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Author(s): Richard F. Johnson, David M. Niles and Sievert A. Rohwer

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HERMON BUMPUS AND NATURAL SELECTION IN THE HOUSE SPARROW *PASSER DOMESTICUS*

RICHARD F. JOHNSTON, DAVID M. NILES, AND SIEVERT A. ROHWER
*Museum of Natural History, Department of Systematics and Ecology,
University of Kansas, Lawrence, Kansas 66044*

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On February 1, 1898, after an uncommonly severe storm with snow, rain and sleet and of long duration, several samples of moribund house sparrows were brought to the biological laboratories of Hermon Bumpus at Brown University, Providence, Rhode Island. Almost half these birds died as a result of stress from the storm, and Bumpus assumed that he could get new information on the operation of natural selection if he properly exploited this differential survival. He accordingly made specimens of all the birds, recording gross body weight at the time, and later took measurements of eight size variables, six of them of skeletal elements. In roughly a year he had reported (Bumpus, 1899) the results of his study.

Judging by his introductory remarks (p. 209), Bumpus fully expected that the study would become a standard reference for later students of the evolutionary process, and at the end of his analysis he proceeded to publish in full the basic data matrix of 136 specimens by 9 characters, arranged by survivors, nonsurvivors, sex, and age of males. Bumpus was right; in the 73 years since he wrote, there have been three published univariate statistical reanalyses of his data, emphasizing improvements on Bumpus' statistical methodology (Harris, 1911; Calhoun, 1947; Grant, 1972) and his general conclusions on stabilizing selection are frequently cited in textbooks on evolution and population genetics.

Yet for all the interest in the data and what they purport to show, it has never been remarked that because Bumpus' conclusions were formulated a posteriori they represent hypotheses that cannot be

tested by the data. In fact they can be tested only experimentally now (or fortuitously in the event that a similar storm presses again on a sparrow population that people can find). So in one sense it does not matter that Bumpus was statistically casual; his hypotheses exist and they are really what attract our attention.

Such attention ultimately leads us again to look at the data, but our interest should be in whether they legitimately led Bumpus, and Calhoun and Grant, to their hypotheses. Accordingly, this paper is an examination of how the hypotheses of stabilizing and directional selection came to be suggested by the data, and whether they are plausible today. We begin by considering the descriptive adequacy of the character variables and proceed to a multivariate examination of the data matrices. Bumpus himself (1899:217) resorted to an intuitive multivariate assessment of his sparrows, and he probably would have used computationally adequate multivariate analysis had the technology of his time permitted. It would seem that multivariate analytic techniques provide an optimal way to examine the data, although the present report seems to be the first to employ them. Multivariate analyses not only allow each individual to be examined over its total character-states set (which is likely to be the way in which storm-stress "examines" an individual) but also provide techniques for the visual display of results that enhance verbal summaries. This paper presents results of principal component and discriminant function analyses over the full sets and certain subsets of the Bumpus data. We will also show the extent to which presence and absence of certain char-

acter variables affects Bumpus' historic hypothesis and those that followed, and we will examine some previously unanalyzed size relationships affecting sexual dimorphism of survivors and nonsurvivors.

ADEQUACY OF THE CHARACTER VARIABLES

Ornithologists think the measurements of total body length and of alar spread in birds are subject to sufficient observational error to be unreliable for the study of morphologic variation. Today no one uses these variables, but they are precisely the two external size characters that Bumpus chose to measure. Expected high variability for these characters does not actually materialize in the Bumpus specimens, and coefficients of variation for body length and wingspread are consistent with those for wing and tail length in sparrow samples from elsewhere in North America. Nonetheless, use of these variables leaves us uneasy.

Body weight, for which surviving birds averaged less than nonsurvivors, is almost certainly an inadequate character in the Bumpus sparrows. Bumpus tells us virtually nothing about how he treated the birds on receipt in his laboratory, but we assume that had surviving birds been fed after he obtained them Bumpus surely would have mentioned it in his discussion on page 211, and that all survivors lived longer than any nonsurvivor. These assumptions are sufficient to allow an explanation of observed differences between the weights of survivors and nonsurvivors that has nothing to do with presumed selection by the storm. Survivors would have continued to process digestive tract contents, voiding wastes frequently as wild house sparrows do on any disturbance in confinement. Also, having survived cold stress longer than some of the nonsurvivors, survivors would have been characterized by a continuous expenditure of energy ultimately to be reflected in a loss of body weight (cf. Packard, 1967:77-78, who discusses daily weight fluctuations of around

7% in free-living sparrows not stressed by cold).

