EVOLUTION IN THE HOUSE SPARROW—VI. VARIABILITY AND NICHE WIDTH

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ABSTRACT.—Degree of secondary sexual size dimorphism in House Sparrows, *Passer domesticus*, varies from small at low latitudes to large at high latitudes. This organization of size dimorphism is an expression of geographic variation of locality variance in body size. For North American populations variance in body size is inversely correlated with number of interspecific competitors, and may result from the interplay between interspecific competition tending to decrease size variation and intraspecific competition tending to increase size variation. For European populations variance in body size is inversely related to number of congeneric species of *Passer*, but possible causal factors seem to be more complicated than they are for North American House Sparrows. Nevertheless, in either set of continental populations, degree of body size variation at a locality may reflect relative niche width. *Received 12 July 1976, accepted 30 November 1976.*

STUDIES associating morphologic structure of organisms with ecologic structure in environments have approached the topic from many angles, and apart from the more strictly paleontologic (Ashton and Rowell 1975) include those that correlate anatomic parts with prey size (Hespenheide 1966, 1973; Pulliam and Enders 1971; Willson 1971; Willson and Harmeson 1973), that assess interspecific competition and food availability (Lack 1947, MacArthur 1972, Soulé 1966, Schoener 1970), that emphasize relative abundance of conspecifics (Van Valen 1973), that predict competitor coexistence (e.g. Pulliam 1975), and that relate morphologic variance to niche width (e.g. Van Valen 1965, Rothstein 1973). We think comparisons of morphologic variation in populations of House Sparrows, *Passer domesticus*, in Europe and North America provide additional insight concerning the adaptive interplay between morphology and environment as this is mediated by intra- and interspecific competition. In particular, we wish to examine geographic variation in degree of secondary sexual size dimorphism (Johnston and Selander 1973) that is expressed in clinal trends of variance in overall size in putative accord with variation in niche width.

SAMPLES, TECHNIQUES, AND METHODS

The data are skeletal measurements of 1,571 House Sparrows from 14 North American localities and 842 specimens from 22 European localities (Table 1). In North America, elevations of sample sites range from sea level to 1,260 m. All sites except one are in prairie or grasslands to maximize environmental, or habitat, similarities and minimize altitudinal differences. Oaxaca, Mexico is not representative of grasslands but is used because it has the lowest elevation of the extreme southern populations with specimen data. In Europe, localities encompass a wider variety of habitats but a smaller range of altitudes, between sea level and 1,000 m. All data were extracted from a larger data matrix assembled by the junior author (cf. Johnston and Selander 1973).

Fourteen skeletal measurements per specimen are the bases from which overall body size is determined; the 14 were measured according to Johnston and Selander (1971), but narial width and femur width were omitted. A subset of skeletal measurements, consisting of skull width and length, premaxilla, dentary, and mandible lengths, provide the input for calculating "bill size." All measurements of "bill size" deal with the morphology of selecting, cracking, and ingesting seeds. Skull length and width are included, since they provide information on muscle attachments, critical factors in granivory. All specimens were collected between 1962 and 1972.

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TABLE 1. Skeletal samples of House Sparrows used in this study

