

Maximum herd efficiency in meat production

III. Feeder–breeder dimorphism

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Feeder–breeder dimorphism is advantageous when large offspring for slaughter is obtained from small breeding animals. The effect of feeder–breeder dimorphism on herd efficiency is evaluated for terminal crossbreeding and growth modification by biotechnological or dietary means. Selection criteria for breeds or lines in terminal crossbreeding can be derived from economic weights relating to herd efficiency, i.e. from the value of the percentage relative gain in herd efficiency for a given percentage relative gain in a component.

Slagdier–teeldier-dimorfisme is voordelig wanneer groot nageslag vir verslagting verkry word vanaf kleiner teeldiere. Die effek van slagdier–teeldier-dimorfisme op kuddedoeltreffendheid is geëvalueer vir terminale kruisteelt en vir groeimanipulasie by wyse van biotegnologie of dieetmodifikasie. Seleksiekriteria vir rasse en lyne in terminale kruisteelt kan afgelei word van ekonomiese gewigte wat op verwantskappe met kuddedoeltreffendheid berus, oftewel van die waarde van die persentasie relatiewe toename in kuddedoeltreffendheid vir 'n gegewe persentasie relatiewe toename in 'n komponent.

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Introduction

Over the same maturity interval, feed efficiency and body size are genetically uncorrelated (Taylor, 1987). This means that, to a first approximation, cumulate growth feed efficiency at mature mass can be assumed constant. This approximation together with the expression for herd efficiency derived in Roux (1992a), can be used to quantify the advantage of feeder–breeder dimorphism when large offspring for slaughter is obtained from small breeding animals. This advantage follows since any system with large feeders from small breeders must be more efficient than one with feeders and breeders of equivalent size, simply because small dams eat less than large ones.

A comparison, later on in this paper, to other studies gives good agreement between predictions under the assumption of constant cumulate growth efficiency at maturity, and comparable results taken from the literature, for situations where such an assumption does not feature in the experimental or simulation procedure at all. However, if circumstances should exist where the assumption of constant cumulate efficiencies at maturity is inapplicable, a correction for changes in growth efficiency is possible from equations (13b) or (13c) in Roux (1992b).

Terminal crossbreeding

An easy way of obtaining feeder–breeder dimorphism is by terminal crossbreeding, when a large sire breed or line is used on a small dam breed or line and all terminally crossbred offspring are sold for slaughter. If a system is considered where the breeding population size is kept constant, it means that male members of the breeder type will also be sold for slaughter, unless sex-control of offspring is possible. Let $e_h(\text{br})$ be the herd efficiency of the breeder population, and $e_h(\text{fe})$ the herd efficiency of the feeder (terminally crossbred) offspring from the breeder herd. Let a proportion $(1 - q)$ of the

offspring sold be of the breeder type and a proportion q of the feeder type. Then the ratio of the herd efficiency of the terminal crossbred system $e_h(\text{sys})$, to that of the breeder population $e_h(\text{br})$ is:

$$\begin{aligned} e_h(\text{sys})/e_h(\text{br}) &= (1 - q)e_h(\text{br})/e_h(\text{br}) + qe_h(\text{fe})/e_h(\text{br}) \\ &= (1 - q) + qe_h(\text{fe})/e_h(\text{br}). \end{aligned} \quad (18)$$

Then, under the assumptions of (i) negligible differences due to b; (ii) equal cumulate growth efficiencies at maturity and (iii) equal values of Q since both feeders and breeders have similar dams, it follows from (6b) in Roux (1992a) and (18), for $\Delta e_h(\text{sys}) = e_h(\text{sys}) - e_h(\text{br})$, that:

$$\Delta e_h(\text{sys})/e_h(\text{br}) = q[\alpha_m(\text{fe})/\alpha_m(\text{br})]^{1-b} - q, \quad (19a)$$

where $\alpha_m(\text{fe})$ and $\alpha_m(\text{br})$ are body masses of feeders and breeders at corresponding degrees of maturity. Let P_d be the proportion of the female herd mated to sires from the dam line/breed and P_s be the proportion of the female herd mated to sires from the sire line/breed, $P_d + P_s = 1$. Then:

$$q = P_s/(P_s + P_d/2), \quad (19b)$$

since only male offspring from the dam line/breed are assumed sold.

The minimum value of P_d for replacement proposes is given by:

$$P_d = 2R/r, \quad (19c)$$

on the assumption of a sex ratio of unity.

Substituting (19c) into (19b) gives:

$$q = (r - 2R)/(r - R). \quad (19d)$$

Comparison to other studies

For a value of $q = 0,85$ and $\alpha_m(\text{fe})/\alpha_m(\text{br}) = 1,4$, Taylor *et al.* (1985) predicted a value for $\Delta e_h(\text{sys})/e_h(\text{br})\%$ between 11 and 13%. For $b = 0,5 - 0,6$ from Roux & Meissner

(1984), equation (19a) predicts 12—16%, under the same assumptions, in reasonable agreement to Taylor *et al.* (1985).

