

A FURTHER ANALYSIS OF BUMPUS' DATA: THE INTENSITY OF NATURAL SELECTION

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Received September 25, 1972

On February 1, 1898, a very severe snowstorm hit New England. A number of English sparrows, presumably exhausted in the storm, were brought to the Anatomical Laboratory of Brown University in Providence, Rhode Island. Out of a total of 136 birds, 72 survived and the rest died. Bumpus (1898) measured nine characters on the birds. They were also classified by sex and the males into young and adults. The characters measured were the following: (i) total length in millimeters; (ii) alar extent from tip to tip of the wings, in millimeters; (iii) weight in grams; (iv) length of head in millimeters; length of (v) humerus, (vi) femur, (vii) tibio-tarsus, (viii) bones across skull and (ix) sternum, all measured in inches to three decimal places. These data have been analysed several times by different authors.

Most recently, Johnston et al. (1972) have applied principal component analysis to the data to examine the differences between the surviving and dead birds. Their analysis of the nine characters confirms Bumpus' own calculations which showed that the main differences were in the means and mean deviations of the characters of total length, wingspan, lengths of humerus and femur and weight. Johnston et al. analysed the data in more detail when the characters of total length, wingspan and weight were excluded. Weight must necessarily depend largely on the condition of the birds and should obviously be excluded from the calculations. But total length and wingspan were excluded on the grounds that ornithologists consider them to be too variable and too subject to error to be useful. Since total length is not more variable than the other characters in Bumpus' data,

this seems an inadequate reason for excluding it. I have calculated simple discriminant functions from Bumpus' data, using the characters of total length, and length of humerus and femur, since these were the characters that were most obviously subjected to selection in the storm. I have then used the statistics of the surviving and dead birds to calculate the proportion of selective deaths and the variance in fitness according to various models of natural selection (O'Donald, 1968, 1970).

A severe snowstorm is a very extreme environment which animals are exposed to on only a few occasions each winter. But on these occasions, a population may well be subjected to a large part of the total selection imposed upon it in the whole year. If so, most of the selective deaths will then be suffered at these times. The variance in fitness will also be much increased. The actual selective values should therefore vary much more widely and it is interesting to calculate what variations in fitness affected the sparrows that Bumpus observed.

BUMPUS' DATA

Bumpus' own calculations show that there is little or no selection affecting most of the characters. Only for total length and the lengths of humerus and femur do the means and variances change significantly after selection. Not surprisingly, the lengths of humerus and femur are very highly correlated. The calculation of a discriminant function to maximize the difference between the survivors and the dead by the measurements of humerus and femur showed that the length of the femur contributed very little to the discrimination. Thus the selection is almost entirely concentrated on the

TABLE 1. *Statistics and statistical tests on length of humerus.*

	Females		Males	
	Survivors	Dead	Survivors	Dead
No. in sample	21	28	51	36
Mean	0.72833	0.72604	0.73914	0.73019
Variance	0.0002679	0.0006721	0.0004460	0.0006470
Student's <i>t</i>		0.356		1.787
Fisher's <i>z</i>		0.460*		0.186
5% point of <i>z</i>		0.361		0.253
	Both Sexes			
	Survivors	Dead		
No. in sample	72	64		
Mean	0.73599	0.72837		
Variance	0.0004140	0.0006518		
Student's <i>t</i>		1.932		
Fisher's <i>z</i>		0.227*		
5% point of <i>z</i>		0.201		

* Indicates significance at a probability of 0.05.

total length and the length of the humerus. I have studied the selection of these two characters separately and together in the form of a discriminant function.

Bumpus originally classified his data into the birds that survived or died, males and females, and the males into young and adults. However there were only 28 young males of which 16 were survivors and they are obviously too few to be analysed separately from the rest of the males. I have therefore calculated the statistics for all birds and for each sex separately.

The length of humerus.—Table 1 gives the values of mean and variance among survivors and dead for each sex and for both sexes together. The values of *t* for the test of significance of means and *z* for the test of significance of variances are also given. The table shows that the variance in females and in both sexes together is significantly greater in the dead birds. Selection has therefore acted to reduce the variance. Since the means have not changed significantly the selection presumably favoured a bird with an optimum near the mean value. But the change of mean does nearly reach a level of statistical significance also.

