A SYSTEMS ANALYSIS APPROACH FOR STUDYING THE EFFECT OF REPRODUCTION-ENHANCING BIOTECHNOLOGIES ON THE GENETIC IMPROVEMENT OF BEEF CATTLE

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ABSTRACT

A function is presented to which nonlinear programming techniques could be applied to quantify the potential of super-ovulation, embryo transfer, sexed semen, in vitro fertilization and in vitro maturation of oocytes used singularly or in combination to improve genetically beef cattle growth and(or) reproductive efficiency. The function to be maximized adds genetic gain times the sale price of the additional product brought about by the genetic selection program, and any income change due to change from the normal replacement rate of females, and subtracts the additional costs of the breeding program over a random breeding program. All this is expressed on a per-calf-sold basis to arrive at the economic return of the breeding program per calf raised to market age. The rate of increase in inbreeding can be restricted as desired. It is assumed that a progeny testing procedure is practiced for the selection of sires. The power of nonlinear programming to find maximums of functions with many variables and to measure how sensitive the genetic and economic returns are to various success rates for the biotechnologies mentioned above is discussed.

(Key Words: Beef Cattle, Biotechnology, Nonlinear Programming.)

Introduction

The developed and developing biotechnologies of super-ovulation, embryo transfer, in vitro fertilization, in vitro maturation of oocytes and possibly sexed semen raise questions about their combined potential to affect genetic change, and for which specific biotechnologies it would be most useful to have high efficacy (Van Vleck, 1981). Continuing to improve the biological efficiency of beef cattle, particularly with respect to reproductive efficiency, increases the consumption options of the U.S. population and increases the economic viability of the producers of beef cattle by decreasing the capital investment in land resources and cattle per unit of market product. This paper presents a complex, nonlinear function that relates success rates of biotechnologies, economic return from genetic gain and costs of the biotechnologies. A thorough understanding of the components of the function provide some depth of understanding of the issues involved. The considerable potential for nonlinear programming techniques to provide in-depth information about the relationships is discussed.

Experimental Procedure

A systems analysis approach can be used to study the interaction among the reproduction-enhancing techniques of super-ovulation, embryo transfer, sexing of semen, in vitro fertilization and in vitro maturation of oocytes within the context of a genetic selection program. Thus the approach can be used to determine success rates of biotechnologies that will maximize genetic improvement per year and economic return per year. This approach can also determine if success rates less than the optimums will substantially lower genetic improvement. This can be done subject to the restriction that the level of inbreeding in the population of animals does not increase any more than a specified amount (e.g., 5% in 20 yr). The results can be expressed in terms of...
discounted genetic gains (Everett, 1975; Van Vleck and Everett, 1976), i.e., income from genetic gain can be discounted for interest and inflation rates and investment time period. In other words, the procedure could allow the determination of the break-even amount of money to be invested in each mating for the purpose of obtaining an animal that is sold as product. Gene flow and survival rates can be taken into account. Product output can be measured in actual production, rather than age- and sex-adjusted product. It will be assumed in this paper that a progeny testing procedure is practiced for the selection of sires.

The details of the function are presented in three parts. Genetic gain per year is first discussed and then income and costs.

**Genetic Gain Per Year.**

\[ AG = \frac{rSD DSD + rDD DDD + rDS DDS + rss DSS + 2P0 rsel Dsel}{LSD + LDD + LDS + LSS + 2(Lsel - Lsamp)Po} \]

