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Optimum Proportions Selected with Unequal Sex Numbers

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Summary. Optimum proportions selected for each sex, giving the maximum selection response up to some specified time, have been investigated. Selection was carried out from a constant number of individuals scored per generation. It has been shown that the maximum response after t generations of selection is obtained when the number of individuals scored and the proportion selected is the same for males and females every generation. Specific situations, where the sex-ratio among scored or breeding individuals or the selected proportion of males or females is taken as given throughout the whole selection process, have been studied, optimum strategies being described in each case. The procedures leading to maximum advance at the selection limit have also been considered in all these situations.

Key words: Sex-Ratio - Maximum Selection Response - Unequal Sex Numbers

Introduction

In a model of many unlinked additive loci, all with small effects when individual selection is carried out from a constant number T of individuals scored per generation, it has been shown by Robertson (1970) that the proportion selected giving the maximum selection response after t generations is a function of t/T. The maximum advance at the selection limit is achieved when selecting the best T/2 individuals every generation (Dempster 1955; Robertson 1960). These results assume equal numbers of males and females in the scored and the selected groups. In this paper, we shall be concerned with extending Robertson's results to populations with unequal sex numbers. This problem has been considered by Smith (1969) regarding immediate response to selection. An experimental check of the theory has been reported by Ruano, Orozco and López-Fanjul (1975).

Results

Consider that M males and F females ($F = cM$) are scored every generation ($M + F = T =$ constant) and from those m males and f females ($f = km$) are selected. The proportions selected in each sex are then $p_m = m/M$ and $p_f = f/F$ and the intensities of selection for each sex are $i_m = z_m/p_m$ and $i_f = z_f/p_f$, where z_m and z_f are the ordinates at the point of truncation of the distribution of the trait, assumed to be normal, for each sex respectively. In the population so defined, the effective population size N_e is given by $N_e = 4mf/(m+f)$ and the total selection intensity $i = (i_m + i_f)/2$.

For a trait with genetic and phenotypic variances σ_A^2 and σ^2, respectively, the gain $\Delta G(t)$ after t generations of selection, all with a selected proportion p, is given approximately (Robertson 1970) by

$$\Delta G(t) = 2N_e\, i\, \sigma_A^2(1 - e^{-t/2Tp})/\sigma.$$

In our case, this expression becomes

$$\Delta G(t) = UV(1 - e^{-tW/T}) \qquad (1)$$

where

$$U = 4T\,\sigma_A^2/\sigma$$

$$V = (cz_f + kz_m)/(1+c)(1+k)$$

$$W = (1+c)(1+k)/8kp_m\,.$$

Since $p_f/p_m = k/c$, only four variables in equation (1) (e.g. c, k, p_m and t/T) are independent.

Considering t/T as a constant and differentiating expression (1) with respect to the three remaining variables and setting these three equations equal to zero, after some rearrangement we have

$$k = (z_f - x_f\, p_f)/(z_m - x_m\, p_m) \tag{2}$$

$$\sqrt{p_m}/(z_m - x_m\, p_m) = \sqrt{p_f}/(z_f - x_f\, p_f) \tag{3}$$

$$x_m + x_f = (x_m + x_f + 8VW^2 t/T)\, e^{-Wt/T} \tag{4}$$

where x_m and x_f are the abscissae corresponding to the values of z_m and z_f in the normal curve.

The function $\sqrt{p}/(z - xp)$ can be shown to be monotonically decreasing for increasing values of p. Accordingly, equation (3) necessarily implies $p_m = p_f$, involving $k = 1$ from equation (2) and as a consequence $c = 1$. Therefore, the general solution of the system giving the absolute maximum is equation (4) for $k = c = 1$ and $p_m = p_f = p$, which then becomes

$$2x = (2x + zt/p^2T)\, e^{-t/2pT}\ . \tag{5}$$

Equation (5) is also the algebraic expression of the particular solution given graphically by Robertson (1970) in his figure 1. In other words, the maximum selection response after t generations is obtained when for both sexes the number of individuals scored and the proportion selected are equal.