There is a much higher proportion of survivors among the males. They have a mean chance of survival of $\bar{w} = 51/87 = 0.586$ compared to the females' chance of survival of $\bar{w} = 0.429$. However, for this difference $\chi^2 = 2.526$ for one degree of freedom, which is not significant.

Total length.—Table 2 gives the statistics for total length. There is strong selection shown here against the longer birds. The dead birds are very significantly longer in the males and in both sexes. The survivors are therefore shorter on average than the population before selection. Selection must have been in favour of an optimum length considerably shorter than the average.

A discriminant function of the characters.—Any measurement of a character is necessarily arbitrary: many different points may be chosen to define the character and many scales may be used to measure it. We can define new characters as various combinations of the others, altering their scales of measurement in any way we please. The simplest way of defining a new character is to choose a discriminant function that will make the difference between the survivors and the dead a maximum. If the total length is *x* and the length of humerus

TABLE 2. *Statistics and statistical tests on total length.*

	Females		Males	
	Survivors	Dead	Survivors	Dead
Mean	157.381	158.429	159.255	162.083
Variance	11.048	15.069	8.2337	8.6500
Student's <i>t</i>	0.933		4.482**	
Fisher's <i>z</i>	0.155		0.0246	
	Both Sexes			
	Survivors	Dead		
Mean	158.708	160.484		
Variance	9.6461	14.6029		
Student's <i>t</i>		2.987**		
Fisher's <i>z</i>		0.207*		

** Indicates significance at a probability of at least 0.01 and

* Indicates a probability of 0.05.

is y , then we can define sums of squares and products within the two groups—survivors, s , and dead, d —as follows:

$$\begin{aligned}
 w_{11} &= \sum x_s^2 - n_s \bar{x}_s^2 + \sum x_d^2 - n_d \bar{x}_d^2 \\
 w_{12} &= \sum x_s y_s - n_s \bar{x}_s \bar{y}_s + \sum x_d y_d - n_d \bar{x}_d \bar{y}_d \\
 w_{22} &= \sum y_s^2 - n_s \bar{y}_s^2 + \sum y_d^2 - n_d \bar{y}_d^2
 \end{aligned}$$

In these equations n_s and n_d are the numbers of survivors and dead, \bar{x}_s and \bar{y}_s are the means of survivors and \bar{x}_d and \bar{y}_d are the means of the dead. It is then easy to show that for a function $D = \lambda x + \mu y$, Student's t will be a maximum when

$$\begin{aligned}
 w_{11}\lambda + w_{12}\mu &= \bar{x}_s - \bar{x}_d \\
 w_{12}\lambda + w_{22}\mu &= \bar{y}_s - \bar{y}_d
 \end{aligned}$$

TABLE 3. *Statistics and statistical tests on the discriminant function, $D = -0.02285x + 0.3075y$.*

	Females		Males	
	Survivors	Dead	Survivors	Dead
Mean	-0.13565	-0.13875	-0.13661	-0.14583
Variance	0.00003542	0.00004539	0.00004193	0.00004473
Student's <i>t</i>		1.614		6.448**
Fisher's <i>z</i>		0.124		0.0323
	Both Sexes			
	Survivors	Dead		
Mean	-0.13633	-0.14273		
Variance	0.00003970	0.00009734		
Students <i>t</i>		4.558**		
Fisher's <i>z</i>		0.448**		

For both sexes together, we have the values $w_{11} = 1604.86$, $w_{12} = 6.15108$ and $w_{22} = 0.0704600$ giving $\lambda = -0.002285$ and $\mu = 0.3075$. Within males alone $\lambda = -0.006820$ and $\mu = 0.6652$ and within females alone $\lambda = -0.003453$ and $\mu = 0.4415$. Since it is only the relative values of λ and μ that are important, the discriminant functions within the sexes and for both sexes are very similar. The discriminant function within males gives $t = 6.728$ while the general discriminant function calculated for both sexes together gives $t = 6.448$ when tested on males alone. The general discriminant function is therefore almost as effective in discriminating between surviving and dead males as the particular discriminant function calculated for the males alone. The particular discriminant function for females is almost identical to the general function and gives $t = 1.616$ compared to $t = 1.614$. These values of t for the females are not of course significant and show that neither function significantly discriminates between the surviving and dead females.

Table 3 gives the means and variances of the discriminant function $D = -0.002285x + 0.3075y$ in each sex and in both sexes to test the differences between survivors and dead. The discriminant function shows that the selection is mainly for an increase of mean D in the males. The mean and variance of D do not differ significantly between surviving and dead females.