where \( \sigma_G \) is the genetic standard deviation of the trait or linear combination of traits for which selection is practiced, \( r \) is the accuracy of genetic evaluation (between 0 and 1.0), D is the selection intensities and \( L \) is the generation intervals (Van Vleck, 1979). The subscripts SD, DD, SS and DS refer to sires of dams, dams of dams, sires of sires and dams of sires, respectively. This formula is not restricted to single trait selection because \( \sigma_G \) can include more than one trait. The need to assume economic weights for each trait in this situation is acknowledged. The \( Po \) is the proportion of the female population reproducing naturally to which sires that have been selected (sel) from the sampled (samp) sires are mated. "Females reproducing naturally" are mothers of only one calf per year (using artificial insemination, possibly sexed semen; or natural service). In other words, these are all the reproducing females in the population excluding recipients (surrogates) and females (DS and DD) from which eggs are collected either via super-ovulation or collection of the entire ovary for in vitro oocyte maturation. The number of cows reproducing naturally is \( N - N_{DD} - N_{DS} - N_{recp} = N^* \). This is assuming that DD and DS are females that are involved with super-ovulation and(or) in vitro maturation of oocytes. Of these \( N^* \) cows, \( (1-Po) \) are mated to sampled sires; of the \( poN^* \) left that are mated to \( N_{otherS} \) sires, \( p_m \) proportion are mated to male sexed semen and \( p_f \) are mated to female sexed semen (\( p_m + p_f = 1.0 \)).
<table>
<thead>
<tr>
<th>Variable</th>
<th>Definition</th>
</tr>
</thead>
<tbody>
<tr>
<td>$p_o$</td>
<td>Proportion of the female population reproducing naturally to which are mated sire that have been selected from the sampled sires. $(1-p_o)$ is the proportion of naturally reproducing female population mated to sample sires.</td>
</tr>
<tr>
<td>$N_{samps}$</td>
<td>Number of sires sampled per year with a progeny test (number of sampled sires).</td>
</tr>
<tr>
<td>$p^m$</td>
<td>Proportion of naturally reproducing females serviced with male sexed semen.</td>
</tr>
<tr>
<td>$NSD$</td>
<td>Average number of lifetime progeny of a sire of a dam.</td>
</tr>
<tr>
<td>$NSS$</td>
<td>Average number of lifetime progeny of a sire of a sire.</td>
</tr>
<tr>
<td>$n$</td>
<td>Average number of progeny with one record each on which is based the evaluation of each sampled sire.</td>
</tr>
<tr>
<td>$ns$</td>
<td>Average number of offspring per year of a sire from naturally reproducing females.</td>
</tr>
<tr>
<td>$nDD$</td>
<td>Average number of progeny of a dam of a dam.</td>
</tr>
<tr>
<td>$nDS$</td>
<td>Average number of progeny of a dam of a sire.</td>
</tr>
<tr>
<td>$f_a$</td>
<td>Probability of an ampule of unsexed semen causing a conception when exposed to an egg in vivo capable of conception, i.e., fertility of unsexed semen.</td>
</tr>
<tr>
<td>$f_n$</td>
<td>Fertility of eggs exposed to semen in vivo.</td>
</tr>
<tr>
<td>$f$</td>
<td>Probability that an embryo handled as a transferred embryo will survive to be born alive.</td>
</tr>
<tr>
<td>$f_b$</td>
<td>Probability of a male calf from male sexed semen.</td>
</tr>
<tr>
<td>$f_b$</td>
<td>Fertility in vitro of male sexed semen.</td>
</tr>
<tr>
<td>$f_e$</td>
<td>Fertility in vitro of eggs exposed to male sexed semen.</td>
</tr>
<tr>
<td>$s$</td>
<td>Number of eggs obtained per year from one cow.</td>
</tr>
<tr>
<td>$b$</td>
<td>Number of eggs a bull can fertilize with male sexed semen in 1 yr.</td>
</tr>
<tr>
<td>$L$</td>
<td>Proportion of the N females replaced per year. $r$ would initially be set at .2 and might remain at about that value, i.e., $r$ would initially be a variable that is listed in table 2.</td>
</tr>
<tr>
<td>$P_c$</td>
<td>Probability of a female calf from female sexed semen.</td>
</tr>
<tr>
<td>$f_c$</td>
<td>Fertility in vitro of female sexed semen.</td>
</tr>
<tr>
<td>$s$</td>
<td>Number of eggs a bull can fertilize with female sexed semen in 1 yr.</td>
</tr>
<tr>
<td>$f_g$</td>
<td>Fertility in vivo of male sexed semen.</td>
</tr>
<tr>
<td>$f_{ge}$</td>
<td>Fertility of eggs exposed to sexed semen in vivo.</td>
</tr>
<tr>
<td>$f_c$</td>
<td>Fertility in vivo of female sexed semen.</td>
</tr>
<tr>
<td>$b^*$</td>
<td>Number of male sexed ampules of semen a bull can produce in 1 yr.</td>
</tr>
<tr>
<td>$c^*$</td>
<td>Number of female sexed ampules of semen a bull can produce in 1 yr.</td>
</tr>
<tr>
<td>$C_1$</td>
<td>Difference between the cost of an artificial insemination service and a natural service.</td>
</tr>
<tr>
<td>$C_2$</td>
<td>Cost of obtaining a mature egg in vitro.</td>
</tr>
<tr>
<td>$C_3$</td>
<td>Cost of obtaining a unit of male sexed semen over and above the cost of a natural service.</td>
</tr>
</tbody>
</table>
TABLE 1. (CONTINUED) LIST OF VARIABLES AND THEIR DEFINITIONS
FOR WHICH NO FIXED VALUE WILL BE ASSumed

