OVERWINTER MORTALITY AND SEXUAL SIZE DIMORPHISM IN THE HOUSE SPARROW

RICHARD F. JOHNSTON AND ROBERT C. FLEISCHER

Museum of Natural History and Department of Systematics and Ecology,
The University of Kansas, Lawrence, Kansas 66045 USA

ABSTRACT.—Overwinter mortality in House Sparrows (*Passer domesticus*) in eastern Kansas in 1978–1979 accentuated sexual size dimorphism. Males were significantly larger after winter, females significantly smaller, meaning that large females and small males were at a lowered survival fitness. We propose that birds of intermediate size are at a competitive foraging disadvantage under conditions of persistent snowcover. Such an effect would be most pronounced at latitudes higher than that at Lawrence, Kansas. The relationship of this to the possible splitting of the foraging niche suggests a modification of earlier thinking, which put emphasis on interspecific competition for food. *Received 4 October 1980, accepted 21 January 1981.*

THE long-term maintenance of sexual dimorphism in size appears to be largely genetic in birds (Lande 1980). Even so, because size is a polygenic character (probably including both sex-linked and autosomal loci), there is a tendency for a significant part of each new generation to be of intermediate size relative to parents (Falconer 1960). This is apparent in House Sparrows (*Passer domesticus*), in which there is, nevertheless, highly significant sexual size dimorphism in high and mid-latitude populations (Johnston and Selander 1973). Current highly significant degrees of dimorphism are probably explained by overwinter mortality that is disproportionately heavy on individuals of intermediate size (Bumpus 1899, Rising 1973, Johnston et al. 1972), which increases the differences in mean sizes of the sexes. This conclusion, nevertheless, remains to be effectively established; thus, this report gives details on mortality in House Sparrows in eastern Kansas over the winter of 1978–1979, in which a modest amount of genetically based, sexual size dimorphism was translated into a larger degree of dimorphism by compelling ecologic events [unusually heavy snowfall (Matson and Wiesnet 1981) and persistent subfreezing temperatures].

Fieldwork for this study was organized around the temporal sequence in which ecologic events occurred. The sampling of sparrows made it relatively easy to sort out the apparent contributions of historically or *phylogenetically early selection* (now genetically coded) and *contemporary selection* (not yet so coded) to size dimorphism in these birds. Darwinian sexual selection is presumably the source of underlying genetic differences in sizes of the sexes. The focus of this work is on the possible influences of wintertime conditions on physiology, ecology, and behavior that result in the modification of the size distribution in a population. Among possible factors, intraspecific fighting for feeding rights is demonstrated to be probably responsible for a frequency-dependent mortality pattern that can significantly enhance the degree of sexual size dimorphism in a population.

MATERIALS AND METHODS

Specimens for this study were secured by mist-netting in seven farmyard colonies within a single population of about 6,000 birds in an area 3.2 km in radius in northeastern Kansas [Lowther (1979) presents details]. Each farm contributed about equal proportions to the fall and spring samples. Some 242 birds were taken in November 1978 and 197 in March 1979; all were prepared as whole skeletons and then measured for 14 variables of bony size (Table 1).

The fall sample was sorted for age; birds-of-the-year, those with skulls not completely ossified ("SNCO"), were distinguished from the other age cohorts, those with skulls completely ossified ("SCO").

TABLE 1. Character-state means for the six subsets of specimens[a] used in this analysis.

Variable	Females[b]			Males[b]		
	Fall SNCO $n = 62$	Fall SCO $n = 40$	Spring total $n = 81$	Fall SNCO $n = 81$	Fall SCO $n = 59$	Spring total $n = 116$
Premaxilla L	7.12	7.14	7.14	7.09	7.09	7.15
Skull W	15.25	15.25	15.30	15.35	15.44	15.39
Skull L	30.20	30.23	30.26	30.16	30.37	30.32
Dentary L	6.22	6.29	6.22	6.22	6.30	6.32*
Mandible L	20.41	20.42	20.45	20.41	20.48	20.46
Coracoid L	17.75	17.76	17.60*	17.94	18.07	18.05
Sternum L	22.78	22.93	22.61	23.12	23.43	23.40**
Keel L	21.40	21.54	21.21	21.95	22.48	22.24*
Sternum D	10.30	10.26	10.30	10.50	10.59	10.60
Humerus L	18.46	18.46	18.26**	18.60	18.72	18.76*
Tibiotarsus L	27.91	27.98	27.76	27.86	28.00	28.03
Ulna L	20.72	20.70	20.57	21.19	21.35	21.35*
Femur L	17.46	17.42	17.31*	17.40	17.44	17.49
Tarsometatarsus L	19.01	19.00	18.76	18.91	19.11	19.07
PC I	−0.36	−0.26	−0.64	0.05	0.53	0.43**

