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Maximising a Function of the Selection Differential

J.W. James, School of Wool and Pastoral Sciences, University of New South Wales, Kensington (Australia)

Summary. It is shown that some problems of optimising selection response can be solved without assuming a specific form of distribution for the trait of interest. To maximise the selection limit using selection among a fixed number every generation, all above the mean should retained. If a fraction of a population is set aside as a sire breeding nucleus, and selection is at one stage, maximum response per generation occurs when the nucleus as a fraction of the whole population is the square root of the sires: dams ratio. When a trait has an optimum, but declines in value at different rates A above and B below the optimum, the population mean should be chosen so that a fraction $B/(A + B)$ are above the optimum.

Introduction

The selection differential plays an important part in quantitative genetics, since the rate of change of the population mean under selection depends upon it. When divided by the population standard deviation it is called the standardised selection differential. For a given proportion p selected for a trait, the maximum standardised selection differential i is obtained by truncation of the distribution at a point x standard deviations from the mean so as to give the required proportion selected. In many applications there is an optimum fraction p selected, and to find the optimum the appropriate criterion function of the selection differential is differentiated with respect to p in order to obtain stationary values. The distribution is usually taken as normal for this purpose, since such traits of interest as fleece weight and milk production are nearly normally distributed. Only occasionally are other distributions discussed, e.g. James (1966). It will be shown here that some problems may be solved without assuming a specific form of distribution.

Results and Discussion

Let U be a continuous variate standardised to have mean zero and variance unity, with probability density function $f(u)$. If a fraction p is selected by truncation at x to give a standardised selection differential i, then

$$p = \int_x^\infty f(u)du, \qquad (1)$$

and

$$i = p^{-1} \int_x^\infty uf(u)du. \qquad (2)$$

From (1) and (2) it follows at once that, if $z = f(x)$,

$$\frac{dp}{dx} = - z \qquad (3)$$

and

$$\frac{d(pi)}{dx} = - xz \qquad (4)$$

so that

$$\frac{d(pi)}{dp} = x. \qquad (5)$$

However,

$$\frac{d(pi)}{dp} = p\frac{di}{dp} + i$$

and so

$$\frac{di}{dp} = -\frac{i - x}{p} \qquad (6)$$

and

$$\frac{di}{dx} = \frac{(i - x)z}{p}. \qquad (7)$$

For a normal distribution $i = z/p$ and this, together with the result that $dz/dx = - xz$, is often used. Among many others examples can be found in Robertson (1957, 1960, 1970) and James (1966, 1972). We now consider some examples in which general solutions can be obtained.

Example 1.

Robertson (1960) showed that the ultimate limit to selective advance is a monotonic increasing function of Ni, where N is the number of parents used. If a total of T animals are available for selection each generation and a fraction p are selected, $N = Tp$ and total advance is a monotonic increasing function of pi. We thus want to maximise pi and find from (5) this occurs when $x = 0$. We should therefore select all animals above the mean. For a symmetrical distribution this implies $p = 0.5$ as Robertson found for a normal distribution. For skewed distributions the optimum will be to select some fraction other than 0.5.

Example 2.

If a breeding program is set up so that only progeny of the best dams, which have been mated to the best sires, are considered as potential sires, then as shown by Dickerson and Hazel (1944), the rate of genetic change is proportional to $S = i_{MM} + i_{MF} + i_{FM} + i_{FF}$, where i_{MM} is the standardised selection differential applied to males used to breed males, i_{MF} is for males used to breed females, and so on. We assume selection is carried out at a single stage and that the age structure and generation interval are fixed. The vital statistics are such that a fraction a of all female progeny are needed as replacements and the ratio of breeding males to females is b:a. The fraction of breeding females used to breed potential sires is q. What value of q will maximise S and thus the rate of genetic gain? The selection intensity for females to breed females is a, and since a fraction q are parents of males the selection intensity for females to breed males is aq. The selection intensity for males to breed males is b, but since males to breed females come only from a fraction q of the population, their selection intensity is b/q. Then if i (p) denotes the standardised selection differential for a fraction p selected, we have

$$S = i(b) + i(b/q) + i(aq) + i(a).$$

Therefore

$$\frac{dS}{dq} = ((i(b/q) - x(b/q)) - (i(aq) - x(aq)))/q.$$

Thus for $\frac{dS}{dq} = 0$ we require

$$i(b/q) - x(b/q) = i(aq) - x(aq).$$

If $i - x$ is a one-to-one function of p this implies that $b/q = aq$. Thus for all distributions for which $i - x$ differs for all values of p the proportion of females used to breed males should be the square root of the ratio of sires to dams, $q = (b/a)^{1/2}$. In Australian Merino sheep it is customary to use 2 rams per 100 ewes, so about one-seventh of the total flock should be used to breed male replacements under the conditions assumed here. Many distributions are such that $i - x$ determines p (e.g. normal) but not all are (e.g. exponential).

Example 3.

This example in the case of a normal distribution was shown to me by Mr. I.R. Hopkins. Suppose that a particular character has an optimum, and that an animal's economic value declines linearly with deviation from the optimum. The rate of decline of economic value is asymmetrical, being A per standard deviation above, and B per standard deviation below the optimum. Degree of fatness of the carcase in meat animals may be such a character. A population has a fixed form and variance, but its mean can be shifted. What mean for the character will maximise the average economic value of the population? Define the loss per individual as the amount by which it is below the maximum economic value. Let the optimum be x standard deviations from the mean so that a fraction p are above the optimum with standardised selection differential i. Then the standardised selection differential for the fraction $(1 - p)$ below the optimum is $- pi/(1 - p)$. The mean loss for those above the optimum is $A(i - x)$ while for those below the optimum the mean loss is $B(pi/(i - p) + x)$. Thus the average loss over the whole population is

$$L = pA(i - x) + (1 - p)B(pi/(1 - p) + x)$$
$$= (A + B)p(i - x) + Bx.$$

Then

$$\frac{dL}{dx} = - p(A + B) + B$$

and on setting $\frac{dL}{dx} = 0$ we find the mean should be shifted to a point where the fraction above the optimum is $B/(A + B)$. When the rate of decline is symmetrical ($A = B$) this gives the intuitively obvious result that half the population should be above and half below the optimum. When the population is not skew, then the mean and optimum coincide. However, in general, unequal fractions above and below the optimum will be superior.

In these examples solutions can be found without assuming a specific form of distribution. This cannot always be done. James (1972) dealt with the sum of discounted returns from a breeding programme of fixed size, and showed that the criterion to be maximised is $pi/(2TRp + 1)$, where T is the number of animals available for selection and R is the discount rate. From the above results the maximum occurs when

$$\frac{x}{p(i - x)} = 2RT.$$

This equation has to be solved for the particular distribution involved. James gave a solution for the normal distribution. Although general solutions are not always possible, it seems worthwhile to use the approach developed here in case there may be a general solution, since particular solutions for specific distributions can be obtained as special cases.

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Dr. J.W. James
School of Wool and Pastoral Sciences
University of New South Wales
Kensington (Australia) 2033