			Number of specimens	
Locality	Latitude	Year collected	Female	Male
		North America		
Peace River, Alberta	56.25	1972	12	14
Edmonton, Alberta	53.57	1963	45	45
Sisseton, South Dakota	45.65	1967	15	27
Manhattan, Kansas	39.18	1971	91	119
Quinter, Kansas	39.07	1966	16	18
Topeka, Kansas	39.03	1966	73	76
Lawrence, Kansas	38.97	1962–70	141	281
Hays, Kansas	38.88	1968–69	81	90
Kit Carson, Colorado	38.75	1968–69	84	97
Udall, Kansas	38.00	1967	14	35
Bastrop, Texas	30.12	1962	22	47
Houston, Texas	29.75	1962	27	61
Progreso, Texas	26.50	1962	12	7
Oaxaca, Oaxaca	17.08	1963	10	11
		Total	643	928
		Europe		
Oslo, Norway	59.93	1970	9	11
Ostermalma, Sweden	58.83	1969	7	7
Aarhus, Denmark	56.17	1969	15	12
Malmö, Sweden	55.58	1970	34	28
Warsaw, Poland	52.83	1964	28	16
Oxford, England	51.77	1962	52	57
London, England	51.50	1969	25	15
Mainz, Germany	50.00	1969	8	5
Oberstenfeld, Germany	48.90	1962	20	19
Ludwigsburg, Germany	48.90	1962	26	41
Paris, France	48.86	1969	18	18
Stuttgart, Germany	48.78	1962	24	15
Radolfzell, Germany	47.73	1969	16	14
Sempach, Switzerland	47.22	1970	21	25
Geneva, Switzerland	46.22	1969	7	19
Karlovač, Yugoslavia	45.50	1970	9	8
Mantova, Italy	45.17	1965	17	27
Parma, Italy	44.80	1965, 70	14	14
Comacchio, Italy	44.70	1965	18	26
Titograd, Yugoslavia	42.47	1970	8	16
Cantalupo Sabino, Italy	42.30	1965	8	16
Cagliari, Sardinia	39.22	1965	23	26
		Total	407	435

Both multivariate (principal component, discriminant function, and multiple regression) and bivariate (linear regression and correlation) analyses were applied to European and North American characters and character sets. Principal component (PC) analysis provides an analytical technique for detecting morphologic covariation in characters and produces factors that represent linear combinations of an original suite of variables. The variation explained by the 14 skeletal measurements is expressed through PC analysis by 14 eigenvectors that are orthogonal to one another (lacking statistical correlation).

Principal component analysis based on the variance-covariance matrix was applied to both the original 14 variables of body size and the 5 variables of bill size; the two sexes were analyzed separately and combined. In all instances PC I appears to represent size variation (Tables 2 and 3), since character loadings tend to make equal contributions to the first eigenvector and are of the same sign (Morrison 1967, Blackith and Reyment 1971). Standard statistics, including mean and variance of PC I scores, were then calculated for each locality; correlation between locality variances of PC I scores and latitude was tested using Spearman's rank correlation analysis. Stepwise multiple regression analysis was performed on data sets from each continent separately, testing the ability of mean PC I scores and latitude to explain variation in locality variance of PC I scores. Partial correlations from multiple regression were used to determine whether change in variance of body size merely reflects change in average body size.

Most computations were done at The University of Kansas Computation Center; later revisions were conducted at the University of Maryland Computation Center. Programs employed include NT-SYS (Rohlf et al. 1969), UNIVAR (Power MS), and SPSS (Nie et al. 1970).

TABLE 2. Character loadings from variance-covariance matrices onto the first Principal Component in a 14-character set of skeletal variables from North American and European House Sparrows. F = females, M = males

Variable	North America[a]			Europe[b]		
	F	M	F + M	F	M	F + M
Premaxilla length	0.115	0.120	0.111	0.138	0.154	0.137
Cranial width	0.151	0.155	0.174	0.191	0.186	0.199
Skull length	0.390	0.396	0.380	0.493	0.563	0.518
Dentary length	0.111	0.125	0.114	0.128	0.149	0.135
Mandible length	0.294	0.304	0.282	0.382	0.378	0.366
Coracoid length	0.412	0.404	0.432	0.494	0.472	0.514
Sternum length	0.482	0.492	0.560	0.681	0.683	0.731
Keel length	0.523	0.612	0.704	0.741	0.754	0.854
Sternum depth	0.210	0.246	0.271	0.276	0.263	0.290
Humerus length	0.437	0.380	0.428	0.523	0.502	0.527
Ulna length	0.479	0.459	0.534	0.607	0.576	0.654
Femur length	0.570	0.387	0.441	0.501	0.483	0.480
Tibiotarsus length	0.732	0.770	0.716	0.883	0.828	0.838
Tarsometatarsus length	0.584	0.522	0.520	0.668	0.645	0.646
% of variation explained by PC I	45.1	51.1	49.4	59.0	60.6	60.4

[a] ♀♀, $N = 643$; ♂♂, $N = 928$.
[b] ♀♀, $N = 407$; ♂♂, $N = 435$.

