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CENTRIPETAL SELECTION AND THE HOUSE SPARROW

P. R. GRANT

Abstract

Grant, P. R. (Dept. of Biology, McGill Univ., Montreal, Canada) 1972. Centripetal selection and the House Sparrow. Syst. Zool., 21:23–30.—In 1898 H. C. Bumpus compared morphological measurements of House Sparrows which survived a severe storm and those which did not. He observed that the group of birds which survived had fewer extreme measurements than did those which died, and suggested that selection had eliminated extreme individuals.

The data, given in full by Bumpus, have been analyzed statistically in the present study. The results support the suggestion made by Bumpus. It is found that among females the survivors varied significantly less than did those which died, in four measurements; weight, length of humerus, length of tibiotarsus and length of sternum. There are no significant differences in variation in any measurement among the males. Females suffered proportionately heavier mortality than the males.

It is not possible to identify the target of selection because the four dimensions involved are strongly correlated with each other. It is suggested that females suffered particularly heavy mortality because they were at least partly denied access to food by the socially dominant males. It is also suggested that the extreme individuals were selected against in the storm because the largest birds were unable to mobilize energy reserves rapidly enough, and because the smallest birds exhausted their energy reserves and were unable to replace them. [Selection; House Sparrows; Bumpus.]

The House Sparrow, or English Sparrow (*Passer domesticus*), has undergone adaptive change in North America. Following the original introduction from Europe in 1851 and additional introductions thereafter (Calhoun, 1947), it spread rapidly throughout most of North America, and has become geographically differentiated (Calhoun, 1947; Johnston & Selander, 1964, 1971; Lack, 1940; Packard, 1967, 1968; Selander & Johnston, 1967). In several size and colour characteristics it shows a pattern of variation which can be related to environmental variables. The colour shifts may be purely phenotypic responses, since it is known that feather pigment is under the direct influence of such environmental factors as humidity (Beebe, 1907). Likewise the size of some exposed parts is influenced by temperature (Allee and Lutherman, 1940). But certain changes in the proportions of exposed parts, and hence shape, cannot so easily be explained as phenotypic responses, and it is therefore reasonable to conclude, as did Johnston & Selander (1964, 1971), that genetic changes have occurred in the North American environment as a result of directional selection.

With the exception of Calhoun (1947), these authors have paid little attention to the fact that more than 70 years ago Bumpus (1899) presented evidence in support of the *process* of natural selection acting on this species. There has been debate on the validity of this evidence (e.g., Calhoun, 1947; Harris, 1911; Robson and Richards, 1936). In view of the current interest in the patterns of geographical variation in this species which might have been produced by selection, it is appropriate to re-examine the evidence given by Bumpus, making use of statistical procedures not available to him.

THE BUMPUS DATA

One hundred and thirty six sparrows were brought to the Anatomical Laboratory of Brown University on February 1, 1898, immediately after an uncommonly severe storm of snow, rain and sleet. Sixty-four of them died, presumably due to the stresses of the storm rather than the laboratory, although this presumption has been questioned (Robson and Richards, 1936). Bumpus reports that nine morphological characters were measured in each of the 136 specimens. These were total length, alar extent, weight, length of beak and head, length of humerus, length of femur, length of tibiotarsus, width of skull and length of keel of sternum. He compared the survivors with those which died, separated according to three sex and age groups he was able to recognize; adult males, young males and adult plus young females. He found several small mean differences between survivors and those which died, which led him to the general conclusion that survivors tended to be "shorter and weigh less (i.e., are of smaller body)", but to have "longer wing bones, longer legs, longer sternums and greater brain capacity [skull width]" p. 213.

Bumpus also combined the data for the different age and sex groups, and compared total survivors with all those which died. He noted a tendency for the extremely large and extremely small to be disproportionately represented in the sample which died. This led him to the conclusion that "the process of selective elimination is most severe with extremely variable individuals, no matter in what direction the variations may occur." p. 219.

Thus, in a single study, he appears to have detected the operation of two forms of selection, which are now referred to as directional and centripetal or stabilizing selection (Mather, 1953), mediated through the agency of climatic factors.