The remaining six variables are of sizes of bones. Bumpus measured two dimensions of the skull, two from the pectoral girdle-wing assembly, and two from the hind limb. These seem to be perfectly ordinary measurements; none violate any expectation. We can get a fractional test of their reliability as unbiased variables by examining the degree and direction of sexual dimorphism of each; if they show "normal" sexual dimorphism, we may assume they are normally adequate in indicating size. As Table 3 shows, the skull and hind limb variables of the total sample tend toward monomorphism and the sternum and humerus show dimorphism of 1-4%, owing to larger male size, and this is the condition found repeatedly in North American sparrow samples (cf. Johnston and Selander, 1971; Johnston, 1972). In large samples femur length and skull width tend to be sexually dimorphic, but in small samples of heterogeneous ages this trend is not necessarily seen (Johnston, 1972).

We assume that the skeletal characters are adequate for testing the likelihood that what Bumpus hypothesized was derivable from the data, but that body length and wing spread are less adequate, and body weight unacceptable, as useful variables. Analyses beyond examine size relationships of survivors and nonsurvivors of both sexes over the entire nine-character set and also of the six-character set of skeletal variables only.

CONSIDERATION OF HYPOTHESES STEMMING FROM DIFFERENTIAL MORTALITY

The Nine-variable Character Set

Although there are reasons for believing that three of the character variables are inadequate for an analysis of character variation of any sort, much less for assessing possible directional or centripetal selection, the full set of characters needs to be examined because of its historical

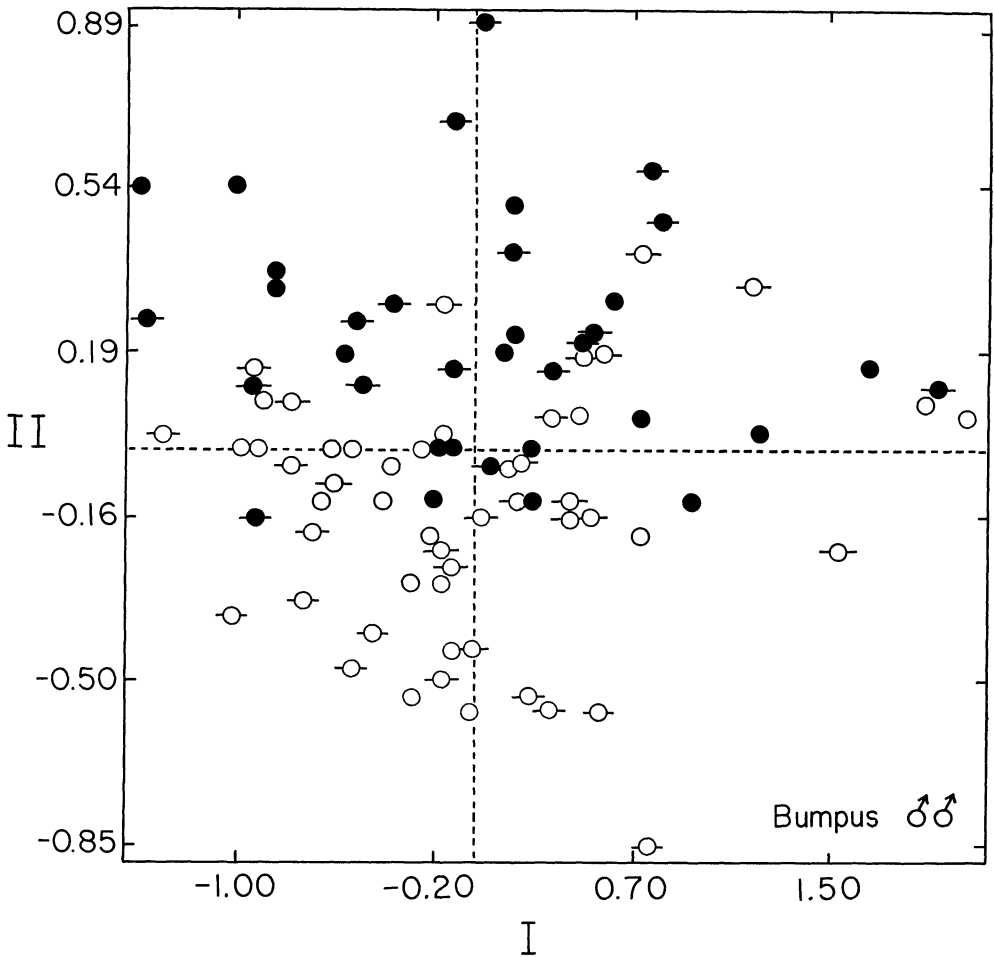


FIG. 1. Plot of two-dimensional positions of individual males in the Bumpus sparrow sample on principal components I and II from the nine-character set of variables. Open circles, survivors, closed circles, nonsurvivors; horizontal lines on circles indicate adults, and no lines indicate subadults. See Table 1.

importance. Principal component analysis was employed. Since the original nine variables do not constitute a homogenous character set, principal components were extracted from matrices of character correlations for each sex. We computed component scores (or projections) as

$$\mathbf{P} = \mathbf{D} \times \mathbf{F} / \sqrt{p}$$

where \mathbf{D} is the standardized individual \times character data matrix, \mathbf{F} the matrix of character loadings (which were first normal-

ized by dividing each eigenvector of \mathbf{F} by the square root of the eigenvalue), and p is the number of characters. Division by \sqrt{p} makes the scores range over approximately the same scale when plotted. Loadings of the original nine characters on the first three principal components (= eigenvectors) are shown in Table 1, and projections of individuals onto the first two principal components are plotted in Figs. 1 and 2.

