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A comparison of Bonus and Quota mating systems for utilising the sex-determining region Y gene in terminal sire beef cattle breeding

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Abstract The use of the sex-determining region Y gene in terminal sire beef cattle breeding was investigated, assuming that fertile transgenic bulls carrying this gene on an autosome can be created. The benefit of these transgenic bulls arises from having an increased proportion of calves with a male phenotype. Two mating strategies utilising the transgenic bulls were devised and compared; the Quota scheme whereby a quota of normal bulls is used alongside the transgenic bulls in a breeding nucleus, and the Bonus scheme in which a phenotypic bonus is assigned to transgenic bulls indicating the added value of their offspring. Bonus and Quota breeding schemes were comparable, in terms of the value of offspring of the bulls, for the first 6 years of selection, after which time the Quota breeding scheme was superior. For time horizons less than 10 years, and large assumed phenotypic superiorities of male calves, breeding schemes with transgenic bulls were superior to traditional breeding schemes without transgenic bulls. If the time horizon was longer, or if the assumed superiority of male calves was small, then traditional breeding schemes were generally superior to those utilising transgenic bulls. Scenarios were observed, however, where transgenic bulls were always superior to normal bulls, in terms of their value as sires. Equations were derived to predict genetic gain and the equilibrium genetic lag between normal and transgenic bulls in Quota breeding schemes.

Key words Beef cattle · Sex ratio · Selection
Sex-determining region Y gene · Transgenic animals

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Introduction

The sex-determining region Y (SRY) gene controls the presence of testes (i.e. maleness) in mammals. This has been demonstrated by Koopman et al. (1991) who developed XX mice carrying the SRY transgene on an autosome. These mice were phenotypically male, although they were infertile. However, a fertile XY male with a copy of the SRY gene on an autosome should, theoretically, produce a greater proportion of offspring which are phenotypically male. This would be advantageous, for example, in breeding terminal beef sires, where male calves are more valuable than females calves on commercial farms. The possible use of beef cattle transgenic for the SRY gene was investigated by Bishop and Woolliams (1991) who found that there were small genetic advantages in breeding schemes using these bulls compared to traditional breeding schemes, although there may be practical problems in running such schemes. Their findings pertained to a restricted mating strategy (the "quota" system) and a restricted time horizon (15 years), however.

This paper investigates the possible application of the SRY gene considering different mating strategies and a flexible time horizon. It also derives a theoretical framework describing genetic progress in breeding schemes utilising the SRY gene.

Materials and methods

Genetic model

It is assumed that fertile transgenic bulls can be produced with the genotype [XY; AoAm], where Ao is a normal autosome and Am is an autosome with a segregating insert containing one or more copies of the SRY gene. When mated to a cow, there will be four potential genotypes amongst the calves, all occurring with equal frequency, i.e. [XY; AoAm], [XY; AoAo], [XX; AoAm] and [XX; AoAo], designated as super male, normal male, pseudo male and female, respectively. In other words, there will be three male phenotypes to every female. The super male has only a 0.25 chance of propagating its own genotype, compared to a 0.5 chance with the normal male, and the super males also sire normal males. This has two consequences (Bishop and Woolliams 1991). Firstly, greater selection pressure can be applied and faster genetic progress achieved with normal males than with super males. Secondly, as a result of this first observation, if selection ignores the distinction between normal and super males, super males will become extinct after several generations.

Two mating strategies were investigated for operating a terminal sire beef breeding scheme that utilises bulls transgeneic for the SRY gene, taking account of the reproductive properties of normal and super males. In the first, a quota of normal bulls to be used along with transgenic bulls was defined, where the proportion of normal males used was Q. The second strategy, the "bonus" system, involved assigning super males a phenotypic bonus (b) representing their superiority as terminal sires and then selecting bulls on their phenotype for the production trait of interest regardless of whether the bull is a super male or a normal male. In both strategies pseudo males were assumed to be infertile, in line with the experimental findings of Koopman et al. (1991) in which the transgenic mice were essentially pseudo males.

Quota breeding scheme

Genetic progress in a Quota breeding scheme was simulated by Bishop and Woolliams (1991), with the general results that (1) inclusion of super males always reduces genetics progress in the breeding scheme itself and (2) there is always a genetic lag between normal and super males in the breeding scheme, which stabilises after several generations of selection. This genetic lag and the rate of genetic gain can be estimated after observing that the expected proportion of animals born in each sire to son combination are: normal males from normal males, $0.5Q$; normal males from super males, $0.25(1-Q)$; super males from super males, $0.25(1-Q)$.