SUBSEQUENT ANALYSES

The chief limitation of the analysis performed by Bumpus is the absence of statistical evaluation of the differences between survivors and those which died. Harris (1911) drew attention to this, and re-analysed the Bumpus data. He calculated means and standard deviations of each of the nine characters, and the "probable errors" associated with each. He commented "For the individual comparisons those differences less than the probable error will be considered of no significance, those between one and two times their probable errors as possibly significant, and those over thrice their probable errors as probably significant" p. 315. He thereupon made the comparisons, and found support for Bumpus' contention that the survivors were smaller in body size, but larger in body part size, than were those which died.

Some of the standard deviations given by Harris are as different, in relation to the probable errors, as are the means, but Harris was unwilling to consider these differences as satisfactorily demonstrated. "Bumpus has discussed this question in detail in his lecture, but to me it seems that the standard deviations as given here do not justify any final conclusions concerning the relation of selection to variability: the problem is too complicated and the data are too few" p. 317.

The only other analysis of the Bumpus data known to me is that by Calhoun (1947). On the basis of his experience he believed that two of the measurements given by Bumpus could be made with consistent accuracy, and concerned himself with only these; the lengths of femur and humerus. He applied *t* tests to the means, and found no significant differences between the survivors and those which died. He also assessed differences in variation in these two dimensions by grouping the data in 0.5 mm classes, and by comparing the median and extreme groups of survivors and those which died in a 2×2 χ^2 contingency table. This can hardly be described as a sensitive test performed in this way, and not surprisingly the differences were found to be not significant.

These analyses leave questions unanswered. Are there mean differences between survivors and those which died, in dimensions other than length of femur and humerus? The data given in tables by Harris (1911) indicate that there are. The question can be answered by applying *t* tests. The point concerning reliability of measurement will be deferred until the *t* tests have been performed. Secondly are there differences in variation? Again, data given by Harris indicate that there are. Differences can be assessed by applying *F* tests to pairs of variances, or to pairs of coefficients of variation squared where the means are significantly different (Lewontin, 1966).

PRESENT ANALYSES

Differences between means

Four significant differences were revealed by the *t* tests. The surviving adult males were smaller than those which died in weight ($P < 0.05$) and total length ($P < 0.001$). The surviving young males were also smaller than their dead counterparts in weight ($P < 0.025$), but larger in combined length of beak and head ($P < 0.05$). There were no significant differences between means among the females.

In all three age and sex groups survivors were either ostensibly or significantly shorter in total length and smaller in weight than those which died, so the conclusion of Bumpus concerning selection against large body size, is supported by these results. However, diurnal fluctuations in body weight (e.g., Baldwin and Kendeigh, 1955; Snow and Snow, 1963) make this character not a completely reliable indicator of body size. Total length is likely to be even less reliable. As pointed out by Phillips (1915) in this context, it is not a dimension usually measured by ornithologists. With the exception of weight, all the other dimensions are rigid (bone or feathers) and may be expected to change to a small extent in size over a period of time due to drying (bone) but not to change size while being measured. Total length, on the other hand, is difficult to measure reliably due to the suppleness of the backbone or, in the case of specimens prepared for a Museum, due to the capacity of the skin to stretch and fold. Unfortunately Bumpus does not give details of how the measurements were made. It is possible, although perhaps unlikely, that the surviving birds were measured in a different way from those which died. For example they may have been sacrificed and measured (for total length) in rigor mortis, while those which died naturally may have been measured post rigor mortis. Hence the significant differences in weight and length should be treated with caution. Calhoun (1947) was correct to point out that some of the dimensions could not be measured reliably enough, although he did not make it clear why the bone measurements, such as length of tibiotarsus, should not be considered reliable.

I conclude that the data presented by Bumpus provide weak evidence for directional selection against large body size in males of this species, and possibly also against small head and beak length in the young males.

Differences between variances

When total survivors are compared with all those which died it is found that the latter vary significantly more than the survivors in two dimensions, weight and length of humerus ($P < 0.05$). To find out if these differences are manifested within the sex and age groups, the comparisons are made with each group treated separately. Now four differences are significant, they are all in the female group and they are all in the same direction; weight, length of humerus, length of tibiotarsus and length of sternum vary more in the sample which died than in the sample which survived (Table 1). Weight and humerus variances differ significantly in both treatments (diurnal fluctuations in body weight, which might influence a comparison of means, p. 25, are less likely to affect a comparison of variances). Therefore differences between variances in the total samples are probably largely due to the differences in the female samples.

These differences support the contention of Bumpus that selection has acted against extreme individuals (see also Fig. 1) although he did not appreciate that it was so conspicuous among the females. Likewise

TABLE 1. A COMPARISON OF VARIANCES OF FEMALES WHICH SURVIVED (S) AND THOSE WHICH DIED (D). SAMPLE SIZES ARE 21 AND 28 RESPECTIVELY.