The sex-ratio among scored (c) or breeding (k) individuals may not be equal to one under a specific type of management or in a given domestic species. In these cases, the proportion selected in a selection programme may not be the optimal. We shall then proceed to study the local maxima when c, k or p_m take a constant value but not necessarily the ones leading to the solution of absolute maximum. In all cases t/T is assumed to be a constant.

Case 1; c or k constant:

Differentiating expression (1) with respect to k and p_m and setting the two equations equal to zero, we obtain after some rearrangement equation (4) and

$$c = (z_m - x_m\, p_m)/(z_f - x_f\, p_f)\ . \tag{6}$$

For the limiting case of t/T → ∞, corresponding to the maximum advance at the selection limit, equation (4) reduces to the somewhat surprising result of $p_m = 1 - p_f$. Under this condition, the values of equation (6) were arithmetically determined and are graphically shown in Fig.1. Of course, for $c = 1$, it gives $k = 1$ and $p_m = p_f = 0.5$ in agreement with theory.

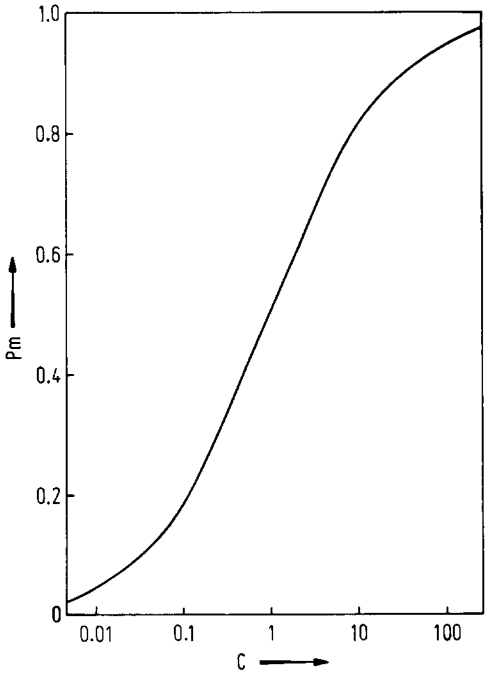

Fig.1. Relation between the sex-ratio among scored individuals (c) and the proportion of males (p_m) selected every generation which gives the maximum advance at the selection limit when T individuals are measured every generation (Case 1; c constant and t/T → ∞)

The function z - xp can be shown to be monotonically increasing for increasing values of p. For a constant value of t/T, solutions of the system formed by equations (4) and (6) were determined arithmetically and they are represented graphically in Fig.2 for different values of c. The limiting values found for t/T → ∞ taken from Fig.1 are shown on the right-hand side of the graph for each of the values of c considered. Values of t/T around two approach very closely these limiting values.

Due to the symmetry of the equations, the solutions already represented in Figs.1 and 2 have the same form for the case of k constant. The values of the ordinate are now those of p_f and the curves represent solutions of the system for the different values of k equal to the values of c stated on the figure.

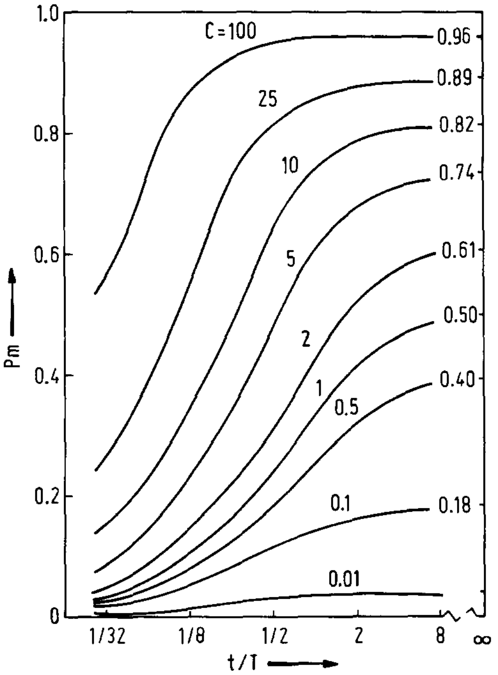

Fig.2. Proportion of males (p_m) selected every generation from T individuals measured which gives the maximum advance in t generations for different values of the sex-ratio among scored individuals (c) (Case 1; c constant)