Genetic Lag (δ)

Assume that the trait under selection is normally distributed and has a phenotypic standard deviation of 1.0. Let f(X) be the normal distribution probability density function, $F(X)$ be the integral of $f(X)$ from X to infinity, and $i(X)$ be the standardised selection intensity from the Normal distribution when truncation is at X, i.e. $f(X)/F(X)$. Then:

$$\delta = 0.5h^2[i(\text{normal male sires}) - i(\text{super male sires})]$$

$$= 0.5h^2\left[\frac{0.5Qi(N) + 0.25(1-Q)i(S))}{0.5Q + 0.25(1-Q)} - i(S)\right]$$

$$= \frac{Qh^2[i(N) - i(\text{S})]}{(1+Q)} \tag{1}$$

where N and S are truncation points defining selection intensities for normal and super males, defined relative to the super male mean.

Now, normal male sires are chosen from both a pool of animals sired by both normal and super males, and the normal male selection intensity must take account of these two distributions, i.e:

$$\text{i}(N) = k(i(NN) + \delta) + (1-k)i(NS) \tag{2}$$

where NN and NS are truncation points in the distributions of normal and super males such that $NS = NN + \delta$. Substituting Eq. 2 into Eq. 1 and rearranging gives:

$$\delta = \frac{Qh^2[k\,i(NN) + (1-k)i(NS) - i(S)]}{1 + Q(1-kh^2)} \tag{3}$$

Let p be defined as the selection proportion when $Q = 1$, then the selection proportions for any value of Q for super males are $\text{F}(S) = 2p$ and for normal males are $F(NN) + F(NS) = 2pQ/(1+Q)$. Therefore:

$$k = \frac{(1+Q)F(NN)}{2pQ} \quad \text{and}$$

$$(1-k) = \frac{(1+Q)F(NS)}{2pQ}$$

Substituting k and $(1-k)$ into Eq. 3, using the relationships outlined above between $f(X)$, $F(X)$ and $i(X)$, and rearranging gives:

$$\delta = \frac{h^2[f(NN) + f(NN+\delta) - 2pQi(S)/(1+Q)]}{2p - F(NN)h^2} \tag{4}$$

This equation can be solved iteratively for any value of p, Q and h^2, using the relationship that $F(NN) + F(NN+\delta) = 2pQ/(1+Q)$, using a polynomial approximation to calculate the $F(NN)$ values. This equation ignores the reduction in genetic variation due to selection that affects both the heritability and the phenotypic standard deviation. These effects are predictable given the selection intensities, however, and should be used to rescale δ each iteration when solving the equation.

Genetic Gain (ΔG)

Let L(sire) and L(dam) be the male and female generation intervals, then genetic gain may be defined as follows:

$$\Delta G = \frac{h^2[i(\text{sire}) + i(\text{dam})]}{L(\text{sire}) + L(\text{dam})}$$

Let N and F be truncation points for selection of normal males and females, relative to the normal male mean, and let S be defined as above. Therefore:

$$\Delta G = \frac{h^2\left[\frac{(0.5Qi(N) + 0.25(1-Q)(i(S) - \delta)}{0.5Q + 0.25(1-Q)} + i(F)\right]}{L(\text{sire}) + L(\text{dam})}$$

$$= \frac{h^2[(2Qi(N) + (1-Q)(i(\text{S}) - \delta) + (1-Q)i(F)]}{(1+Q)(L(\text{sire}) + L(\text{dam}))} \tag{5}$$

Now $i(N) = k\,i(NN) + (1-k)(i(NN+\delta) - \delta)$ and k is defined above. Substituting and rearranging:

$$\Delta G = \frac{h^2\left[\frac{f(NN) + f(NN+\delta)}{p} + \frac{(1-Q)i(S)}{(1+Q)} - \delta\left\{\frac{F(NN+\delta)}{p} + \frac{(1-Q)}{(1+Q)}\right\} + i(F)\right]}{(L(\text{sire}) + L(\text{dam}))} \tag{6}$$

Equation (5) is computationally easier, especially when calculating genetic gain in small populations, however Eq. 6 shows more clearly the genetic gain from different sources. Equations (5) and (6) can be solved using polynomial approximations to the F and i values, accounting for small sample size effects for normal males when Q is small and for super males when Q is large. As with equation (4) empirical corrections to take account of the reduction in genetic variation with selection should be done when estimating genetic gain.