[a] Sample abbreviations: Fall SNCO, specimens with skulls not completely ossified in November 1978; Fall SCO, Spring Total, specimens with skulls completely ossified in either November 1978 or March 1979.
[b] An asterisk shows means for the postwinter sample that differ significantly by t-test from means for the SNCO prewinter sample at the 5% level; two asterisks show differences at the 1% level.

Some of the birds with SNCO may have been only about 5 months old, hatched as late as mid-July 1978, but most were 6 or 7 months old. Most thus had completed their linear body growth and could be expected as a class to be similar in size to birds with SCO (around 17 months old at a minimum to more than 6 yr old). Some of the smallest birds probably are the youngest in the SNCO sample (Rising and Johnston MS). Nevertheless, it is worth noting (Table 1) that character-state means for SNCO birds are by no means uniformly smaller than those for SCO birds.

RESULTS

SEXUAL SIZE DIMORPHISM

Variation in single characters.—Mean values of the 14 variables are presented in Table 1 for the three samples of each sex. In males the SNCO birds have the smallest means, and the two samples of SCO birds share the largest. In females the SCO birds from 1979 have the smallest means, and both classes from 1978 share the larger means. If we look only at spring versus fall SNCO means, 9 of the 10 postcranial variables in females in the spring sample are smaller (3 significantly so) than those for the fall SNCOs; for males, all 14 variables are larger in spring relative to fall, and 5 of the postcranial variables are significantly larger than those of the SNCOs. These differences from fall to spring are here assumed to represent the results of overwinter mortality; they are the bases on which the changes in sexual size dimorphism were realized.

Figure 1 presents an assessment of sexual dimorphism for the three samples over the 14-character set of variables. There are two tendencies: (1) variables of the skull and hindlimb show no or little sexual dimorphism, but those of the body core and wing show significant dimorphism; and (2) the degree of dimorphism in the birds from the spring of 1979 is consistently greater than that for either fall sample. In fall SNCO birds, 6 variables are significantly dimorphic, in SCO birds from that fall 7 are dimorphic, but for the spring birds 11 are dimorphic. Differences in sample sizes pose a problem, however, and, if the SNCO sample sizes had been the same
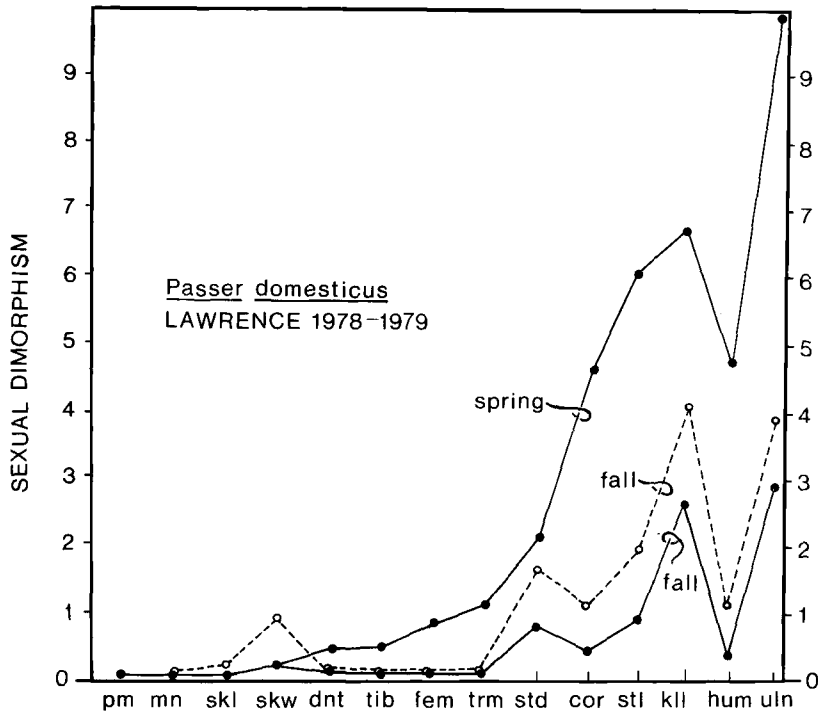
Fig. 1. Degree of sexual size dimorphism in 14 morphometric variables for three samples of House Sparrows from Lawrence, Kansas. The solid line labelled "fall" represents subadults for 1978, the dashed line is for adults taken in 1978, and the solid line labelled "spring" is for the sample from March 1979. The scale for dimorphism is the value of the F-ratio/10 from analyses of variance for each variable for the two sexes; the smallest F-ratio achieving statistical significance is that of the fall subadults for skull width ($F = 3.75$). Abbreviations for the variables; pm, premaxilla length; mn, mandible length; skl, skull length; skw, skull width; dnt, dentary length; tib, tibiotarsus length; fem, femur length; trm, tarsometatarsus length; std, sternum depth; cor, coracoid length; stl, sternum length; kll, keel length; hum, humerus length; uln, ulna length.