RESULTS

Variance in body size.—House Sparrow populations show greater variation in body size at northern latitudes and are more homogeneous in size in the south. This clinal pattern is supported by positive correlation between the variance of PC I scores depicting overall size of the pooled sexes (here called PC I variance) and latitude in both North America ($r_s = 0.807$; $n = 14$; $P \leqslant 0.01$) and Europe ($r_s = 0.423$; $n = 22$, $P \leqslant 0.05$).

Stepwise multiple regression indicates that latitude contributes more to the explanation of variation in PC I variance than does the mean of PC I scores describing overall size (hereafter called PC I mean). In both North American and European data sets, latitude is the first variable to enter stepwise multiple regression (0.001 = tolerance, 0.01 = F to enter) followed by the second and final variable PC I mean. Latitude explains 62.9% ($R^2 = 0.629$) of PC I variance in North American and 18.1% in European samples. PC I mean accounts for a proportionate increase in explained variation of 3.2% and 10.5% in the respective continental data samples. This increase is determined from the squared partial correlation coefficients.

Because average body sizes of House Sparrows increase clinally with increasing latitude in North America (Johnston and Selander 1973) it was possible that clinal increase in body size variance simply reflected increase in overall size. A higher correlation between PC I variance and latitude than between PC I variance and PC I mean within the North American populations suggests factors other than mean body size produce the latitudinal gradient of variance in body size. In European House Sparrows a significant positive latitudinal cline in body size variance occurs despite a negative latitudinal cline in mean body size (Johnston and Selander 1973).

Spearman's correlation between PC I variance and latitude for males and females separately within their respective continental samples produces a significant relationship ($P < 0.05$) in only one case. North American females correlate positively with latitude ($r_s = 0.728$; $n = 14$; $P \leqslant 0.01$) and adhere to the general pattern of increased variation in body size within House Sparrow populations at higher latitudes.

TABLE 3. Character loadings from variance-covariance matrices onto the first Principal Component in a five-character set of skeletal variables associated with feeding from North American and European House Sparrows

	North America[a]			Europe[b]		
Variable	F	M	F + M	F	M	F + M
Premaxilla length	0.208	0.214	0.211	0.233	0.235	0.234
Cranial width	0.178	0.184	0.186	0.154	0.192	0.178
Skull length	0.575	0.564	0.569	0.751	0.703	0.726
Dentary length	0.183	0.196	0.191	0.194	0.213	0.204
Mandible length	0.461	0.447	0.453	0.510	0.529	0.521
% of variation explained by PC I	69.7	72.4	70.8	69.1	73.7	71.2

[a] ♀♀, $N = 643$; ♂♂, $N = 928$.
[b] ♀♀, $N = 407$; ♂♂, $N = 435$.

Bill size variation.—Continental differences between House Sparrows appear in geographic patterns of bill and cranial measurements. In European samples variance of PC scores derived from bill and skull measurements of the pooled sexes (hereafter called BS I variance) correlates positively with latitude ($r_s = 0.555$; $n = 22$; $P \leq 0.01$), but means of the same PC scores (hereafter called BS I mean) describe a negative association (BS I $\bar{x} = 1.76 - 0.035$ lat., $P \leq 0.008$). Neither BS I variance nor BS I mean correlate significantly with latitude in North American samples ($r_s = 0.035$; $n = 14$; $P > 0.05$; BS I $\bar{x} = 0.077 - 0.004$ lat., $P = 0.514$).

The most pronounced clinal variation in bill variance occurs in samples in which sexes are pooled, and not within each sex. Correlations relating BS I variance to latitude for males and females separately are not statistically significant ($P > 0.05$). This observation holds for both Old and New World samples.

Sexual differences.—Differences between the sexes are reflected in mean bill size on each continent. Average bill size in males follows a strong cline along a latitudinal gradient, but latitudinal trends in female bill size are weak and statistically nonsignificant. Geographic change in average bill size is directly correlated with the change in mean body size. Both average body and bill sizes in males increase with increasing latitude in North America (BS I $\bar{x} = -0.981 + 0.027$ lat., $P \leq 0.01$) and decrease with increasing latitude in Europe (BS I $\bar{x} = 1.67 - 0.036$ lat., $P \leq 0.02$).