Bonus breeding scheme

If a bonus breeding scheme is to be considered, the phenotypic bonus to be applied to super males should reflect the added value from using the super male as a terminal sire. Let the difference in performance between male and female calves from the terminal sires be d. Super males are expected to sire male to female calves in the proportions 0.75:0.25, compared to 0.5:0.5 for normal males, giving super males of the same genetic merit an advantage of 0.25*d*. Truncation points *S* and *N* for selection should be set such that the value of the super male sires of phenotype *S* is the same as the value of normal male sires of phenotype *N*, and by definition the bonus (b) = N–S. Let the super male mean be S_ave, the normal male mean be N_ave and $\delta = N\_ave - S\_ave$, then b can be derived by observing that:

$$0.5(N\_ave + h^2(N - N\_ave)) = 0.5(S\_ave + h^2(S - S\_ave)) + 0.25d$$

$$= 0.5(N\_ave - \delta + h^2(N - b - N\_ave + \delta)) + 0.25d$$

$$\text{Therefore: } b = \frac{0.5d - \delta(1 - h^2)}{h^2}$$

It is important to note that b changes from year to year as δ changes.

Comparison of breeding schemes

The two mating strategies were compared in a simulated breeding scheme, with two comparison criteria being used. The first was the average expected performance of commercial progeny of all bulls from the breeding scheme, where this average includes the difference in performance between female and male phenotypes, and the second was the value of super males from the two types of breeding schemes. The results discussed in this paper descirbe a simulated breeding scheme with a population size of 1000 cows, a heritability for the trait under selection of 0.5 and mass selection with the selection proportion being 0.10. For the quota system, simulations were undertaken for Q values of 0, 0.1, 0.2, up to 1.0. This simulation scheme is described in more detail in Bishop and Woolliams (1991). The results were then intepreted for values of d of 0, 0.5, 1.0 and 2.0 standard deviation units. The bonus system was simulated with bonuses pertaining to the same d values starting at $Q = 0$, adjusting b as δ changed. All mating strategies were simulated 50 times. Comparisons between the two strategies were made for time horizons of 5, 10 and 15 years.

Results and discussion

Simulated quota scheme

For the simulated quota system, the optimal Q value varied according to the time horizon considered and the actual difference in performance between male and female calves (d). Q values which maximise the value of bulls as terminal sires for selection schemes with different time horizons and for different performances advantages of males over female calves are shown in Table 1. When the average value of all males from the breeding scheme is the evaluation criterion, only for scenarios when the time horizon is short and d is large are breeding schemes utilising super males beneficial. If the difference between male and female progeny is small or of the time horizon is large, i.e. more than 10 years, the breeding schemes with transgenic bulls can not compete with traditional breeding schemes.

When the average value of super males from the breeding schemes is the evaluation criterion, then the Q value has little effect for the first 4 years (two male generations) after which an optimum Q of between 0.8 and 0.9 is attained for all values of d (Table 1). For the time horizons considered it was observed that for values of d which were greater than 0.75 and Q equal to 0.8, then super males were always more valuable as terminal sires than males from a traditional breeding scheme, i.e. a breeding scheme with $Q = 1$, despite the fact that they were genetically inferior for the trait under selection. This superiority depends on d and can be equated to the number of years of selection, e.g. approximately 1, 2 and 4 years for $d = 0.8$, 1 and 2, respectively.

Simulated bonus scheme

Simulated selection under the "bonus" scheme resulted in a continual change in the observed Q values (Fig. 1), the cow age structure in the breeding herd (because the number of female calves born is a function of Q) and the actual bonus itself. When the parameters given above are used, Q approached an equilibrium of 1.0 for all d values less than 0.9. This process happened very quickly for small d values.

The effect of selection on bonus values (b) is tabulated in Table 2. For scenarios where the difference in performance between male and female calves was small, b tended to zero after several generations, reflecting the fact that super males eventually became extinct in these schemes. For schemes with intermediate d values, those where Q approached an intermediate equilibrium, b decreased over time to an equilibrium value, e.g. to approximately 0.9 for $d = 1.0$. For schemes with large d values, e.g. $d = 2.0$, the bonus did not change because nearly all the selected males are super males and, hence, no genetic lag built up between normal and super males.