<table>
<thead>
<tr>
<th>Variable</th>
<th>Definition</th>
</tr>
</thead>
<tbody>
<tr>
<td>C_4</td>
<td>Cost of one embryo transfer.</td>
</tr>
<tr>
<td>C_5</td>
<td>Cost of obtaining a unit of female sexed semen over and above the cost of a natural service.</td>
</tr>
</tbody>
</table>

Inbreeding increase per year (Falconer, 1981) is approximately:

\[ \Delta F = \frac{N_S + N_D}{8(N_SN_D)} \]

where

\( N_S \) is the number of sires used each year \((N_{otherS} + N_{samps})\) and \( N_D \) is the number of dams used each year \((N - N_{repl})\). It is this function that can be restricted, e.g., .0025 or less.

The selection intensities \((D)\), accuracies \((r)\) and generation intervals \((L)\) for the sires are as follows:

\[
D_{SD} = \frac{\text{selection intensity factor associated with picking } N_{SD} \text{ from } N_{samps}}{n_{SD} (n_{SD} + (4 - h^2) / h^2)}
\]

\[
D_{SS} = \frac{\text{selection intensity factor associated with picking } N_{SS} \text{ from } N_{samps}}{n_{ss} (n_{ss} + (4 - h^2) / h^2)}
\]

\[
D_{sel} = \frac{\text{selection intensity factor associated with picking } N_{otherS} \text{ from } N_{samps}}{t + n_{SD} - n_{ns}}
\]

\[
r_{SD} = \left[ \frac{n_{SS}/(n_{SS} + (4 - h^2) / h^2)}{h^2} \right]^{-1}
\]

\[
r_{sel} = \left[ \frac{n_{SD}/(n_{SD} + (4 - h^2) / h^2)}{h^2} \right]^{-1}
\]

\[
L_{SD} = t + \frac{n_{SD} - n_{ns}}{n_{SD}}
\]

\[
L_{SS} = t + \frac{n_{SS} - n_{ns}}{n_{SS}}
\]

\[
L_{samp} = t + \frac{n_{SD} + n_{SS} - n_{ns}}{2}
\]

TABLE 2. LIST OF VARIABLES AND THEIR DEFINITIONS
FOR WHICH FIXED VALUES WOULD BE ASSumed

<table>
<thead>
<tr>
<th>Variable</th>
<th>Definition</th>
</tr>
</thead>
<tbody>
<tr>
<td>( \sigma_G )</td>
<td>Genetic standard deviation of the trait or linear combination of traits for which selection is practiced.</td>
</tr>
<tr>
<td>( N )</td>
<td>Total number of breeding age females in the population. This could be initially set at something like 500,000.</td>
</tr>
<tr>
<td>( t )</td>
<td>Age at which progeny records become available. This would be set at 2.</td>
</tr>
</tbody>
</table>

Sale price per unit of male product |
Sale price per unit of female product |
Sale price of a culled cow |
Heritability of \( G \)
The selection intensities (D), accuracies (r) and generation intervals (L) for the dams are as follows:

\[ D_{DD} = \frac{N_{DD}}{N_{samD} + N_{otherDm} + N_{otherDf}}; \]
\[ D_{DS} = \frac{N_{DS}}{N_{samD} + N_{otherDm} + N_{otherDf}}; \]
\[ r_{DD} \text{ can be assumed to be based on one individual record and } n_{DD} \text{ progeny with one record each;} \]
\[ r_{DS} \text{ can be assumed to be based on one individual record and } n_{DS} \text{ progeny with one record each;} \]
\[ L_{DD} = t + n_{DD} \text{ and } \]
\[ L_{DS} = t + n_{DS}. \]

These expressions for \( L_{DD} \) and \( L_{DS} \) are assuming that cows selected to be DD and DS are cows that have raised a calf each year.