For males each of the nine variables

TABLE 1. *Character loadings from correlation matrices onto the first three principal components of variation in the nine-character set of male and female Bumpus sparrows.*¹

Character	Component of variance ²					
	I		II		III	
	M	F	M	F	M	F
Total length	-0.620	-0.790	0.603	-0.351	-0.210	-0.358
Alar spread	-0.836	-0.835	0.224	-0.044	-0.055	-0.362
Body weight ^{1/3}	-0.571	-0.536	0.361	-0.639	0.507	0.334
Skull length	-0.669	-0.874	-0.404	0.093	-0.069	0.092
Skull width	-0.595	-0.776	0.038	-0.080	-0.655	0.445
Keel length	-0.612	-0.716	-0.375	-0.273	0.020	-0.144
Humerus length	-0.888	-0.906	-0.118	0.212	0.064	-0.120
Femur length	-0.898	-0.838	-0.097	0.383	0.108	0.184
Tibiotarsus length	-0.841	-0.837	-0.116	0.401	0.186	0.035

¹ Loadings for males exceeding 0.211 and 0.275, and for females exceeding 0.285 and 0.369, are significant at $\alpha = .05$ and $\alpha = .01$, respectively.

² Per cent of trace: males, I = 54.3%, II = 9.8%, III = 8.8% (total = 72.9%); females, I = 63.8%, II = 10.8%, III = 7.2% (total = 81.8%).

loads significantly on component I, which is a general size factor accounting for 54% of the variation in the data set; component II represents an inverse relationship between total length, wingspread and weight against skull length and keel length and accounts for 10% of the variation. Scattergrams for scores on components I and II (Fig. 1) provide reasonably good separation of survivors and nonsurvivors, most of which is effected by component II. Overall, the disposition of individuals along component I might generate the hypothesis that males were subject to directional selection in which large individuals had a higher probability of surviving than small ones, but Fisher's exact probability ($p = .274$) computed for a median test (Siegel, 1956) did not show this ordering to be significant. (Hereafter exact probabilities will be given for similar tests without further explanation.) Additionally, for small individuals (those right of the vertical line) there is a suggestion that the effects of severe winter weather were not as drastic on those that had already lived through at least one winter (as any adult would have), as on those in their first year of life.

Scores for survivors and nonsurvivors are remarkably well-separated on com-

ponent II ($p \leq .001$), in part owing to the high positive loadings from total length, wingspread, and weight. Influence of these peculiar characters is thus of primary importance in generating any hypothesis concerning differential survival, and we assume that Bumpus' ideas were significantly ordered by them.

An additional point of interest is that most survivors had relatively long keels and skulls, giving them relatively large negative component II scores. Bumpus included length of bill (as premaxilla) in his measurement of skull length, but his measurement of skull width was taken exclusively on the cranium. Skull width loaded positively (and insignificantly) on this component, suggesting that if skull length loaded significantly negatively, it is the premaxillary element of "skull length" that is responsible for its importance on this axis of variation. If so, then it is possible that birds with the relatively large premaxillae were best fit to survive that winter storm.

For females each of the nine variables also loads significantly on component I, which accounts for 64% of the variation; component II represents an inverse relationship of total length and body weight against femur and tibiotarsus lengths, ac-