A comparison of optimal simulated quota and bonus breeding schemes is shown in Table 3, along with the Q values that optimised the quota scheme. The bonus

Table 1 Optimal Q values in a Quota breeding scheme for criteria of (1) average value of all males and (2) average value of super males as terminal sires. Values in bold indicate that value as terminal sire is greater than for selection schemes with no super males, i.e. $Q = 1$

d^a	Time Horizon (years)					
	5		10		15	
	All Males	Super Males	All Males	Super Males	All Males	Super Males
0.0	1.0	0.8	1.0	0.9	1.0	0.8
0.5	**0.6**	**0.8**	1.0	**0.9**	1.0	**0.8**
1.0	**0.3**	**0.8**	1.0	**0.9**	1.0	**0.8**
2.0	**0.0**	**0.8**	**0.4**	**0.9**	1.0	**0.8**

[a] d = male-female difference, in standard deviations

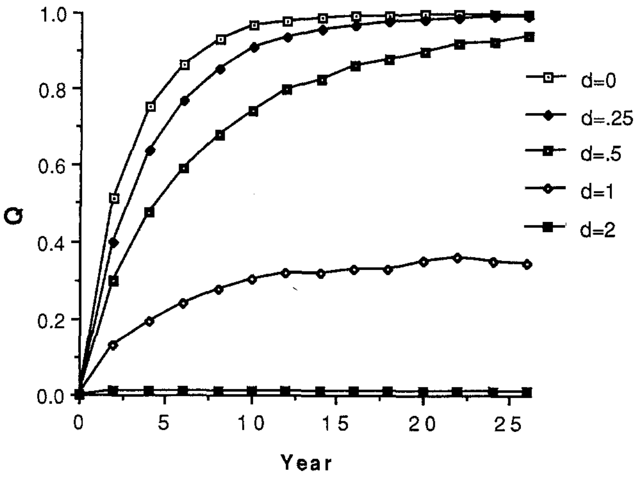

Fig. 1 Observed Q values from optimised bonus scheme

Table 2 Observed bonus values[a] in simulated Bonus breeding scheme

Year	d[a]				
	0.25	0.5	0.8	1.0	2.0
0	0.25	0.50	0.80	1.00	2.00
5	0.19	0.43	0.73	0.94	2.00
10	0.16	0.41	0.72	0.92	2.00
15	0.07	0.38	0.68	0.91	1.99
20	0.07	0.31	0.65	0.89	1.99
25	0.02	0.18	0.64	0.91	1.99

[a] Bonus $(b) = (0.5d - \delta(1 - h^2))/h^2$
[b] d = male-female performance difference (SD units)

system was approximately equal to the optimal quota system for the first two generations of male selection, i.e. until year 6, but thereafter fell behind the optimal quota scheme both in terms of the average value of super males and the average value of all males. This outcome occurs because the bonus scheme picks bulls to optimise the value of terminal sire offspring, accounting for the difference between males and females and also accounting for the different reproductive characteristics of normal and super males. However, by doing this it foregoes immediate genetic progress in the actual nucleus itself with the consequence that in the longer term animals from the bonus scheme are inferior to animals from a quota scheme.

Evaluation of prediction equations

Genetic lag (δ) between super and normal males, predicted from the equation accounting for the loss in genetic variation as a result of selection, is compared to simulation results in Table 4. There is close agreement between the two estimates of δ, except for large Q values where the theoretical δ values were less than the simulated values. It should be realised that the theoretical values are not exact insofar as polynomial approximations of the F values were used rather than tabulated values for computational ease, and for large Q values the super male cohorts in the simulation were very small resulting in reduced selection differentials. In Table 5, δ values are shown for different Q values, selection intensities and heritability values. As Q increases, δ always increases, approximately doubling between $Q = 0.2$ and 0.8. Heritability also has a large effect on δ, with the changes in δ being almost proportional to the changes in heritability. Conversely, selection intensity has a relatively small effect on δ, with δ being slightly smaller at high selection intensities.