The numbers of males and females in each category are mostly functions of \( N_{samp} \) and the fertility and survival rates, number of semen amounts obtainable from a sire per year, number of eggs per year obtainable from a cow, success rate of sexing semen, etcetera. The details follow:

\[ N_{samD} = \frac{N_{samp}}{N_{samD} \cdot (f_a) \cdot (f_e) \cdot (0.8) \cdot (0.8)}, \]
where \( f_a \) is the probability of an ampule of unsexed semen causing conception when exposed to an egg capable of conception, \( f_e \) is the probability of a natural egg being capable of conception and the probability of an embryo surviving to a live birth and the live calf making a record is each 0.8.

\[ N_{DS} = \frac{N_{samp}}{[(.5) \cdot (f_b) \cdot (f_e) \cdot (e)]}, \]
where .5 is the probability that a calf born alive will survive to reproductive age and have enough acceptable reproductive capabilities to be further considered as a parent, \( f_b \) is the probability that an embryo handled as a transferred embryo will survive to be born alive, \( p_b \) is the probability of a male calf from male sexed semen, \( f_{se} \) is the probability that a male sexed amount of semen is capable of causing conception in vitro, \( f_e \) is the probability that the egg exposed in vitro to male sexed semen is capable of conception and \( e \) is the average number of eggs obtained per year from one cow.

\[ N_{SS} = \frac{N_{samp}}{[(.5) \cdot (f) \cdot (p_b) \cdot (f_e) \cdot (e)]}, \]
where \( f \) is the number of eggs a bull can fertilize with male sexed semen in 1 yr. The other terms have been defined previously.

\[ N_{recp} = \text{number of recipients needed to get } \frac{N_{samp}}{[(.5) \cdot (f_e) \cdot (p_b)]}. \]

The .5 probability of the three expressions just described (and the .6 of the next three) is set at an arbitrary value because it is related to management and not to success rates of the biotechnologies focused on here.

If \( r \) is the proportion of the \( N \) females that are culled per year, the number of female replacements is \( rN \). From a genetic improvement point of view, \( r \) can be a value from 0 to 1. However, from an industry point of view, \( r \) may need to be fixed at something like .20 because of limited demand for cull beef cows and overhead costs in raising replacement heifers.

\[ N_{DD} = \frac{rN}{[(.6) \cdot (f_c) \cdot (f_e) \cdot (e)]}, \]
where .6 is the probability that a calf born alive reaches puberty and is phenotypically sound enough to be considered as a parent, \( f_c \) is the probability of a female from female sexed semen, \( f_e \) is the probability of a conception with female sexed semen, and \( e \) is the average number of eggs obtained per year from one cow.
semens. The other terms have been defined previously.

\[ N_{\text{recPD}} = \frac{N}{[(.6) (f) (p_c) (c)]}. \]
\[ N_{\text{SD}} = \frac{N}{[(.6) (f) (p_c) (c)]}, \]
where \( c \) is the number of eggs a bull can fertilize with female sexed semen in 1 yr. The other terms have been defined previously.

\[ N_{\text{other}} = \text{maximum of } \frac{p^m N^*}{[f_m f_b b^*]} \text{ and } \frac{p^f N^*}{[f_m f_b f^*]}, \]
where \( f_m \) is the probability that male sexed semen will cause a conception in vivo, \( f_b \) is the probability of a natural egg being capable of conception by sexed semen, \( f^* \) is the probability that female sexed semen will cause a conception in vivo, \( b^* \) is the number of male sexed ampules of semen a bull can produce in a year and \( g^* \) is the number of female sexed ampules of semen a bull can produce in a year. The other terms have been defined previously.

**Income.** The break-even amount invested per calf sold (\( N^* \) of them because the recipients are raising calves to be DS, DD, SD and SS) in the breeding program would be \( \Delta G \times \) the “discounted genetic gains” factor (Everett, 1975; Van Vleck and Everett, 1976) \( \times (p_o \times p^m \times \text{sale price per unit of male product} + p_o \times p^f \times \text{sale price per unit of female product} + (1-p_o) \times \text{average price per unit of male and female product}) + (r-.2)N \times \text{the sale price of cull cows.} \) The .2 is the normal replacement rate for beef cattle females. The sale prices might be adjusted downward to compensate for the additional costs (feed for instance) to produce additional product.

**Costs.** A selection program incurs costs over and above that of a random breeding program in which no genetic change occurs.

The costs involve the same variables that determine \( \Delta G \). The cost per \( N^* \) calf obtained would be the sum of the following nine products divided by \( N^* \). The income minus the costs indicates the economic advantage or disadvantage to selection programs that use reproduction-enhancing biotechnologies.