as the spring samples (while preserving the mean values recorded in Table 1), skull width and humerus length would have achieved significant dimorphism.

Variation in overall size.—It is necessary to pay close attention to single characters in studying sexual dimorphism, but it is also necessary to use multivariate means of assessing such variation. Two such techniques have been used here: first, principal components of variation (Sneath and Sokal 1973) were extracted for each specimen; means were then computed for each subsample, and these appear in Table 1 for the first principal component (PC I). PC I is a rendering of overall size, because 13 of the 14 variables load significantly on this axis, and all have the same sign. Overall, PC I summarizes 50.8% of the variation in the 14 variables. Negative scores are for small specimens, positive for larger ones, and it is clear that males are larger than females. The largest males are from the fall of 1978 and the smallest females are from the spring of 1979.

An assessment of size dimorphism is perhaps best realized by using PC I, and this is done in Table 2. Values of t comparing differences in mean sizes of the sexes are relatively large for both the fall SNCO and spring samples; the t for the spring sample, however, being $2.5\times$ larger, shows that appreciably greater differences in

TABLE 2. Comparison of sexual size dimorphism by means of scores on Principal Component I ("Overall Size") in two samples of House Sparrows.

| | | Sample size | Principal component I | | t | P |
			Mean	SD		
Fall SNCO	♀♀	60	−0.364	0.916	2.49	0.01
	♂♂	81	0.049	1.010		
Spring ALL	♀♀	81	−0.642	0.889	8.15	0.001
	♂♂	115	0.428	0.908		

sizes of the sexes are found there than in the fall SNCOs. As noted above, there is a problem with sample sizes; if, for instance, the fall SNCOs had the sample sizes of the spring birds (while preserving their size characteristics), they would have achieved a value of $t = 2.91$; likewise, if the spring samples were to have been of the sizes of the fall SNCOs, they would have had $t = 6.93$. But, whichever way these are calculated, the increase in sexual size dimorphism by the spring birds over the fall SNCOs is considerable.