Table 4 Comparison of expected and simulated genetic lag between normal and super males in a Quota breeding scheme[a]

	Q						
	0.1	0.2	0.5	0.8	0.9	0.95	0.98
Expected lag	0.05	0.08	0.12	0.16	0.17	0.18	0.24
Simulated lag	0.05	0.09	0.12	0.16	0.20	0.23	0.34
±SE	±0.01	±0.01	±0.01	±0.01	±0.03	±0.03	±0.06

[a] Hertability = 0.5 and selection proportion is equivalent to 0.1

Table 3 Value of males from Bonus and optimal Quota breeding strategies as terminal sires[a]

Year	d								
	0.5			1.0			2.0		
	Bonus scheme	Quota scheme	Q[b]	Bonus scheme	Quota scheme	Q	Bonus scheme	Quota scheme	Q
1	0.06	0.06	0	0.13	0.12	0	0.25	0.25	0
2	0.07	0.06	0	0.13	0.12	0	0.25	0.25	0
3	0.26	0.25	0.2	0.31	0.30	0.1	0.43	0.42	0
4	0.26	0.25	0.3	0.31	0.30	0.2	0.43	0.42	0
5	0.37	0.37	0.6	0.41	0.40	0.2	0.52	0.52	0
6	0.39	0.40	0.6	0.43	0.43	0.3	0.55	0.54	0.1
7	0.50	0.52	0.8	0.51	0.53	0.8	0.61	0.61	0.1
8	0.55	0.58	1	0.56	0.59	0.8	0.64	0.65	0.3
9	0.65	0.68	1	0.63	0.69	0.8	0.71	0.74	0.4
10	0.71	0.76	1	0.69	0.76	1	0.74	0.79	0.4

[a] Expressed in SD units
[b] Q value required to optimise Quota strategy given the time horizon and d value

Table 5 Expected genetic lag[a] between normal and super males in a Quota breeding scheme

p^b:	0.05		0.10		0.20	
h^2:	0.3	0.5	0.3	0.5	0.3	0.5
0.2	0.05	0.07	0.05	0.08	0.06	0.10
Q: 0.5	0.08	0.12	0.08	0.12	0.10	0.15
0.8	0.09	0.15	0.10	0.16	0.12	0.19

[a] Lag expressed in standard deviation units

[b] p = proportion of bulls selected if Q were to be 1.0

Table 6 Genetic gain (ΔG)[a] and relative contributions of normal males, super males and females[b]

Q	*Simulated* ΔG	*Expected* ΔG	Relative contributions from:		
			Normal Males	Super Males	Females
0.0	0.10	0.10	–	91.7	8.3
0.2	0.12	0.13	41.7	48.6	9.6
0.5	0.14	0.14	67.2	22.1	10.7
0.8	0.16	0.17	79.6	7.0	13.3
1.0	0.17	0.18	81.9	–	18.1

[a] Calculated for heritability = 0.5 and P = 0.1; units are SD/year

[b] Contribution expressed as proportions × 100, estimated from Eq. 5

A comparison of simulated and expected genetic gains for the Quota breeding scheme, calculated using Eq. 5 and accounting for the loss in genetic variation as a result of selection, are shown in Table 6. There is close agreement simulated and expected rates of genetic gain. The proportions of genetic gain contributed by selection on normal males, super males and females are also tabulated. For the example shown, most of the genetic gain is achieved through selection on normal males, unless Q is very small. This result is true, regardless of the selection intensity or heritability evaluated. The importance of female selection increases as Q increases, however this is simply a consequence of more females being available for selection as Q increases. Inspection of Eq. 6 indicates that genetic gain is affected negatively by δ, however when the equations were numerically solved this effect was found to be trivial.

General

The results show that breeding schemes utilising bulls transgenic for the SRY gene may be superior, in the short term, to traditional breeding schemes provided that male calves on commercial farms are superior to female calves. If d is sufficiently large, e.g. greater than 1 SD, and the breeding scheme is evaluated only by the value of the super males it produces, then breeding schemes utilising the SRY gene may be superior to traditional breeding schemes for time horizons in excess of 15 years, although the benefits will be small. For very short time horizons, e.g. up to 6 years, a bonus breeding strategy is an effective means of maximising the value of bulls as terminal sires; however for longer time horizons a more structured breeding system must be considered in order to balance the immediate value of selected bulls against potential genetic progress within the nucleus. The quota system investigated here fulfilled this criterion, however other methods could also be devised.

The equation presented for predicting genetic gain and δ for the quota system give an accurate description of the selection process, and they can easily be adapted to a wide variety of scenarios. As discussed by Bishop and Woolliams (1991), an obvious example is where multiple ovulation and embryo transfer (MOET) are used in conjunction with embryo sexing to attempt to obtain optimal proportions of super male and female calves. Given that half of the embryos (pseudo and normal males) from super male sires will be undesirable under these circumstances and should ideally be discarded, this objective is unlikely to be realised. Therefore, likely selection differentials for females, super and normal males should be calculated and substitued into these equations and compared to optimum MOET schemes in the absence of super males.

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