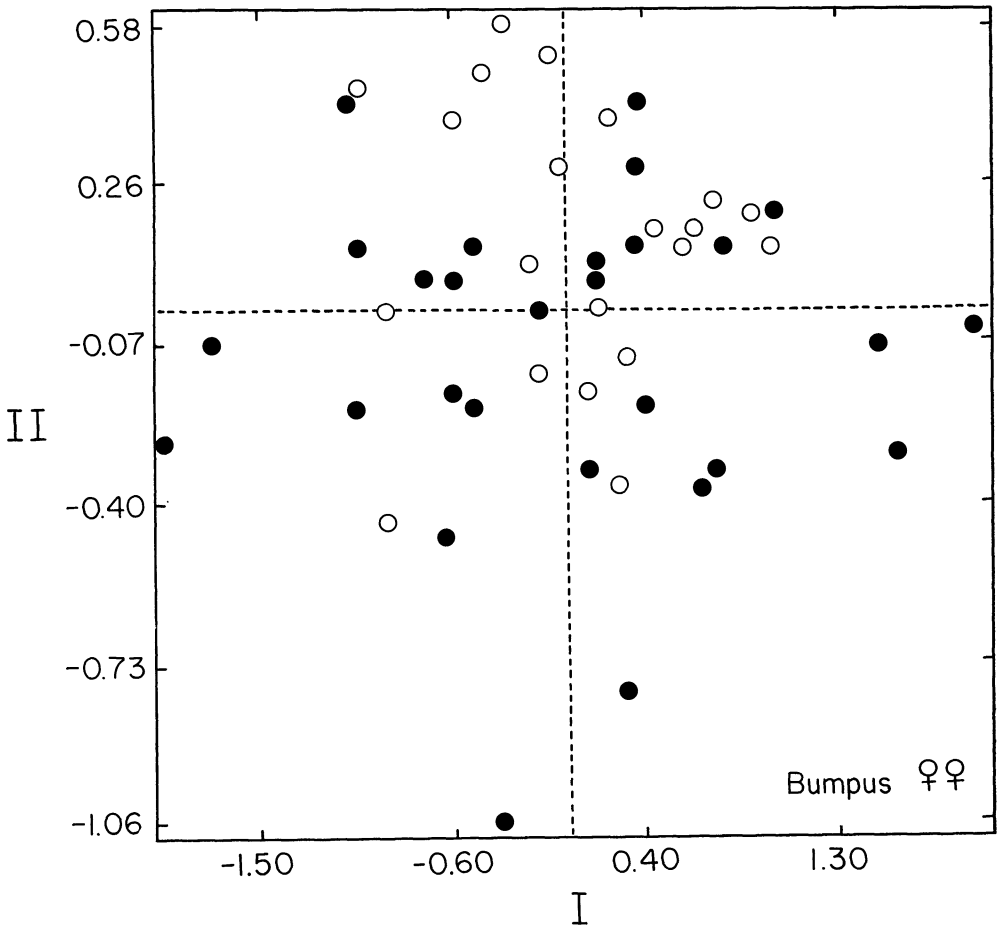


FIG. 2. Plot of two-dimensional positions of individual females in the Bumpus sparrow sample on principal components I and II from the nine-character set of variables. Open circles indicate survivors, closed circles, nonsurvivors. See Table 1.

TABLE 2. Character loadings onto the first three principal components of variation from variance-covariance matrices in the six character set of male and female Bumpus sparrows.¹

Character	Component of variance ²					
	I		II		III	
	M	F	M	F	M	F
Skull length	-0.447	-0.681	0.071	-0.081	0.455	0.387
Skull width	-0.178	-0.301	-0.021	0.034	0.085	0.102
Keel length	-0.640	-0.732	0.655	0.664	-0.120	-0.089
Humerus length	-0.514	-0.510	-0.089	-0.044	-0.032	-0.010
Femur length	-0.531	-0.561	-0.120	-0.154	-0.027	0.006
Tibiotarsus length	-0.947	-0.932	-0.356	-0.357	-0.117	-0.245

¹ Loadings for males exceeding 0.211 and 0.275, and for females exceeding 0.285 and 0.369, are significant at $\alpha = .05$ and $\alpha = .01$, respectively.

² Per cent of trace: males, I = 65.1%, II = 18.2%, III = 7.6% (total = 90.9%); females, I = 70.8%, II = 16.8%, III = 6.4% (total = 94.0%).