MEASURES OF SELECTION

The proportion of selective deaths suffered by a population is measured by the quantity

$$I = (w_0 - \bar{w})/w_0$$

where w_0 is the fitness of the most fit phenotype and \bar{w} is the mean fitness (Van Valen, 1965). I is usually called the intensity of selection which Haldane (1954) originally proposed to measure as $1 - e^{-I}$. A more general measure of selection is given by the quantity V_w/\bar{w}^2 where V_w is the variance in fitness. This has the advantage that it does not depend on knowing w_0 . If fitness varies as a linear function of the value of a character, it will be entirely arbitrary what value is chosen to give w_0 . The intensity of selection then has no meaning. But selection can still be measured by calculating V_w/\bar{w}^2 . This measure of selection has the advantage that it is related to the change in the mean fitness produced by the selection. It is easy to show (see O'Donald, 1970) that for changes of phenotypic values

$$\Delta\bar{w}/\bar{w} = V_w/\bar{w}^2$$

which is therefore the proportionate increase in mean fitness. If V_w were solely determined by the additive effects of different genes, or if V_w were the heritable component of the variance and determined by additive genetic effects, then the equation for $\Delta\bar{w}/\bar{w}$ would give the proportionate increase in mean fitness to be expected in the following generation.

The values of I and $\Delta\bar{w}/\bar{w}$ can be calculated from the changes in the mean and variance of the character. Particular models of selection must be assumed. Thus selection may vary directly with the values of the character: fitness may be a linear or quadratic function of these values. Such "fitness functions" usually give reasonable values of the fitnesses in the range of values of the character but may give negative fitnesses at extreme values. However they have the advantage that the change of mean and variance is given by the moments

of the distribution of the character and do not depend on assuming a particular distribution, usually a normal distribution, of the character. On the other hand, if fitness is related to the values of the character by a curve of the shape of the normal distribution, negative fitness cannot then occur, but the change of mean and variance can only be obtained if the character is also normally distributed. In practice, since we are not concerned with extreme values, the quadratic and normal fitness functions give similar results and the normal is only seriously in error if the character is very skew in its distribution.

O'Donald (1970) gave the formulae for the values of I and $\Delta\bar{w}/\bar{w}$ according to the various fitness functions. If fitness varies as a linear function of the character, then

$$w = J + Kx$$

$$\text{and} \quad \Delta\bar{w}/\bar{w} = (\Delta\bar{x})^2/V_x$$

where $\Delta\bar{x} = \bar{x}' - \bar{x}$ and \bar{x} and \bar{x}' are the means of the character before and after selection. V_x is the variance of the character.

If the fitness function is quadratic and $w = 1 - \alpha - K(\theta - x)^2$ where θ is the optimum value of the character so that at the optimum $w_0 = 1 - \alpha$, then it can be shown that

$$\Delta\bar{x} = \frac{2V_x(\theta - \bar{x}) - \mu_{3x}}{\phi - (\theta - \bar{x})^2 - V_x}$$

and

$$(\Delta\bar{x})^2 + \Delta V_x = \frac{V_x^2 - \mu_{4x} + 2\mu_{3x}(\theta - \bar{x})}{\phi - (\theta - \bar{x})^2 - V_x}$$

where $\phi = (1 - \alpha)/K$. From these equations ϕ and θ can be estimated if $\Delta\bar{x}$ and $\Delta V_x = V_x' - V_x$ are known. The equations for I and $\Delta\bar{w}/\bar{w}$ are given by O'Donald (1970) in terms of θ and ϕ . However if x is normally distributed, we obtain

$$I = \frac{\Delta V_x [\Delta V_x + 2(\Delta\bar{x})^2] + (\Delta\bar{x})^2 [V_x + (\Delta\bar{x})^2]}{\Delta V_x [\Delta V_x + 2(\Delta\bar{x})^2 - 2V_x] - (\Delta\bar{x})^2 [V_x - (\Delta\bar{x})^2]}$$

$$\Delta\bar{w}/\bar{w} = \frac{(\Delta\bar{x})^2}{V_x} + \frac{1}{2} \left\{ \frac{(\Delta\bar{x})^2 + \Delta V_x}{V_x} \right\}^2.$$