COMPETITION AND VARIATION IN NICHE WIDTH

Bill size and body size both have been used by ecologists as indicators of prey size. Larger-billed birds generally take larger items of food than smaller-billed birds (Hespenheide 1966, Myton and Ficken 1967, Newton 1967, Willson 1971). Larger-bodied individuals generally select larger food items than smaller-bodied individuals (Pulliam and Enders 1971, Brown and Lieberman 1973; for literature review see Hespenheide 1973: 216). Population variance in body size and/or bill size may indicate the range in size of food items taken by individuals in a population, in other words, intraspecific competition (within-phenotype competition) bears on niche size—stiff competition will tend to increase niche width.

Range in prey sizes selected by House Sparrows is in turn influenced by the distribution and abundance of other taxa—we note the dependence on plant productivity (House Sparrows are mostly granivorous in winter) and the influence of interspecific competition. Under heavy competitive pressure from other granivores the variety of seed sizes available to House Sparrows, and thus niche width, may be reduced. But, to the point, we suggest that reduction in the size range of available foods results in reduced variance of House Sparrow body or bill size. Support for this contention is found in the differential occurrence of potential competitors along a north–south continental transect. And, as we will show beyond, interspecific competition correlates inversely with latitude and inversely with degree of variability in overall size of House Sparrows.

Pianka (1966) noted that interspecific competition is likely to vary with latitude. In modeling variation in food abundance for a species, Lack (1947), Van Valen (1965), Willson (1969), and Rothstein (1973) were prepared to believe that relative food abundance diminishes where number of congeneric species increases. In western Europe there are three species of *Passer* (Summers-Smith 1963), but only *P. domesticus* occurs effectively in North America (populations of *P. montanus* occur in low densities around St. Louis, Missouri—e.g. Anderson 1973). Possible competitive pressure in North America is applied by a variety of granivorous birds that variously share House Sparrow habitats and, in effect, replace the pressure of congeneric competitors.

The competition index.—A competition index, C, was designed to test for variation in competitive pressure and to measure interspecific competition at specific localities, differentially weighting the effects of competing species. A comparison of C-indices from localities differing latitudinally provides a technique to detect latitudinal change in competitive pressure. The C-index takes the form:

$$C = \sum_{j=1}^{n} w_j d_j N_j,$$

where C = locality interspecific competition index, n = total number of competing species, w_j = average body weight of species j, d_j = fraction of diet in species j identical to that of *P. domesticus*, and N_j = total number of individuals of species j.

Competing species possessing numerous individuals (large N), sharing a large fraction of the House Sparrow diet (large d), and maintaining a large body size (large w) contribute heavily to competitive pressure; small, rare species with marginal dietary overlap with *P. domesticus* add little to the pressure of interspecific competition and to the C-index. A large C value indicates that House Sparrows at a given locality can experience appreciable interspecific competition.

In testing competition, only North America was considered, since necessary census data were not available for Europe. Competing species included only those that share all or part of the House Sparrow habitat (Table 4) and feed on at least one of the kinds of seeds listed by Martin et al. (1961) as comprising the wintertime diet for prairie House Sparrows—bristlegrass, corn, crabgrass, elm, knotweed, oats, ragweed, smartweed, sorghum, and sunflower. Average weights of species were obtained from Tordoff and Mengel (1956), direct field measurements (Peter Lowther, unpubl. data) and average weights of museum specimens in The University of Kansas Museum of Natural History. Competitors' diets were derived primarily from Martin et al. (1961), but see Table 4.

Number of individuals for each competing species was calculated by averaging observations from the 1967 and 1968 Christmas Bird Counts (Cruickshank 1967, 1968). The number of individuals per species was divided by party hours for each locality; species represented by seven individuals or less were omitted to eliminate bias favoring sightings of rare birds. Initially, total number of competing individuals

TABLE 4. House Sparrow competitors, average competitor weights, and percent of competitor diets identical to that of *P. domesticus*