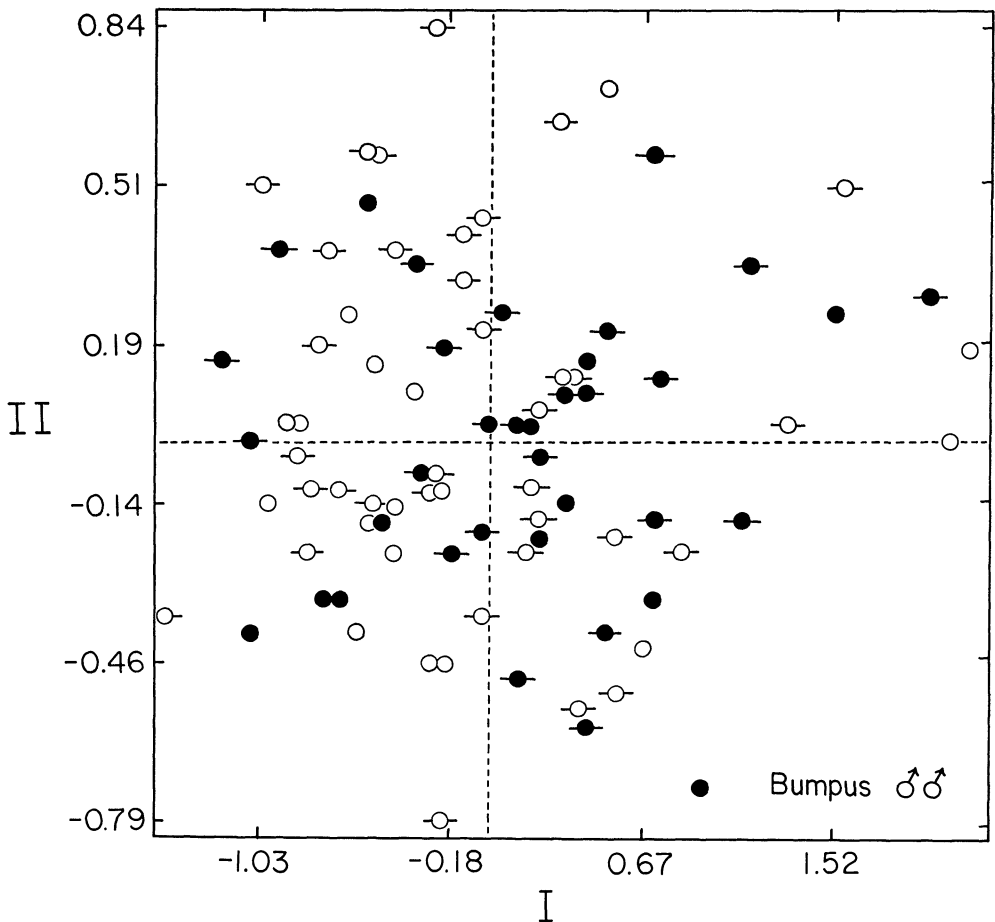


FIG. 3. Plot of two-dimensional positions of individual males in the Bumpus sparrow sample on principal components I and II from the six-character set of variables. Open circles, survivors, closed circles, nonsurvivors; horizontal lines on circles indicate adults; no lines indicate subadults. See Table 2.

counting for 11% of the variation. The loadings do not provide (Fig. 2) a separation of survivors of the same sort as for males. Along component I, which is a general size factor, individuals with some aspects of their morphology rendering them relatively large or relatively small were subject to a higher risk of death than were individuals of intermediate size. Bumpus was impressed by essentially the same distribution in formulating his ideas about stabilizing selection in the birds, although he treated the sexes simultaneously. Component II projections also tend to separate

survivors and nonsurvivors in females ($p = .080$), but not so clearly as in males. Females with relatively large character-states for femur and tibiotarsus lengths and relatively small states for total length and body weight were more likely to survive than those with converse sets of character-states.

So if all nine character variables are used in principal component analyses of both sexes, the major contentions of Bumpus and Grant and Calhoun are seen to be suggested by the data: that stabilizing selection for intermediate size occurred

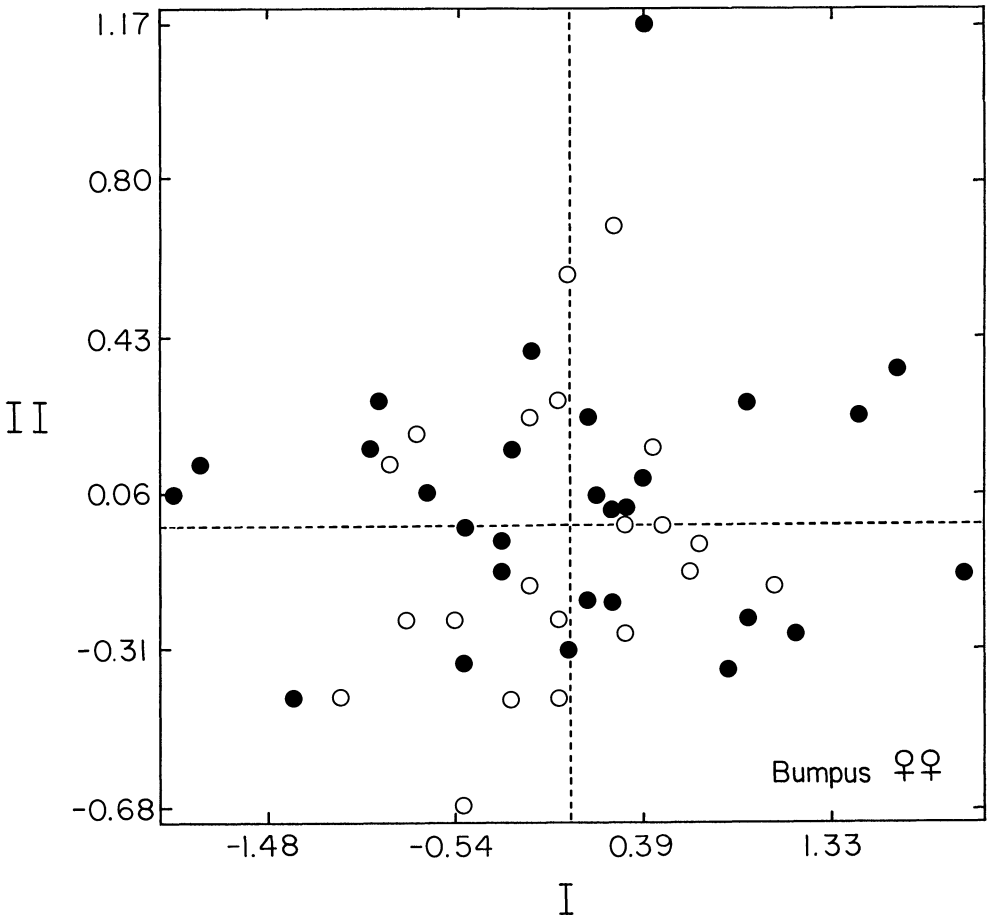


FIG. 4. Plot of two-dimensional positions of individual females in the Bumpus sparrow sample on principal components I and II from the six-character set of variables. Open circles, survivors, closed circles, nonsurvivors. See Table 2.

in females and directional selection for large size occurred in males. From the present analysis it also could be suggested that age-related survival occurred in males such that relatively small individuals had a slightly greater chance of surviving the storm if they were adults; and males with relatively large premaxillae may have had a better chance of surviving.