Notter *et al.* (1979) appear to have assumed an average of 50% terminally crossbred matings, implying a value of $q = 2/3$, under the assumption that all non-terminally bred females are used for replacements. Hence, with 2,5% heterosis, a value of $\alpha_m(\text{fe})/\alpha_m(\text{br}) = 1,025 (800 + 500)/2 \times 500 = 1,33$, in equation (19a) predicts:

$$\Delta e_h(\text{sys})/e_h(\text{br})\% = 8—10\%,$$

in reasonable agreement to the 6—11% (9—14% minus 3% due to heterosis for weaning rate) improvement by terminal crossbreeding predicted by Notter *et al.* (1979).

Direct experimental evidence on the advantage of feeder-breeder dimorphism is available for sheep (Large, 1970), and is summarized in Table 1. Suffolk rams were used on different sized ewes, including Scottish Halfbred and Devon Longwool ewes of equal average body mass, referred to as Controls in Table 1, and Kerry Hill as well as Welsh Mountain ewes.

The observed efficiencies were calculated as weighted averages from the efficiencies of singles, twins and triplets given by Large (1970). It is evident from Table 1 that large rams \times small ewes form a more efficient system than large rams \times large ewes, where Large (1970) defined efficiency as (mean carcass mass of a lamb \times number of lambs \times 100)/(food eaten by the ewe + food eaten by the lambs), which corresponds to the basic idea behind equation (19a), except that replacement rate is ignored.

The reproductive efficiency of the Control ewes mated to Suffolk rams, $e_r(\text{Control})$, is from (6):

$$e_r(\text{Control}) = \alpha_m(S \times C)/Q(C).$$

Likewise, the reproductive efficiency of the Welsh ewes is:

$$e_r(\text{Welsh}) = \alpha_m(S \times W)/Q(W),$$

where C = Control, W = Welsh and S = Suffolk. Assume that:

$$\alpha_m(W)/Q(W) = \alpha_m(C)/Q(C) \quad (20)$$

or

$$Q(C)/Q(W) = \alpha_m(C)/\alpha_m(W)$$

i.e. that the reproduction efficiencies in the corresponding purebred systems are invariant with body size. Furthermore, assume that lamb carcass masses are proportional to the limit masses, i.e. that:

$$\alpha(S \times W)/\alpha(S \times C) = 14,9/20,1 = 0,74,$$

from Table 1.

From (20), and analogous to the derivation of (19a), it

follows for the total efficiencies of the crossbred systems that:

$$\begin{aligned} \Delta e_h &= e_h(\text{Welsh})/e_h(\text{Control}) - 1 \\ &= [\alpha_m(S \times W)Q(C)/\alpha_m(S \times C)Q(W)]^{1-b} - 1 \\ &= [\alpha_m(S \times W)\alpha_m(C)/\alpha_m(S \times C)\alpha_m(W)]^{1-b} - 1 \quad (21) \\ &= (0,74 \times 78,6 / 33,4)^{0,45} - 1 \\ &= 0,28. \end{aligned}$$

Likewise,

$$\begin{aligned} \Delta e_h &= e_h(\text{Kerry})/e_h(\text{Control}) - 1 \\ &= [(20,7 / 20,1) \times (78,6 / 57,6)]^{0,45} - 1 \\ &= 0,17. \end{aligned}$$

From the standard errors in Table 1 it is clear that the observed gains in herd efficiencies agree well with the efficiencies predicted by this method.

Useful approximations

It follows from (19a) that a 20% increase in the $\alpha_m(\text{fe})/\alpha_m(\text{br})$ ratio will result in an approximate improvement in the ratio $e_h(\text{sys})/e_h(\text{br})$ of:

$$20(1 - b)q\%. \quad (22)$$

Let $\alpha_m(\text{sl})$ and $\alpha_m(\text{dl})$ be corresponding sire and dam line limit masses. Then, with complete favourable dominance:

$$\alpha_m(\text{fe})/\alpha_m(\text{br}) = \alpha_m(\text{sl})/\alpha_m(\text{dl}), \quad (23)$$

and with complete additivity:

$$\alpha_m(\text{fe})/\alpha_m(\text{br}) = [(1 + \alpha_m(\text{sl})/\alpha_m(\text{dl}))]/2. \quad (24)$$

Thus, under complete favourable dominance an increase of 20% in sire/dam line limit mass will result in:

$$\Delta e_h(\text{sys})/e_h(\text{br}) = 20(1 - b)q\%. \quad (25a)$$

Under complete additivity, a 20% increase in sire/dam line limit mass will result in:

$$\Delta e_h(\text{sys})/e_h(\text{br}) = 10(1 - b)q\%, \quad (25b)$$

due to division by 2 on the right-hand side of (24).