Potentially competing species	Average weight (g)	References for weight[a]	% diet identical to House Sparrows[b]
Starling, *Sturnus vulgaris*	95	M	2
Evening Grosbeak, *Hesperiphona vespertina*	55	M	5
Snow Bunting, *Plectrophenax nivalis*	35	M	60
Black-billed Magpie, *Pica pica*	150	T	15[c]
Common Redpoll, *Carduelis flammea*	14	M	60
Harris' Sparrow, *Zonotrichia querula*	36	L	75
Pine Siskin, *Carduelis pinus*	18	L	5
Common Grackle, *Quiscalus quiscula*	100	L	65
Dark-eyed Junco, *Junco hyemalis*	22	L	30
Field Sparrow, *Spizella pusilla*	14	M	30
Cardinal, *Cardinalis cardinalis*	48	L	12
Song Sparrow, *Melospiza melodia*	20	T	60
White-throated Sparrow, *Zonotrichia albicollis*	26	L	60
White-crowned Sparrow, *Zonotrichia leucophrys*	25	M	70
Common Crow, *Corvus brachyrhynchos*	475	M	50
Tree Sparrow, *Spizella arborea*	19	M	37
Mourning Dove, *Zenaida macroura*	130	M	55
American Goldfinch, *Carduelis tristis*	15	L	20
Brown-headed Cowbird, *Molothrus ater*	45	M	55
Red-winged Blackbird, *Agelaius phoeniceus*	60	M	50
Savannah Sparrow, *Passerculus sandwichensis*	18	T	30

[a] M = mean weight of five specimens (Museum of Natural History, KU); T = Tordoff and Mengel (1956); L = Peter Lowther (unpublished).
[b] From Martin et al. (1961).
[c] From Kalmbach (1927).

divided by party hours and a C-index were calculated for 14 North American and Canadian localities, comprising a latitudinal transect through the Great Plains. Regressions of individual competitors on latitude and of the C-index on latitude are significant (*Number of competitors* $= 93.5 - 1.89$ lat., $P < 0.01$; $C = 245 - 5.02$ lat., $P < 0.01$).

Because localities of Christmas bird counts and our collecting localities were not identical, C-index was computed for 12 new localities with latitudes and habitats comparable to those of specimen sites. No data were available for latitudes corresponding to Peace River, Alberta or Oaxaca, Mexico. Correlation of body size variance on the C-index indicates a strong inverse relationship (Fig. 1); variance in body size is maximal where interspecific competition appears to be least ($r_s = -0.802$; $n = 12$; $P \leq 0.01$).

METHODOLOGICAL NOTES

An important focus of this study has been on the relationship between morphometric character variance and within- and between-species competition. This relationship allows us to approach the core of the niche-variation hypothesis, which states that the amount of within-population character variance is directly proportional to niche width of the population, assuming that variation in competitive pressure will be reflected in variation in niche width (Van Valen 1965, Soulé and Stewart 1970, Rothstein 1973). Our examination within the confines of one species shows significant variation in character variances for both overall size and size of the feeding structures, significant variation in the probable degree of interspecific competition with House Sparrows from other avian granivores, and a significant negative correlation between character variance and interspecific competition. Finally, if some