The Six-variable Character Set

For reasons discussed earlier, removal of total length, wingspread, and body weight from the data set leaves six bony dimensions that could provide an assessment of

the Bumpus sparrows that is more independent of operational error than the data in the above analysis. Since these measurements provide a fairly homogeneous character set, principal components were extracted from variance-covariance matrices; component scores were obtained as described above. The character loadings for each of the first three principal components are shown in Table 2, and projections of individuals onto the first two components are plotted in Figures 3 and 4.

For males component I has significant loadings from all the variables except skull width, and accounts for 65% of the varia-

TABLE 3. *Secondary sexual dimorphism assessed by character-state means for three groupings of Bumpus sparrows.*

Character	Character-state means ¹								
	Total sample			Survivors			Nonsurvivors		
	♂	♀	% ♂:♀	♂	♀	% ♂:♀	♂	♀	% ♂:♀
Total length	160.43	158.04	1.5***	159.25	157.38	1.2*	162.08	158.53	2.1***
Alar spread	247.47	241.33	2.5***	247.41	241.00	2.6***	247.56	241.57	2.4***
Body weight	2.96	2.94	0.7	2.95	2.91	1.4*	2.98	2.96	0.7
Skull length	31.64	31.46	0.6	31.70	31.43	0.9	31.56	31.48	0.3
Skull width	15.33	15.26	0.5	15.35	15.24	0.7	15.29	15.28	0.1
Keel length	21.63	20.83	3.7***	21.76	20.81	4.4***	21.46	20.84	2.9*
Humerus length	18.67	18.47	1.1*	18.76	18.50	1.4*	18.55	18.44	0.6
Femur length	18.13	18.08	0.3	18.21	18.16	0.3	18.01	18.02	-0.05
Tibiotarsus length	28.74	28.87	-0.5	28.84	29.05	-0.7	28.61	28.73	-0.4

¹ Body weight in $\sqrt[3]{\text{g}}$; remainder in mm. Per cent differences significant at $p \leq .05$ (one asterisk) and $P \leq .001$ (three asterisks) judged by F -ratios from single classification analysis of variance.

tion in the six-character set; component II, representing 18% of the variation, has inverse loadings from keel length and tibiotarsus length. Again component I is a general size factor; larger individuals, plotting to the left in Figure 3, are mostly survivors while smaller individuals, plotting to the right, are mostly perishers. Unlike the nine-variable analysis this distribution was significant ($p = .016$), providing a strong basis for the classical hypothesis of size-ordered directional selection in males. In this analysis males were not significantly ordered along component II ($p = .827$).

For females component I has significant loadings from each of the six variables, and these account for 71% of the variation; component II has inverse loadings from keel length and tibiotarsus length, and accounts for 17% of the variation. Most of the survivors fall toward the center of the principal component I scores, which is consistent with the plot obtained from the nine-variable analysis above (cf. Fig. 2). A parametric test showed the variance in principal component I scores to be significantly smaller for survivors than for nonsurvivors ($F \text{ max} = 2.905$; $p \leq 0.05$), thus supporting Bumpus' classical conclusion. Unlike the nine-character analysis, females are scarcely distinguished along component II in this analysis ($p = .380$).

ANALYSIS OF SEXUAL DIMORPHISM

As we mentioned in the introduction, we used an analysis of secondary sexual character dimorphism to get information on possible bias in the six skeletal variables in the Bumpus sparrows. It is already well-established that intersexual character dimorphism has a predictable form in house sparrows such that external size variables, body weight, and bony elements in the pectoral girdle and wing are strongly sexually dimorphic and bony elements from the head and hind limb are either monomorphic or only weakly dimorphic (Selander and Johnston, 1967; Johnston and Selander, 1971; Johnston, 1972). We thus expected that Bumpus sparrows would show dimorphism in keel and humerus lengths and monomorphism in skull width and in skull, femur and tibiotarsus lengths. This is precisely the organization of sexual differences for bones of the total sample and of survivors alone. But in nonsurvivors humerus length is not different between the sexes and the difference in keel length is less than in the other samples. As can also be seen in Table 3, the nonsurvivors show reduced dimorphism in body weight and wingspread, but not for total body length (for which the nonsurvivors show the greatest sexual difference).