1) \( N_{\text{amps}} \times n \times b^5 \times C_1; C_1 = \text{difference between the cost of an artificial service and a natural service and } n^5 \text{ is the average number of artificial insemination services needed to get a progeny with a record.} \)

\[ n^5 = \frac{1}{[(f_a)f^1(f^1)(.8)(.8)]}. \]

\[ \times C_2; C_2 = \text{cost of getting an in vitro mature egg.} \]

\[ \times C_3; C_3 = \text{cost per unit of male sexed semen over and above the cost of a natural service.} \]

\[ \times C_4; C_4 = \text{cost of one embryo transfer process.} \]

\[ \times C_2 \]

\[ \times C_5; C_5 = \text{cost per unit of female sexed semen over and above the cost of a natural service.} \]
Example and Description and Discussion of the System Analysis Techniques

This simple example is not based on a simplification of the detailed complex function. However, it does illustrate and describe the experimental procedures that could be used to study the complex function by showing how to determine the break-even investment per mating in switching from a natural, random mating no-record-keeping situation to a natural (no artificial insemination), selective mating situation based on phenotypic records. More importantly, the system analysis techniques are also discussed in general.

In a situation of natural breeding with selection of SS, SD, DD and DS based on the individual record and one record on each of n progeny of a sire and m progeny of a female, ΔG equals o G times the following expression (Van Vleck, 1979).

\[
\text{AG} = \frac{\text{Selection intensity factor associated with } (2/f) + \text{Selection intensity factor associated with } (2(r)/.8)\times\left(\frac{h^2\left(1-(n-1)h^2/4\right)n-(h^2)^2/16}{f\left(1+(n-1)h^2/4\right)n-(h^2)^2/16}\right)^2\times\left(\frac{h^2\left(1-(m-1)h^2/4\right)m-(h^2)^2/16}{f\left(1+(m-1)h^2/4\right)m-(h^2)^2/16}\right)^2+12(n/f+2)+2(m+2)},
\]

where f is maximum number of progeny per sire for 1 yr and is greater than 1 but less than or equal to 20, r is the female replacement rate and h^2 is heritability.

Maximizing this expression over f, n and m constitutes a nonlinear programming problem, since ΔG bears nonlinear relationships with f, n and m. Analytical analysis of this problem reveals that ΔG is increasing in f, implying that f must be increased to as high a value as possible, namely the value 20. Fixing f reduces the problem to the two dimensions n and m. This reduced problem can be subject to direct analysis or numerical analysis when direct analysis fails. Direct analysis constitutes the application of the well-known derivative conditions for a function of two variables (Mangasarian, 1969), namely the conditions that the first-order partial derivatives vanish at the maximum, and that the Hessian comprising the second-order derivatives be negative definite. In other words, we solve the simultaneous equations:

\[
\frac{\partial \Delta G}{\partial m} = 0 \quad \text{and} \quad \frac{\partial \Delta G}{\partial n} = 0
\]

to obtain the solution (m*,n*) and then show that the Hessian matrix

\[
H = \begin{pmatrix}
\frac{\partial^2 \Delta G}{\partial m^2} & \frac{\partial^2 \Delta G}{\partial m \partial n} \\
\frac{\partial^2 \Delta G}{\partial m \partial n} & \frac{\partial^2 \Delta G}{\partial n^2}
\end{pmatrix}
\]

evaluated at (m*,n*) is negative definite. Note that the matrix H is negative definite if for any direction (m,n) relative to (m*,n*), the product

\[(m,n)H(m,n)^T < 0.\]

More precisely H is negative definite if its eigen values are all negative.

Application of the direct analysis reveals that ΔG is minimized when f = 20, m = 1 and n = 20. Then ΔG equals 1.97 kg of weaning weight if h^2 = .25, o G = 13.6 kg and r (the female replacement rate) = .2. Assuming that the survival probabilities of a 2-yr-old heifer to ages 3, 4, 5 and 6 are .82, .68, .52 and .34, respectively; an investment period of 10 yr; and an 8% true discount rate; the number to multiply AG by to account for discounted genetic gains is 2.7681 (Everett, 1975; Van Vleck and Everett, 1976). If the sale price is $1.32 per kg, the amount that can be invested per mating in a record-keeping and genetic evaluation program is 1.97 kg x 2.7681 x $1.32/kg = $7.20. This means that the owners of the cattle will make just as much money in 10 yr investing $7.20 per mating in a genetic selection program as putting $7.20 in the bank at 8% interest for every mating in a random mating breeding program that involves no record-keeping and no genetic selection.