If $\Delta\bar{x} = 0$, then selection acts entirely on the variance V_x . Thus

$$I = \frac{\Delta V_x}{\Delta V_x - 2V_x} = \frac{V_x' - V_x}{V_x' - 3V_x}$$

and

$$\Delta\bar{w}/\bar{w} = \frac{1}{2}(\Delta V_x/V_x)^2.$$

If $V_x = 0$, selection acts entirely on the mean, I is not defined, and

$$\Delta\bar{w}/\bar{w} = (\Delta\bar{x})^2/V_x + \frac{1}{2}[(\Delta\bar{x})^2/V_x]^2.$$

This expression for $\Delta\bar{w}/\bar{w}$ gives similar values to that obtained from the linear model, for the additional term $\frac{1}{2}[(\Delta\bar{x})^2/V_x]^2$ is very small.

If the fitness function is shaped like a normal curve, then $w = (1 - \alpha)e^{-K(\theta - x)^2}$. Assuming that x is normally distributed, the values of I and $\Delta\bar{w}/\bar{w}$ can then be calculated. In general the expressions are (O'Donald, 1970)

$$I = 1 - \sqrt{1 + \Delta V_x/V_x} \cdot \exp \{ (\Delta\bar{x})^2/2\Delta V_x \}$$

$$\Delta\bar{w}/\bar{w} = \{ 1/\sqrt{1 - (\Delta V_x/V_x)^2} \} \times \exp \{ (\Delta\bar{x})^2/(V_x - \Delta V_x) \} - 1$$

Thus if $\Delta\bar{x} = 0$, then

$$I = 1 - \sqrt{1 + \Delta V_x/V_x}$$

$$\Delta\bar{w}/\bar{w} = 1/\sqrt{1 - (\Delta V_x/V_x)^2} - 1$$

and if $\Delta V_x = 0$, I is not defined, and

$$\Delta\bar{w}/\bar{w} = \exp \{ (\Delta\bar{x})^2/V_x \}$$

These expressions all give very similar values to the quadratic model, except when x has a very skewed distribution. The estimates of I and $\Delta\bar{w}/\bar{w}$ are necessarily biased and are slightly inflated as a result of the bias.

Selection for length of humerus.—The only statistically significant effects are the differences between the variances of the surviving and dead birds in females and both sexes. In females the variance of all

birds is 0.00049102 and the variance of survivors is 0.00026793. Therefore $\Delta V_x = -0.00022309$ and from the formulae of the quadratic fitness function

$$I = 0.185 \\ \Delta\bar{w}/\bar{w} = 0.103$$

The normal fitness function gives slightly higher values of

$$I = 0.261 \\ \Delta\bar{w}/\bar{w} = 0.123$$

Selection for total length.—There are no significant effects in the females but a highly significant difference of means of surviving and dead males. For both sexes differences of both mean and variance are significant. In the males we get for the selection acting on the mean

$$\Delta\bar{w}/\bar{w} = 0.142$$

In both sexes the quadratic model gives

$$I = 0.195 \\ \Delta\bar{w}/\bar{w} = 0.072$$

and the normal model gives

$$I = 0.223 \\ \Delta\bar{w}/\bar{w} = 0.076$$

Selection for the character defined by the discriminant function, D.—The change in mean is highly significant in the males. Changes of mean and variance are significant in both sexes together. In the males we have the statistics $\bar{D} = -0.14042$, $V_D = 0.000063412$ and $\Delta\bar{D} = 0.00381218$. This gives by the quadratic model

$$\Delta\bar{w}/\bar{w} = 0.255$$

and by the normal model

$$\Delta\bar{w}/\bar{w} = 0.257.$$

By the linear model

$$\Delta\bar{w}/\bar{w} = 0.229.$$

All these models agree and show that selection is very intense. Dowdeswell (1961) obtained data of very intense selection for spot number on the wings of the butterfly

Maniola jurtina. His data give the values

$$I = 0.227$$

$$\Delta\bar{w}/\bar{w} = 0.042$$

compared to

$$I = 0.370$$

$$\Delta\bar{w}/\bar{w} = 0.169$$

for the selection acting on the sparrows when both sexes are lumped together.