		S	F	P
Total length	S	11.0476	1.36	> 0.1
	D	15.0688		
Alar extent	S	17.4999	1.92	0.05 < 0.1
	D	32.5503		
Weight	S	1.1419	2.35	< 0.05
	D	2.6789		
Length of beak and head	S	0.5313	1.37	> 0.1
	D	0.7284		
Length of humerus	S	0.000268	2.51	< 0.025
	D	0.000672		
Length of femur	S	0.000408	1.97	0.05 < 0.1
	D	0.000805		
Length of tibiotarsus	S	0.000865	2.60	< 0.025
	D	0.002241		
Width of skull	S	0.000171	1.65	> 0.1
	D	0.000283		
Length of keel of sternum	S	0.000884	2.20	< 0.05
	D	0.001943		

Total length, alar extent, length of beak, length of head measured in millimeters, weight in grams, the remainder in inches.

Harris (1911), in whose table of standard deviations I have detected some errors of calculation, did not pay attention to the differences in the female group. The differences established above suggest that centripetal selection was acting on the females only. The suggestion is supported by the fact that females suffered proportionately heavier mortality than either male group. Thus 28 of the 49 females (57.3%) died, in contrast to 24 of 59 adult males (40.7%) and 12 of 28 young males (42.9%).

The comparison between the sexes is artificial in that age groups were separated in the males but not in the females. To show that females behaved differently from males it is necessary to combine the males. When this is done, and variances of all males compared, it is found that surviving males do not vary significantly less than those which died, in any of the nine characters.

It is known that, within the males, selection did not act against one or the other age group; the ratio of adults to young is approximately the same, two to one, among those which survived and those which died. However it is possible that selection acted against one age group in the females, thereby causing a reduction in variance in some of the dimensions. This might take the form of all survivors being in one age group, the 'favoured' one, while those which died are heterogeneous with respect to age. To see if this explanation of the differences in variances within females is feasible we can use the data from males, because age is known. We combine adult and young males which died and compare them, separately, with adult male survivors and young male survivors. The 18 comparisons so made yield only one significant difference, and it runs counter to expectations; the young males which survived vary more in tibiotarsus length than do the young and adult males which died ($P<0.05$). Admittedly young and adult males are not equally represented in the group which died, so heterogeneity with

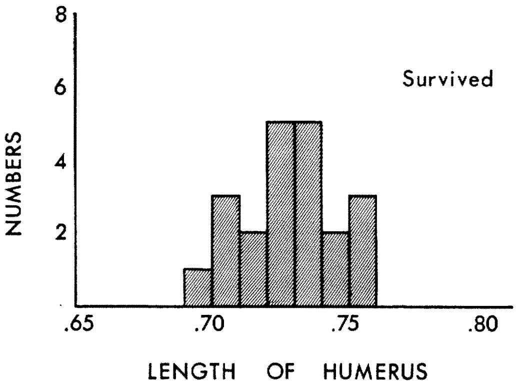

FIG. 1.—Comparison of the distribution of humerus length measurements, in inches, between females which died and females which survived.

respect to age is not maximized by this procedure. Nevertheless, there is no evidence from this test, albeit an indirect one, that the significant differences between surviving and succumbing females are due to selection against one age group.

Finally, it is worth considering the possibility that selection acted against extreme female individuals and not against extreme male individuals (as revealed by the statistical tests) because, at the outset, females varied much more than males. This is assessed by comparing variances of total males and total females. None of these comparisons yield significant differences; females did not vary more than the males initially.

To what extent the established differences in variance are due to the presence of just a few unusual or exceptional individuals in the group which died is a matter difficult to decide. Inspection of the data shows that in most instances extreme measurements are only a little below or beyond neighbouring measurements (see also Fig. 1) so there are no obvious "freaks" in the sense that the individuals are quite different from all others. Bumpus has also pointed out that when the most extreme individuals are removed from consideration, those individuals in the remainder now occupying the extreme positions are mostly from the group which died.

I conclude that, despite limitations of small sample size and attendant possible biases, there is evidence in the data presented by Bumpus of centripetal selection acting on the females.