The second multivariate technique used is that of discriminant analysis (Sneath
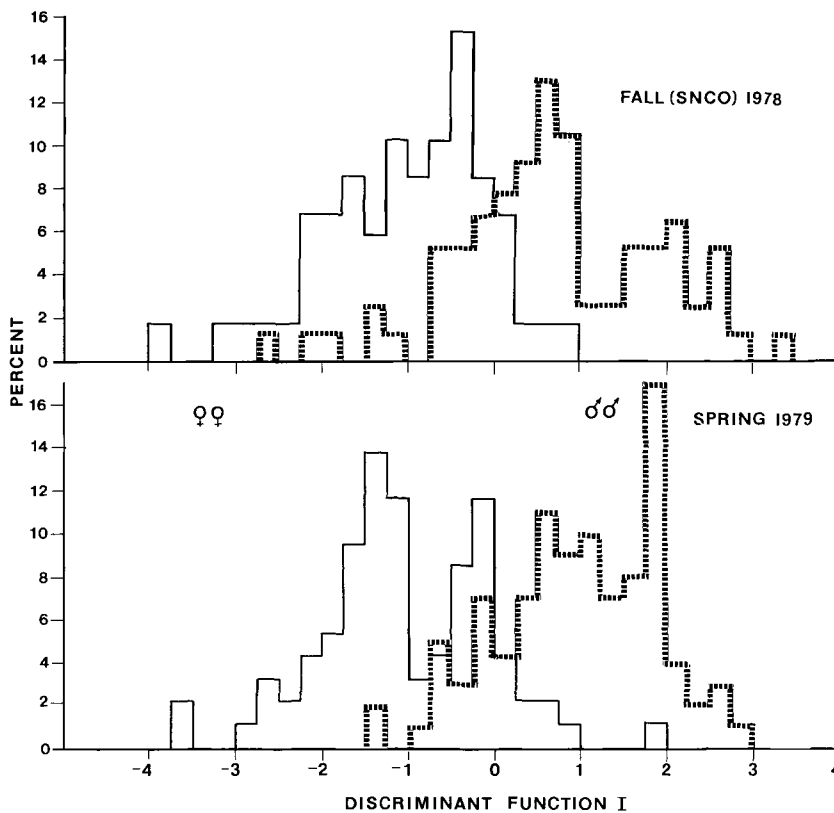

Fig. 2. Frequency distributions of males (broken line) and females (solid line) on the first canonical variate (discriminant axis I, = overall size) of a two-way discriminant analysis of all specimens from 1978–1979. Upper: distributions of 62 females and 81 males from the subadult sample; lower: distributions of 81 females and 116 males from the spring sample.

and Sokal 1973). This technique is ideal for obtaining a maximum estimate of the size differences between males and females; all specimens were entered into a two-group (male and female) discriminant analysis, each specimen accordingly receiving a discriminant score based on its character-states for eight of the 14 variables, of which the most important were lengths of ulna, tibiotarsus, and keel. The frequency distributions of canonical variates scores from the discriminant analysis is depicted for four of the samples in Fig. 2. The histograms tend toward normal distributions, and for a given time period the sexes have extensive overlap. In the SNCO birds the modal size classes for each sex are relatively close in discriminant space; the Mahalanobis distance is $D^2 = 2.98$ ($P = 0.05$). In the birds from the spring of 1979 the modes are more widely separated, and the Mahalanobis distance between the sexes is $D^2 = 4.16$ ($P = 0.01$). The frequency distributions of the SCO specimens from the fall resemble those of the spring specimens, and the Mahalanobis distance is $D^2 = 4.33$ ($P = 0.01$).

THE PATTERN OF OVERWINTER MORTALITY

The histograms (Fig. 2) present a reasonably good visual depiction of the results of disruptive selection (compare Wallace 1968: 384–395). An even better visual depiction is obtained by combining the sexes into single histograms, one before and one after winter mortality. Figure 2 nevertheless shows the point concerning winter mortality—there was a disproportionately heavy loss of individuals from the center of the size distribution and a correspondingly light loss from size classes to either side of the midpoint size. The likelihood of an increase in numbers of a size class following winter was inversely proportional to the number of individuals in the size class before winter. The chance for a decrease in numbers following winter was directly proportional to the numbers in a size class before winter.

Other studies of wintertime mortality in sparrows.—In the basic text of such studies on House Sparrows, at Providence, Rhode Island, Bumpus (1899) found normalizing selection in females, and his data documented directional selection for large size in males (Johnston et al. 1972). Rising's (1973) overwinter study in 1967–1968 of the Bumpus effect at Lawrence, Kansas showed normalizing selection in both sexes (the individual character-state means, although generally larger in males and to some extent smaller in females, were statistically identical before and after winter). In contrast, the present study at Lawrence shows significant directional selection for size in both sexes, females being smaller, males larger, after winter.