The data can also be used to estimate the parameters of the fitness function itself. If the fitness function is

$$w = 1 - \alpha - K(\theta - x)^2$$

then the mean fitness is

$$\bar{w} = 1 - \alpha - K(\theta - \bar{x})^2 - KV_x.$$

But \bar{w} is the proportion of survivors which is known. It can easily be shown that

$$\alpha = \frac{1 - \bar{w} - I}{1 - I}.$$

Using the data of the changes in the mean and variance of D , we get by the quadratic model

$$\alpha = 0.16000$$

$$\theta = -0.11983$$

$$K = 708.23$$

giving the quadratic fitness function

$$w = -9.3293 - 169.72D - 708.23D^2$$

This gives a negative fitness when $D = \bar{D} - 2\sigma_D$ which is the point at which $w = -0.0132$. It is better, therefore, to use the normal fitness function, for which

$$w = (1 - \alpha)e^{-K(\theta - x)^2}$$

where

$$\alpha = 0.19746$$

$$\theta = -0.12968$$

$$K = 3923.2$$

In *Maniola jurtina*, butterflies with three spots are at the value of

$$x = \theta + 5.586\sigma$$

where x is the number of spots. In the sparrows the corresponding value of D is

-0.17209. In *Maniola* at this point the fitness is $w = 0.336$ according to the calculated fitness function given by O'Donald (1970). In the sparrows, the corresponding fitness is $w = 0.00086$. Ford (1971) has pointed out how extreme is the selection acting on the number of spots in *Maniola jurtina*. How much more extreme is it therefore on the character measured by D in the sparrows! These fitnesses however are the fitnesses of particular phenotypes of a quantitative character. The fitnesses affecting the genes at individual loci may well be much less if the genes at each locus only have small effects on the values of the character (O'Donald, 1971).

CONCLUSION

The selection imposed on the sparrows of Providence, Rhode Island by the storm of 1898 was more intense than any which has since been observed acting on particular quantitative characters. This is not surprising in such an extreme environment. All populations are at times exposed to extreme environments and are probably then subjected to a large part of the selection acting upon them. If the quantitative character is determined by genes at many loci, the selection affecting particular alleles will be detectable only in the adverse conditions. Such alleles may determine particular enzyme polymorphisms. If so, this selection may then be responsible for maintaining many enzyme polymorphisms which have been regarded as selectively neutral. This must remain speculative until the selection has been demonstrated experimentally in the particular polymorphisms for which explanations are sought in terms of selective mechanisms.

SUMMARY

Bumpus measured nine characters on a group of sparrows, some of which perished, while others survived, after a storm in Rhode Island. In this paper, the characters on which natural selection had the greatest effect are analysed both singly and when

combined as discriminant functions. According to several different models of selection, the proportion of selective deaths and the variance in fitness can be calculated for the particular characters and the discriminant functions. These calculations show that in the storm very intense selection was acting on the sparrows. The fitnesses of the phenotypes vary between very wide limits.

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ANNOUNCEMENT

FIRST INTERNATIONAL THERIOLOGICAL CONGRESS

The American Society of Mammalogists expects to be able to make small grants to scientists planning to attend the International Theriological Congress at Moscow, U.S.S.R., the 6th to 12th of June, 1974 (see J. Mammal., 54:560, May, 1973). These grants, to partially defray travel costs, will probably amount to \$100-\$250. All professional mammalogists who are residents of the U.S.A., but not employed by the U.S. government, are invited to apply; membership in the Society is not a prerequisite. Requests for information should be sent to: Robert S. Hoffmann, Museum of Natural History, University of Kansas, Lawrence, Kansas 66045.

The Society has also chartered a Pan American World Airways Boeing 707 which will leave New York City on 4 June 1974, arriving in Moscow the following day. Following the Congress, a 5-7 day period is available for post-Congress activities; the charter flight will leave Moscow on 18-19 June 1974 for the return trip to New York City. Capacity of the plane is 179 persons; places will be reserved on a first-come-first-serve basis. Persons may register for space on the charter flight by sending a non-refundable deposit of \$50.00 for each seat, and the name of the registrant(s), to Robert S. Hoffmann. Checks should be made payable to the American Society of Mammalogists.

A further notice concerning passport and visa arrangements, and post-Congress activities, will be published in the November issue of the Journal of Mammalogy. Any questions concerning the Congress may be addressed to Dr. V. E. Sokolov, Chairman, Organizing Committee, International Theriological Congress, Institute of Evolutionary Animal Morphology and Ecology, Academy of Sciences of the U.S.S.R., 33 Leninskii Prospekt, Moscow 117071, U.S.S.R., or to Robert S. Hoffmann, Chairman, Committee on International Relations, American Society of Mammalogists, Museum of Natural History, University of Kansas, Lawrence, Kansas 66045.