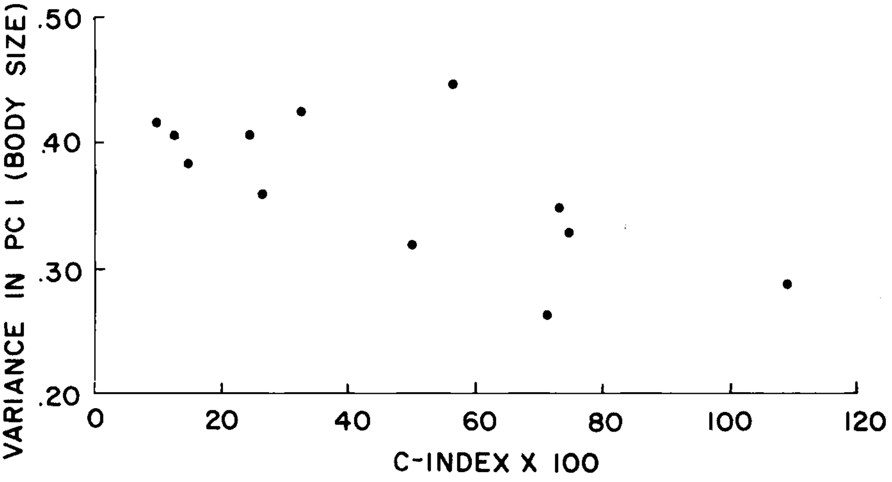

Fig. 1. Variance in Principal Component I (PC I, overall body size) of North American House Sparrows plotted on an index to interspecific competition for food (*C*-index). PC I scores closely approximate body size and were computed from 14 skeletal variables of males and females combined. A large *C*-index indicates potentially intense interspecific competition. Spearman's correlation coefficient between variance in body size and the *C*-index is $r_s = -0.802$ ($P \leq 0.01$; $n = 12$).

dimensions of niche width are conceded to vary in accord with the amount of interspecific competition, then this instance of House Sparrow morphometrics supports the niche-variation hypothesis. An assessment of the strength of this support includes the following, largely methodological, points.

Estimating character variances.—We computed variances for locality specimen sets for PC scores that summarized either five cranial (feeding) dimensions or 14 (overall size) dimensions. Both sets of characters are larger than most such sets employed in examining the niche-variation hypothesis, and the number of specimens is likewise robust. Hence, our estimates of character variances are likely to contain information on lability in feeding apparatus in a much more complete way than is usual, especially since many studies use only bill and tarsus measurements.

Body size in House Sparrows in North America varies from large in the north to small in the south, and since variance scales on size we expected to find parallel variation in variance estimates. Tests for such influence showed it to be of small importance. Fortunately in this regard, body size of European House Sparrows varies from small in the north to large in the south and likewise inversely to size variance. We are satisfied that our variance estimates are free of scaling influences.

Specific unit of analysis.—Our study is done on specimens referable to one species, and this is a departure from most other such analyses based on bird specimens. Since the evolutionary processes lying back of any instance of niche-variation conformity necessarily occur within a species (population), such a taxonomic focus is ideal for our purposes.

Habitat diversity and niche width.—Our specimen samples come from rural, predominantly farmyard, populations. The range in physical habitats sampled is relatively trivial and, although we make no attempt to estimate the range, it is certainly less than that found in species not so strongly commensal with humans. Biotic components of the habitats vary more than physical aspects, and one such source of variation is optimal—wintertime variation in number of granivorous competitors. Another source of variation in habitat is less than ideal, however, and this is that owing to differences in sizes of seeds available to the granivores; such variation can almost never be controlled and is an appreciable source of error in this study.

Temporal diversity and niche width.—The specimen samples were largely netted from fall and winter flocks; most samples were secured prior to mid-winter of any year. Since sparrow populations are known to vary significantly in morphometrics over the winter period (the Bumpus Effect; see Bumpus 1899; Johnston et al. 1972, O'Donald 1973, Johnston and Selander 1973), it is of some consequence to have samples as nearly time-constant as possible. Such time-constancy has been violated in taking some samples for use here, and this is a source of error tending to reduce the precision with which morphometric data can reflect relative niche size.

Granivory, wintertime, and the period of selection.—House Sparrows eat seeds at any time of year, but in winter they are nearly dependent on such food. The winter is also when very powerful selective pressures have been found to operate on size of sparrows (O'Donald 1973); such strong selection, and even lesser pressures (Rising 1973, Johnston and Selander 1973) are known to generate significant increases in degree of sexual dimorphism at a locality. Character variances likewise increase under such differential selection. Individual successes under such selection are partly determined by degree of intraspecific competition. If we now add consideration of interspecific wintertime granivory we should very nearly have touched the major forces generating variation in food aspects of niche width in House Sparrows. Similar views of wintertime as a major source of selective mortality are developed by Lack (1966) and Fretwell (1972).

Sensitivity of the C-index.—Our *C*-index explicitly considers only abundance, relative size, and degree of feeding overlap of actual or potential granivorous competitors, but there is implicit treatment of other aspects of interspecific competition. For example, competitive success among birds is frequently owing to large size. Thus it is that a starling (*Sturnus vulgaris*) can displace all House Sparrows at a feeding site simply by arriving and taking a perch; its size, large relative to a House Sparrow, seemingly is read as a guarantee of aggressive competitive vigor. The *C*-index of course includes size, so some weight is given to this aspect of the psychology of aggressive interaction.