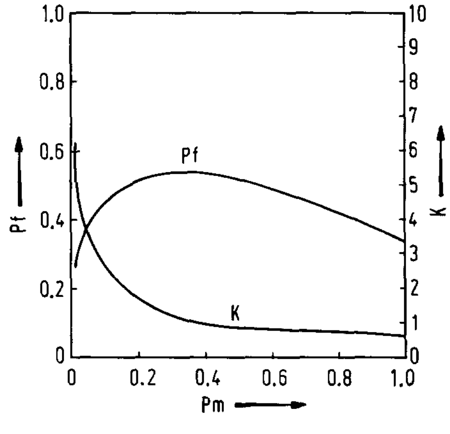

Fig.3. Relation between the sex-ratio among breeding individuals (k) and the proportions selected of males (p_m) and females (p_f) every generation which give the maximum advance at the selection limit when T individuals are measured every generation (Case 2; p_m constant and $t/T \to \infty$)

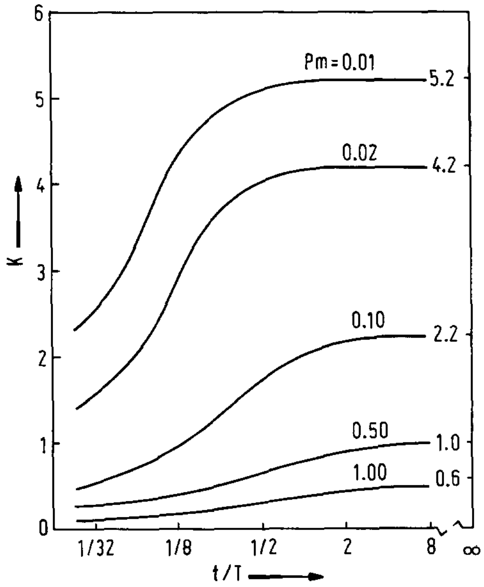

Fig.4. Sex-ratio among breeding individuals (k) which gives the maximum selection advance in t generations from T individuals measured every generation for different selected proportions of males (p_m) (Case 2; p_m constant)

Case 2; p_m constant:

Differentiating expression (1) with respect to k and c and setting these two equations equal to zero, we have

$$kc = 1 \tag{7}$$

$$Y = (Y - UWt/T)e^{-Wt/T} \tag{8}$$

where

$$Y = \{(z_f - x_f p_f) - k(z_m + x_f p_m)\}/(1+c)(1+k) \ .$$

For the limiting case of $t/T \to \infty$, the system reduces to equation (7) and Y = 0. Solutions have been obtained arithmetically and they are shown graphically in Fig.3: p_f increases for values of p_m lower than 0.25 and decreases otherwise.

The general solutions for a constant value of t/T are those of the system formed by equations (7) and (8). These solutions have been represented graphically in Fig.4 for different values of p_m. The limiting values found for $t/T \to \infty$ taken from Fig.3 are also shown on the right-hand side of the graph for each value of p_m considered. Values of t/T of about one approach very closely these limiting values. It is also apparent from the graphs that unless the proportion p_m is very low, the corresponding values of k determining the maximum selection advance in t generations will not be large. Although the whole range of values of p_m have been considered in Figs. 3 and 4, proportions p_m larger than 0.5 imply values of k lower than one and therefore, a male surplus.