In general, nonlinear functions to be maximized can be sufficiently complex to prohibit direct analysis. However, since the advent of the digital computer in the early 1950s, researchers have devised numerous techniques (Luenberger, 1984) to solve nonlinear programming problems numerically on a computer. The state-of-the-art today is rich in numerical methods and can optimize practical problems involving as many as a hundred
variables within reasonable computational times (Lasdon, 1980). Hence these methods can be applied successfully to more complex functions, such as the one involving the described, biotechnology-driven ΔG with its associated success rates and costs. Moreover, it is possible to measure how sensitive the genetic and economic returns are to various success rates for the biotechnologies of super-ovulation, embryo transfer, sexing of semen, in vitro maturation of oocytes and in vitro fertilization. In other words, it is possible to address the question: will low success rates have an impact or do the success rates have to be medium or high, and is effort to further the success rates justified from genetic and economic points of view?

To illustrate a numerical method to solve a nonlinear programming problem, consider figure 2, which displays the contours of a function of two variables. Our objective is to find , the value at which the function is maximized, starting from . Application of the numerical method results in moving along a zig-zag path from to . The direction taken at is the direction of steepest ascent at . This direction may be computed from the partial derivatives of the function at obtained analytically or numerically with the computer. Then a line search algorithm determines , which is the value at which the function is maximized when moving in the steepest ascent direction. Then at , a new steepest ascent direction is computed and the line search algorithm gives . This procedure is continued until is found.

In practice, the numerical method to be deployed depends on the nature of the function to be maximized. But empirical verification is usually necessary to ascertain the efficiency of the method. Other factors affecting the selection of a method are the constraints involved such as inbreeding levels and farm animal population requirements, and the mathematical nature of these constraints.

These techniques can be used to address the issue of local maximums (modes) by using different starting points. If more than one maximum is found, they can each be studied as to their contours. The maximum associated with the maximum genetic and(or) economic return may not be the most desirable because of its sensitivity to success rates. A maximum that does not require such specific values for success rates may be more practical.

**Appendix**

Derivation of genetic gain per year (ΔG):

Following Van Vleck (1979), let be the genetic value of the replacement progeny. The genetic value of the dams of the replacement progeny with genetic value is:

\[ \frac{1}{2} (P - L_{SD} \Delta G + \Delta SD + P - L_{DD} \Delta G + \Delta DD). \]

The genetic value of the sampled sires that were sires of the replacement progeny with genetic value is:

\[ \frac{1}{2} (P - L_{SS} \Delta G + \Delta SS + P - L_{DS} \Delta G + \Delta DS). \]

The genetic value of the other sires that were sires of the replacement progeny with genetic value is the genetic value of the sampled sires when the selected sires were just sampled sires plus the genetic superiority of the selected sires relative to the sampled sires. This is:

\[ \{P - L_{SS} \Delta G + \Delta SS - (L_{sel} - L_{samp}) \Delta G \]
\[ + P - L_{DS} \Delta G + \Delta DS - (L_{sel} - L_{samp}) \Delta G} / 2 + \Delta sel. \]

Since the sampled sires and the selected sires are used in proportions \((1 - p_o)\) and \(p_o\), respectively,

\[ P = .5 \left\{ \frac{1}{2} (P - L_{SD} \Delta G + \Delta SD + P - L_{DD} \Delta G + \Delta DD) \right\} \]
\[ + .5 \left\{ (1 - p_o) \cdot \frac{1}{2} (P - L_{SS} \Delta G + \Delta SS + P - L_{DS} \Delta G + \Delta DS) \right\} \]
\[ + p_o \left\{ P - L_{SS} \Delta G + \Delta SS - (L_{sel} - L_{samp}) \Delta G \right\} / 2 + \Delta sel \}

The \((L_{sel} - L_{samp})\) is just the number of years older, on the average, the selected sires are than the sampled sires.

Solving for \(\Delta G\) and substitution of the respective \(r\) and \(D\) for \(\Delta D\), \(\Delta DD\), \(\Delta SS\), \(\Delta DS\) and \(\Delta sel\) (all of which are multiplied by \(\sigma G\)) results in the expression for \(\Delta G\) given in the paper.

**Literature Cited**


