Hall, and overall size differences might be attributable to interannual variation in environmental conditions.

Influences on size.—Environmental factors are believed to be one influence on overall size in avian species (e.g., James 1970, 1983; Johnston and Fleischer 1981). We found no correlation, however, between average size in the populations and average climatic conditions for their respective regions. Temporally localized weather conditions, such as severe winter storms, are known to influence survival of certain House Sparrow phenotypes (Johnston et al. 1971, Rising 1973, Fleischer and Johnston 1982). In the above cases, in severe winters, large males survive, as do medium and small sized females (Johnston et al. 1971, Johnston and Fleischer 1981). In the present study winters prior to sampling at Woodson and Naples were colder for a longer period of time than winters prior to sampling at White Hall. January snowfall as measured at Jacksonville was, on average, higher in 1982–83 than in 1983–84. Therefore it cannot be ruled out that ordination patterns of the North American populations of *P. montanus* in part are attributable to localized climatic conditions, such that the larger male Woodson and Naples birds suggest a preponderance of large size classes in severe winters, and smaller White Hall females reflect survival by them in milder winters.

Conclusions.—We believe that selective forces acting on the sexes separately and in concert, along with founder-induced ecological differences, such as food availability, account for approximately half of the morphometric variation seen across all populations in this study. Variation in size may be explained in terms of selective pressure from microenvironmental (e.g., severe climatic conditions) sources. Lack of correspondence, however, between genetic and morphometric data does not preclude a lack of genetic constraint on overall size or individual characters. Skeletal characters covary, and therefore are thought to be genetically related to some degree. The magnitude of any genetic influence cannot be assessed within the present study.

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