Case 3; c = 1 and k constant:

This particular case has been studied in detail as it may be more representative of practical situations. The conditions of maximum are now represented by the equation

$$(x_m + x_f)\{x_m + x_f + (z_f + kz_m) \times (1 + k)t/4p_f^2T\} e^{-(1+k)t/4p_fT} = 0 . \qquad (9)$$

This equation reduces to $p_m = 1/(1 + k)$ when $t/T \to \infty$. In both cases $p_f = kp_m$, showing that intense selection in both sexes when k is large will not generally lead to maximum selection advances. The solutions of equation (9) are graphically shown in Fig. 5 for different values of k. The limiting values found for $t/T \to \infty$ are shown on the right-hand side of the graph for each value of k considered. Of course, for k = 1 the curve corresponds to the one given by Robertson (1970) in his figure 1.

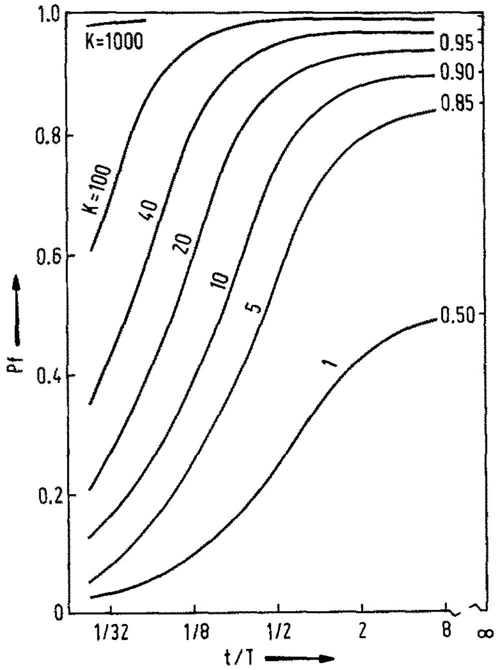

Fig. 5. Proportion of females (p_f) selected every generation from T individuals measured which gives the maximum advance in t generations for different values of the sex-ratio among breeding individuals (k) (Case 3; c = 1 and k constant)

Discussion

A general solution has resulted from the analysis of the model, namely that the maximum response after t generations of selection is obtained when the number of individuals measured and the proportion selected are the same for both sexes every generation. This is a situation seldom encountered in practical animal breeding although it is commonly found in laboratory selection experiments.

In a breeding programme, the intensity of selection attainable in practice will depend on female fecundity and on the number of females which can be served by one male. The consideration of these two factors will determine the value of the sex-ratio among breeding individuals (k). This situation has been studied in Case 1 (k constant), the main conclusion being that large values of k are rarely compatible with strong selection pressures on females (p_f) either in the short- or in the long-term. In the short-term, the values of p_m and c determining the optimum strategies are very insensitive to large changes in the value of the remaining variables in the model. For example, for values of p_f ranging from 5 % to 60 % and values of k from 5 to 100, p_m and c take values between 1.5 % and 2.5 % and 1.3 and 2.5, respectively, t/T being 1/32.

On the other hand, the tolerable rate of inbreeding will also limit the intensity of selection attainable. In practice, the breeder will usually choose an empirical level of inbreeding aimed at balancing short- and long-term selection gains. In our model, the effective population size N_e is given by

$$N_e = 4Tkp_m/(1 + c)(1 + k)$$

and therefore, once a given strategy is chosen (k, c or p_m constant) the rate of inbreeding leading to maximum response up to t generations of selection is already defined. It may then be of some interest to compare theoretical and empirical rates of inbreeding in specific selection programmes, as fixing k and N_e will not in general lead to optimum responses.

In all situations, the distribution of testing facilities among the sexes (c) can be critical. At the optimum, when selection is carried out at a constant c value, small values of p_m will not be compatible with large values of c.

In the cases studied, the optimum proportions selected can exceed 50%. It will then be preferable to select 50% from the scored individuals taking the rest at random from the unscored population, as suggested by Smith (1969). A comparison between short- and long-term selection gains will also depend on the size of the scored population T. The problem of how large T should be in a breeding programme has been discussed by James (1972).

In our model, individual selection has been assumed although values of k larger than one will obviously imply the existence of information on the individual genotype other than its own phenotype. The use of this additional information has not been considered in this paper.

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