It would be useful to be able to generalize over the three studies. Bumpus worked with birds affected by a severe, 1-day storm; both the studies at Lawrence were on birds subjected to an entire winter period. At Providence the bad weather was intense for an overnight period. At Lawrence in 1978–1979 the bad weather was intense for many weeks of the winter; in 1967–1968, however, the winter presented no unusual temperature challenges and was nearly snow-free in cold weather.

Even so, using discriminant analysis, Rising's samples from 1967–1968 showed an increase in size dimorphism (Johnston and Selander 1973), that is, Rising's samples were shown to agree with the earlier Providence (and the later Lawrence) studies on this point. The generalization thus emerges and may be phrased as follows: Under winter stress House Sparrows of intermediate size (large females and small males) are at an overwinter survival disadvantage. Or, conversely, females of average and small size, and males of average and large size, are at an overwinter survival advantage.

Using the latter phrasing, the generalization fits earlier thinking about size and survival (e.g. Fretwell 1972). Small size is an advantage in that less energy is required to maintain it (Kendeigh 1944). Large size results in a lower ratio of surface area to body volume, which increases heat retention and metabolic efficiency. Also, large size is an advantage in winter in that fights over food are usually won by larger birds (Cink 1977).

DISCUSSION

Regeneration of the mid-parent size each year.—Sizes of males and females cannot depart infinitely from one another, but the two would be much farther apart in Kansan House Sparrows if overwinter mortality were to occur each year as it did in 1978–1979. To that point, we have already noted that Rising's (1973) field experiment on the Bumpus effect provided an entirely different degree of overwinter, mortality-generated difference. The one-night calamity documented by Bumpus, although not strictly comparable, demonstrated mortality like that of the present case. At Lawrence the challenges are less stringent in most years, and in some winters mortality from the combination of cold, snowcover, and competitively mediated starvation is modest—as the Rising experiment showed. In such years a great proportion of mid-size birds will live to reproduce, and their descendants will inevitably include a major fraction of medium-sized birds.

Even very large and very small birds that survive overwinter will tend to produce a significant fraction of medium-sized birds in their offspring, partly owing to genetic recombination of the large numbers of genes for size and partly owing to the fact that House Sparrows do not mate assortatively for size (Edward Murphy MS). If we assume that there are autosomal (as well as sex-linked) loci coding for large size, a large male may impart a "large" genotype to both sexes of its offspring, resulting in larger than optimal females. The opposite trend presumably occurs for smaller females, resulting in smaller than optimal males and regeneration of the mid-parent size classes. Thus, there appears to be no persistent tendency at Lawrence for sexual size dimorphism to be greatly modified from the basic amount that is coded from historical, Darwinian sexual selection. There is, nevertheless, significant geographic variation, clinally ordered from south to north, in degree of sexual size dimorphism in North America, to which we will return later.

Disadvantages of intermediate size.—The three studies of concern seemingly demand an explanation for the reduction in frequency of birds of intermediate size through the winter period. Problems of getting food under extreme conditions are likely to be involved. In winter, sparrows are daily subjected to finding enough food for the activities of each day—there is scant nightly carryover of energy reserves (Blem 1973); birds in optimal condition expend 60% of their usable fat in 15.5 h at $-20°C$. Many winter nights are nearly that long, and very many are colder. Above latitude 45°N extreme low temperatures can become a critical challenge when snow covers possible feeding sites for even a fraction of a foraging day. Under these conditions fights between foraging individuals become ever more frequent (Cink 1977). The distribution of food resources thus becomes a function of winning and losing fights; these may go as follows:

Large individuals win aggressive encounters, in stable flocks this is recognized, and such individuals move wherever they want with simple supplanting attacks; this can be considered efficient use of foraging time.

Small individuals lose aggressive encounters, in stable flocks this is recognized,

and such individuals are readily displaced by larger ones; in and of itself, this is efficient use of foraging time and exists over and beyond the energetic benefits of small size.