To obtain a multivariate assessment of

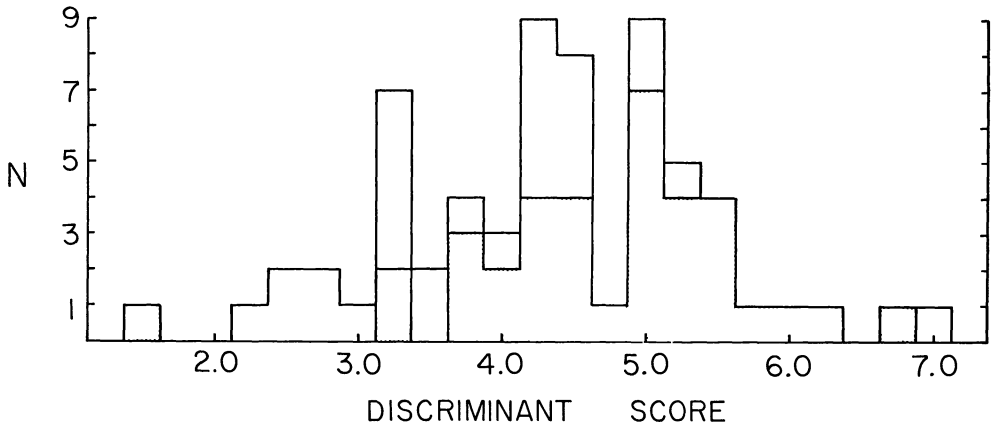


FIG. 5. Frequency distribution of males (stippled) and females (clear) in the nonsurviving set of Bumpus sparrows along the discriminant axis computed for the six skeletal variables using nonsurviving males and nonsurviving females as groups.

sexual dimorphism, two-group discriminant function analyses based on the six skeletal characters were performed on the survivors and on the nonsurvivors, using the two sex classes as groups. Since ordinary (mist-netted) samples of house sparrows are significantly sexually dimorphic in size for two of these six characters, it is of considerable importance that discriminant scores were unable to adequately separate the

sexes of the nonsurvivors (Fig. 5; exact $F = 1.80$ ns). However, survivors were classified according to sex by discriminant analysis with only a small per cent of misclassification (Fig. 6), and the multivariate difference between the means for survivor sex classes was highly significant (exact $F = 4.52$, $p = 0.001$).

More insight into the nature of the differences in sexual size dimorphism between

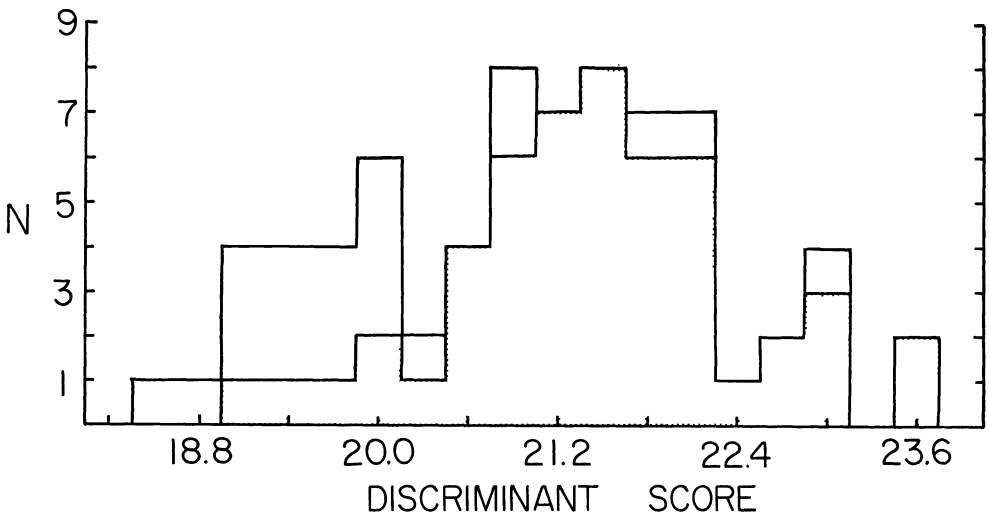


FIG. 6. Frequency distribution of males (stippled) and females (clear) in the surviving set of Bumpus sparrows along the discriminant axis computed for the six skeletal variables using surviving males and surviving females as groups.

TABLE 4. *Relative influence of bony characters in discrimination between males and females in two samples of Bumpus sparrows.*

Character	Nonsurvivors		Survivors	
	Standardized discriminant function	Per cent separation	Standardized discriminant function	Per cent separation
Skull length	0.095	3.33	0.060	1.78
Skull width	0.030	1.05	-0.127	3.77
Keel length	0.708	24.80	1.029	30.54
Humerus length	0.881	30.86	0.773	22.94
Femur length	-0.285	9.98	-0.624	18.52
Tibiotarsus length	-0.856	29.98	-0.756	22.44
Totals	3.369	99.99	2.855	100.00

survivors and nonsurvivors can be obtained from the standardized discriminant coefficients (Table 4), which reflect the relative importance of the six variables in separating the sex classes in each analysis. To assess the differing importances of the characters within each of the two analyses, the per cent of the total separation effected by each character has been computed for survivors and nonsurvivors (Table 4). The per cent separation effected by the four characters contributing significantly to the discriminant function reveals that the importance of humerus and tibiotarsus lengths was increased in the survivors versus the nonsurvivors, while the importance of keel and femur lengths was reduced. Since the discriminant coefficients for humerus and tibiotarsus lengths receive contrasting signs, surviving males had relatively longer humeri than nonsurvivors, and surviving females had relatively longer tibiotarsi than nonsurvivors. Thus, the nonsurvivors included males with short humeri (a "female character") and females with short tibiotarsi (a "male character"), both of which inclusions would generate an increase in homogeneity of the nonsurvivors.