Abundance of the potential granivorous competitor is judged by the wintertime censuses of birds taken by cooperators of the National Audubon Society, but not necessarily at the exact localities from which we obtained samples of sparrows.

DISCUSSION

Two aspects of niche width.—Niche width for a species is comprised of two aspects of variability—that for individuals (individual flexibility) and that for populations (differences between individuals in a population). Our information and our emphasis concern the latter, largely from a position of morphologic inference. The hard data are bony sizes of House Sparrows; this allows us to infer a part of the niche hypervolume for sparrows in general terms, but we nevertheless miss the information on individual flexibility.

We suppose that individual flexibility is likely to be a behavioral, not a morphologic, quality. This is not a polar dichotomy, for behavioral variables are often influenced by morphology, as when North American House Sparrows fight for position at a good foraging site in winter—large individuals win much more often than small ones, whether in Saskatchewan, North Dakota, Nebraska, or Kansas (C. L. Cink, pers. comm.). Even so, we have no way of knowing how much morphologic variation within populations is organized by behavioral interaction, and further assume that some behavioral flexibilities in individuals are neither mediated by nor translated into variation in morphology.

Our approach includes no direct behavioral information on House Sparrows, but we think that were we to have such information the precision with which we could track relationships between morphology and niche width should increase. And, perhaps the degree of scatter of points in Fig. 1 would be reduced if information on behavioral aspects of interspecific competition in House Sparrows were available.

Sociality and niche width.—Hespenheide (1975: 176) has supposed that "the normal means by which [intraspecific] competition is alleviated . . . [is] . . . by the social structure of the population." Furthermore, he notes that territorial species have social structures placing only paired males and females in competition with each other. He views such a problem of competition as being as readily soluble through behavioral and ecologic as through morphologic means. He goes on, "Only in species that feed in social groups on relatively rare food would differences in feeding (bill) morphology be useful in reducing intraspecific competition." Our information on House Sparrows can be taken as reasonable support for Hespenheide's hypothesis. Our information on morphologic differences transcends bill size, but we see no reason to modify the hypothesis. Additionally, food of House Sparrows during wintertime social feeding activities is not often "rare." Yet it is precisely at those times when most food is covered by snow that the advantages of differential size are greatest; it is then that most fighting for food occurs, and any means to feed successfully at opposite ends of a food spectrum would be of pronounced value for individuals. Realization of such value is highest at high latitudinal localities, owing to wintertime competitive release at those localities.

Significance of the European replication.—Because variation in body size of House Sparrows is clinally large to small from south to north in Europe (the opposite of what is found in North American populations), replication of the latitudinal increase in variance in size is extremely important. It not only vitiates any argument that the increase in variance is a mere effect of increase in body size, but also suggests that wintertime competitive release is exploited by different populations of House Sparrows in the same way, irrespective of body size.

Selection for variation in niche width.—The ultimate source of sexual size variation in House Sparrows probably involves Darwinian sexual selection. Phyletic considerations (Johnston and Klitz 1977) suggest the most recent ancestor of the House Sparrow was sexually dimorphic both in plumage and size, for its closest relative (*Passer hispaniolensis*) shares such sexual dimorphism. We envision sexual selection preceding any selection defining niche width—males became slightly larger than females owing to size advantages in intrasexual battles followed by female choice of winners as mates. Males were thus suited to using a larger range in seed sizes than females, who in turn could specialize on a set of smaller seeds. In this view males and females each comprise distinct selective populations, and each is a major component of the other's environment. Such a view also reduces the utility of earlier distinctions between "within-species" and "between-species" factors generating variation in niche width.

ACKNOWLEDGMENTS

We are happy to thank B. Amerson, S. Fretwell, F. James, P. Humphrey, N. Slade, and S. Rothstein for various kinds of assistance in the course of this study. H. Hespenheide provided reviewer commentary that we found very helpful. Support of the National Science Foundation (DEB-72-02374) and the General Research Fund of The University of Kansas (3952-5038) likewise has been helpful.

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