Intermediate-sized individuals win some encounters and lose some, and against other medium-sized birds the prospects of winning cannot be readily estimated; in stable flocks, therefore, individuals of intermediate size must spend more time in agonistic encounters than either large or small birds, and this has to be reckoned as inefficient use of foraging time.

In other words, individuals at the top of a hierarchy tend to initiate agonistic encounters but rarely respond to, or have to respond to, an aggressive attack by avoidance behavior; individuals at the bottom of a hierarchy tend to use avoidance behavior when responding to an aggressive encounter, but they rarely initiate such encounters; but individuals of intermediate hierarchic rank, and size, engage in both agonistic initiation and avoidance behavior.

Clinal variation in sexual size dimorphism.—The degree of size dimorphism in House Sparrows is large at high latitudes and small at low latitudes (Johnston and Selander 1973, Hamilton and Johnston 1978). Hamilton and Johnston suggested that variation in sexual dimorphism in size is a consequence of the merits of niche-splitting—the farther apart in size the sexes are the lesser the likelihood for inter-sexual competition for food. Because of the important role that environmental mod-ification of sexual size dimorphism has here been found to play, however, the hypothesis needs re-examination. The major problem for the hypothesis is that large degrees of size dimorphism are generated by wintertime selection, not by prior genetic coding. Additionally, seemingly heavy competition for food occurs in flocks of sparrows already significantly sexually dimorphic in size. Finally, there is a related problem in that the feeding structures (measured by sizes of skull parts) are nearly sexually monomorphic.

Specifically for granivorous birds, the concept of niche-splitting entails the idea that competition between large and small individuals in a population can be reduced if there is specialization of large individuals on large seeds and vice-versa. Well and good, perhaps, but perhaps not if attainment of effective degrees of size dimorphism is a matter of annual adjustment, sometimes a little and sometimes a lot. Surviving males and females may, as the data from the birds from the winter of 1978–1979 suggest, actually achieve some measure of food specialization, but this will have been only from a considerable number of selective deaths. Such deaths do not readily count as "costs" of evolution (Haldane 1957), for, as noted above, smaller females and larger males tend to regenerate large numbers of offspring of mid-parent size, so the prospect of amelioration of selective deaths as a consequence of disruptive selection is small.

The niche-splitting hypothesis likewise is not helped by the virtual size mono-morphism of the feeding structures in the skulls of sparrows. There is only one variable in the skull complex that regularly achieves significant sexual size dimor-phism—width of skull (and, in the present set of specimens, dentary length: Fig. 1). Although width of skull can be related to relative muscle masses associated with jaw kinetics and hence seed-eating efficiencies, it is not clear what an increase in dentary length can mean without an associated increase in either length of premaxilla or of the skull as a whole. In any event, the condition of significant size dimorphism in two of five skull variables after wintertime mortality cannot be used to support the hypothesis on niche-splitting for the reasons examined in the last paragraph.

TABLE 3. Relative size of adult and first-year specimens of House Sparrows at several North American localities.[a]

Locality	Latitude °N	Females[b]					Males[b]				
		P	S	H	T	U	P	S	H	T	U
Peace River, Alberta	56	−	+	−	−	−	+	+	+	+	+
Edmonton, Alberta	53	−	−	+	−	−	+	+	+	−	+
Regina, Saskatchewan	50	+	−	−	−	−	+	+	+	+	+
Jamestown, North Dakota	46	. . . .					+	+	−	−	−
Burlington, Iowa	40	+	+	+	+	+	+	+	−	+	+
Gunnison, Colorado	38	−	+	+	−	+	±	−	+	−	±
Hays, Kansas	38	+	+	+	+	+	+	+	+	+	+
Manhattan, Kansas	38	+	+	−	−	±	+	±	+	+	+
Lawrence, Kansas	38	+	+	+	+	+	+	+	+	+	+
Houston, Texas	29	+	+	+	+	+	+	+	+	+	+
Las Cruces, New Mexico	32	+	+	+	+	+	+	−	+	+	+
Tampa, Florida	28	+	+	+	+	+	+	+	+	+	+

[a] If adult specimens average larger than first-year specimens, the tabular entry is "+"; if adults average smaller, the entry is "−"; if there is no significant difference, the entry is "±."