For additional examination of increase of homogeneity in nonsurvivors we may turn again to Table 3. For the six bony variables, comparison of the per cent dimorphism values for survivors and nonsurvivors shows that the absolute value of these figures was increased for all six variables in

the survivors. For five of the six, means for males were larger than those for females, which results from the tendency for the overlapping tails of the distributions to be eliminated when the nonsurvivors are removed from the sample (i.e., when the small males and the large females are removed, as they were by effects of storm-stress).

COMMENTS

Bumpus' hypotheses concerning differential survival of the sparrows following the storm of 1898 were formulated after he examined the data from the specimens; the data suggested the hypotheses and thus cannot be used to test the adequacy of the hypotheses lest they become merely self-fulfilling prophecies. Hence, no one can legitimately say that Bumpus showed this or Bumpus showed that. But it is quite another thing to ask whether Bumpus and Calhoun and Grant, were justified in speaking of stabilizing and directional selection after having examined the data. It is clear that the hypotheses are justifiably extracted from the data and that experimental testing of them would now be a worthwhile thing to do.

Bumpus, Harris, Calhoun, and Grant did not look into sexual dimorphism. But there were only indirect suggestions (like directional selection in males) that secondary sexual character differences would have been increased by selective elimination of individuals by a winter storm. Such

a modification in fact occurred; to put it crudely, nonsurvivors conformed to a multivariate "type" much more than sexes of the house sparrow ordinarily do (there is no other such instance on record).

The selective base of such an occurrence is examined below. We may note that the Bumpus sparrows were already sexually dimorphic in conventional ways (Table 3), and we know they stemmed from populations ultimately from western Europe that were (or are) sexually dimorphic in conventional ways (Johnston, 1969). Whether in Europe or North America, the adaptive phenotype of male house sparrows includes relatively large sizes of certain covariant morphologic elements that increase male reproductive fitness—large individuals are likely to win male:male contests for space, nest sites, etc. One assumes that this competition led to classical Darwinian selection at a very early point in the history of the species. Such selection alone could have elaborated secondary sexual dimorphism in house sparrows and as Leigh Van Valen points out (in litt.), size is plausibly related to physical condition of males, both because of effect of a better territory size and because of stress associated with lower rank of smaller birds. In Bumpus sparrows from Providence, it was the smaller males that were more subject to storm-induced mortality. Hence, smaller males were at a double disadvantage. The novelty introduced by this finding is that morphologic covariances presumably adaptive in sexual selection, or enhancing reproductive aspects of fitness, were also apparently adaptive in escaping storm mortality, or in enhancing viability components of fitness.

Females have a covariant character suite that has evolved presumably exempt from selection for size as associated with sexual combat. If there are any strictly reproductive aspects of fitness associated with body size and proportions in females, they might coincide with the sizes associated with viability components of fitness. Or, we could say that the quality of being a female sparrow seemingly entrains certain

size covariances as well as chromosomal, endocrinologic, gonadal and behavioral modalities, and that evolutionarily successful females will violate as few of these entrainments as possible; a parallel statement could be made for males.

In closing, we may note that if males and females are as different as this discussion assumes, we would expect differing sorts of abiotic stress (different kinds of storms, for instance, or heat stress in summer) to consistently express themselves differently on the sexes. In short, we think that each sex represents a distinct, though related, adaptive system.

SUMMARY

The frequency distribution of character-states of morphologic variables in the house sparrows collected after a severe winter storm in Providence, R. I., in February, 1898, by Hermon C. Bumpus are such that they adequately generate the following hypotheses: 1) large males have a selective advantage over small ones under conditions of severe winter cold stress; 2) females of intermediate size have a selective advantage over larger and smaller individuals under conditions of severe winter cold stress; 3) small subadult (= first year) males are at a selective disadvantage relative to small adult males under severe winter cold stress.

Surviving individuals showed normal secondary sexual size dimorphism, but nonsurvivors were almost monomorphic for size of skeletal characters. Many nonsurviving females tended to have male-like proportions and nonsurviving males tended to have female-like proportions; thus, differential storm-induced survival suggests there are viability components of fitness in sizes of the sexes in addition to the reproductive components of fitness that have been invoked to explain general size dimorphism in sparrows.

ACKNOWLEDGMENTS

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