THE TARGET OF SELECTION

Selection may be acting against individuals which possess only one extremely large or small character, or against those which possess several. If the characters were individually responsive to selection we might detect this by finding a lack of correlation among the characters. If on the other hand the characters were strongly correlated, we would not be able to distinguish between selection against individuals with extreme measures of one, or more, characters. Correlation analysis reveals that in the female group all pairs of the nine variables are significantly correlated ($P < 0.05$). In each of the two male groups all but two pairs are correlated. Most of the correlations are significant at the 1% level. The four dimensions in the female group whose variances differ significantly are all correlated with each other to a highly significant extent ($P < 0.01$). Therefore the results do not permit us to distinguish between selection upon single or several characters; but they do account for the observation of Bumpus that among the birds which perished those with one extreme dimension often had other extreme dimensions.

The results conform to those of previous studies of intra-population correlations. Selander and Johnston (1967) have demonstrated significant correlations between pairs of the following characters:—wing length, tail length, bill length, bill width, tarsus length and weight. Additional correlations have been established for some German populations of this species by Grimm (1954) and Löhrl and Böhringer (1957), working with wing length, tail length, weight and bill length.

DISCUSSION

The survival of sparrows under conditions of cold stress is determined by the availability of food and the rate at which food resources can be used to meet the energetically demanding thermoregulatory requirements at low temperature (Kendeigh, 1934, 1944, 1945). In the storm which caused, eventually, the death of 64 of the birds brought to Bumpus, both factors were probably operating. Temperatures were low and, whatever the food supply, probably not much was available to the birds without risk because there is a decrease in feeding activity on rainy and windy cold days (Beer, 1961). An explanation of the centripetal selection on the sparrows can be sought within this framework.

The first question to be considered is why extreme individuals suffered a disproportionately high mortality. As far as body size (weight) is concerned, the heaviest and lightest birds might suffer particularly from cold stress, but for different reasons. The smallest birds have the largest surface/volume ratio, and hence the largest rate of heat loss per unit volume of body. To meet the needs of thermoregulation these birds would have to mobilize the energy reserves at the fastest rate, and would be expected to be the first to exhaust, or to approach complete exhaustion of, energy reserves. The largest birds have the least surface to volume ratio and the greatest absolute quantity of stored energy, but their total existence energy requirements are large (Kendeigh, 1969). Moreover the rate of mobilizing energy reserves may be relatively slow in large birds, and if so this rate may be insufficient to meet the energy demands of thermoregulation fast enough and as a consequence the birds will succumb to the cold stress (Kendeigh, 1945). In support of this are the findings of Kendeigh (1934) that sparrows die at higher body weights when cold stressed than when heat stressed. If these explanations are correct, there is an optimum size determined by opposite tendencies to maximize rate of energy reserve mobilization (small body size) and amount of energy that can be stored (large body size), and to minimize the attendant disadvantages of each.

The remaining three characters subjected to centripetal selection are lengths of sternum, humerus and tibiotarsus. Length of sternum is strongly correlated with body weight in the female group ($P < 0.01$), and probably is another indicator of body size.

Humerus and tibiotarsus are fore-limb and hind-limb bones respectively. Excessively long wings and legs might be selected against under conditions of cold stress, because of the large energy required to compensate for the heat lost from the vascularized surfaces (Brush, 1965; Bartholomew & Cade, 1957; Eliassen, 1963). It is less clear why birds with short limbs would be at a disadvantage under conditions of cold stress, unless it is that short limbs are associated with small body size which is selected against.

The second question to be considered is why extreme females were selected against while extreme males were apparently not. It is possible of course that the extreme males were selected against right at the beginning of the storm and were therefore never found. Even if this were so, an explanation would still be required for the difference in operation of selection on the two sexes.

I suggest that the females may have suffered proportionately heavier mortality than males because access to food was more difficult for them. Although females are aggressive (Johnston, 1969) they are generally subordinate to adult and first year males Watson (1970); for instance, when threatened by adult males, females do not adopt similarly threatening postures, but "merely space out" (Watson, 1970). Under conditions of starvation this might be instrumental in denying females access to food.

It is interesting to note that when a storm decimated a population of Song Sparrows, *Melospiza melodia* on Mandarte Island, British Columbia, survival was influenced by position (Tompa, 1964, 1971). Birds in the shrubbery, mainly adults, suffered proportionately heavier mortality than those, mainly young, in neighbouring (and more exposed) grassland areas. Social interactions had previously determined the spatial distribution of adults and young, and had therefore indirectly led to differential mortality.

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