[b] Abbreviations for characters: P, premaxilla length; S, sternum length; H, humerus length; T, tarsometatarsus length; U, ulna length.

The cline in degree of sexual size dimorphism in House Sparrows is therefore probably a result of progressively more exacting wintertime selection from southerly to northerly localities. If this is true, that is, if sexual size dimorphism is regularly modified as described here but varies clinally in its expression, we should expect to find adult females to be smaller than first-year birds at the most rigorous wintertime sites; adult males should be larger than first-year males at the same localities. This prediction is examined in Table 3, in which it is evident that at the three most northerly localities, where winter stress is greatest, the adult females are indeed smaller than the first-year females (80% of the time). At mid- and low latitudes the trend reverses, and adult females are larger than first-year birds in 84–93% of the cases over a set of seven localities. Males are larger as adults irrespective of locality.

In conclusion, the presumed occurrence of splitting of the seed-eating component of the feeding niche of House Sparrows seems not to apply to birds at southerly or mid-latitudinal stations. The evidence does support the prospect that such niche differentiation occurs, or is in the process of being established, at high-latitude localities in North America. Hamilton and Johnston (1978) were impressed at the contributions that progressive relaxation of interspecific competition at progressively northerly sites could make to the generation of the cline in size dimorphism. The present report has nothing to say on that matter, but the importance of intraspecific competition at high latitudes has been reinforced. It has been reinforced to such an extent that one can expect that future examination of the degree of sexual size dimorphism of House Sparrows at higher latitudes in North America will show a more pronounced level of dimorphism than is found presently.

LITERATURE CITED

BLEM, C. 1973. Geographic variation in the bioenergetics of the House Sparrow. Ornithol. Monogr. 14: 95–121.

BUMPUS, H. 1899. The elimination of the unfit as illustrated by the introduced sparrow. Biol. Lect., Marine Biol. Lab. Woods Hole: 209–226.

CINK, C. 1977. Winter behavior of the House Sparrow. Unpublished Ph.D. dissertation, Lawrence, Kansas, Univ. of Kansas.

FALCONER, D. 1960. Introduction to quantitative genetics. Edinburgh, Oliver & Boyd.

FRETWELL, S. 1972. Populations in a seasonal environment. Monogr. Pop. Biol. No. 5. Princeton, N.J., Princeton Univ. Press.

HALDANE, J. 1957. The cost of natural selection. J. Genet. 55: 511–524.

HAMILTON, S., & R. JOHNSTON. 1978. Evolution in the House Sparrow—VI. Variability and niche width. Auk 95: 313–323.

JOHNSTON R., D. NILES, & S. ROHWER. 1972. Hermon Bumpus and natural selection in the House Sparrow, *Passer domesticus*. Evolution 26: 20–31.

———, & R. SELANDER. 1973. Evolution in the House Sparrow. III. Variation in size and sexual dimorphism in Europe and North and South America. Amer. Natur. 107: 373–390.

KENDEIGH, S. C. 1944. Effect of air temperature on the rate of energy metabolism in the English Sparrow. J. Exp. Zool. 96: 1–16.

LANDE, R. 1980. Sexual dimorphism, sexual selection, and adaptation in polygenic characters. Evolution 34: 292–307.

LOWTHER, P. 1979. Interfarm variation in breeding biology of a Kansas population of House Sparrows (*Passer domesticus*). Unpublished Ph.D. dissertation, Lawrence, Kansas, Univ. Kansas.

MATSON, M., & D. R. WIESNET. 1981. New data base for climate studies. Nature 289: 451–456.

RISING, J. 1973. Age and seasonal variation in dimensions of House Sparrows, *Passer domesticus* (L.), from a single population. Pp. 327–336 *in* Productivity, population dynamics, and systematics of granivorous birds (S. C. Kendeigh and J. Pinowski, Eds.). Warsaw, Polish Sci. Publ.

SNEATH, P., & R. SOKAL. 1973. Numerical taxonomy. San Francisco, W. H. Freeman.

WALLACE, B. 1968. Topics in population genetics. New York, Norton.