The percentage gain in herd efficiency from terminal crossbreeding with favourable complete dominance or complete additive gene action is given in Tables 2 & 3, respectively. These Tables were constructed from equations (23), (24) and (19a) with values of $b = 0,55$ for cattle and sheep and $b = 0,72$ for pigs from Meissner *et al.* (1975), Roux & Meissner (1984) and Siebrits *et al.* (1986). The values of q in (19a) were calculated from (19b) by assuming that only enough purebred females are produced for replacements necessary to keep herd size constant (19c). Thus, with 1/2 of the herd crossbred, $q = 2/3$.

Table 1 The percentage relative gains in herd efficiency with terminal crossbreeding of large (Suffolk) rams to small ewes

Breed of ewe	n	Ewe body mass (kg)	Lamb carcass mass (kg)	Efficiency	Efficiency gains (%)	Predicted gains (%)
Control	46	78,6	20,1	6,29 \pm 0,09	—	—
Kerry	21	57,6	20,7	7,24 \pm 0,19	15 \pm 3,3	17
Welsh	20	33,4	14,9	8,03 \pm 0,19	28 \pm 3,4	28

Table 2 The percentage gain in herd efficiency from terminal crossbreeding with favourable complete dominance

% of herd Crossbred	Sire / dam line body mass			
	1,2	1,6	2,0	3,0
50 (Cattle)	6	16	25	43
67 (Cattle or sheep)	7	19	29	51
75 (Sheep)	7	20	31	55
95 (Pigs)	5	14	21	35

Table 3 The percentage gain in herd efficiency from terminal crossbreeding with complete additive gene action

% of herd Crossbred	Sire / dam line body mass			
	1,2	1,6	2,0	3,0
50 (Cattle)	3	8	13	25
67 (Cattle or sheep)	4	10	16	29
75 (Sheep)	4	11	17	31
95 (Pigs)	3	7	12	21

The replacement and reproduction rates of the different species that will allow the percentages of crossbreeding in Tables 2 & 3, are as given by Large (1976), with the exception of 67% crossbreeding in cattle, which follows from herd statistics of the Nguni herd of the Animal and Dairy Science Research Institute.

The importance of finding crosses with a favourable mode of inheritance and a large difference in mature body mass is obvious from Tables 2 & 3 and a comparison between them.

Sexual dimorphism

To a similar level of carcass finish, the feed conversion rates of steers and heifers are approximately equal (Lowman, 1987). This suggests that the advantage of sexual dimorphism against monomorphism can also be evaluated by (19), where q is the proportion of male surplus reproduction. Hence, $q > 1/2$, since some of the female offspring need to be kept for reproduction.

The advantage in herd efficiency due to sexual dimorphism, in comparison to monomorphism, is given in Table 4. In cattle, average sexual dimorphism (sire/dam mass) is given as 1,4 (Marlowe, 1962, as quoted by Taylor *et al.*, 1985).

Table 4 Percentage gain in herd feed or cost efficiency through sexual dimorphism (in comparison to monomorphism)

% young females Marketed	Sire / dam line body mass		
	1,2	1,6	2,0
50 (Cattle)	6	16	25
67 (Cattle or sheep)	5	14	22
75 (Sheep)	5	13	21
95 (Pigs)	3	7	11

Adjusting (end of test body mass)/(18-month body mass of heifers) between breeds to an average of 1,4, the sexual dimorphism of South African beef breeds, as calculated from Bosman (1980), varies between 1,2 and 1,6.

Biotechnological animal size manipulation

An example of animal size manipulation by biotechnological means is the micro-injection of the structural gene for rat growth hormone into the pronuclei of fertilized mouse eggs by Palmiter *et al.* (1982). An important feature of the experiment was the use of a DNA fragment containing a special promoter gene which was switched on by the feeding of zinc in the diet. Such manipulation would allow modification of market animals only, so that $q = 1$ in equation (22), giving an approximate $20(1 - b)\%$ improvement in the ratio $e_h(fe)/e_h(br)$. In cattle and sheep, achieving $q = 1$ in (19a) or (22) may be worthwhile. Otherwise the advantage to biotechnological size manipulation in comparison to terminal crossbreeding will have to come from an increase in the $\alpha_m(fe)/\alpha_m(br)$ ratio. The gain in herd efficiency from feeder-breeder dimorphism achievable by size manipulation, is given in Table 5.

Table 5 The percentage gain in herd efficiency by size manipulation of all market animals

Feeder-breeder mass	1,2	1,6	2,0	3,0
% Gain in cattle or sheep	9	24	37	64
% Gain in pigs	5	14	21	36

Dietary induction of feeder-breeder dimorphism

Falconer (1960) selected mice in two directions for growth rate on two diets differing in energy concentration and found that gains in environments least favourable for the expression of a trait, carried over to more favourable environments, but that the converse was not true. Although not universally true, this result recurred often enough to be considered the most likely response in most situations (Bateman, 1974).

In cattle it is common practice to keep cows on natural pasture, and to prepare weaners to market finish in feedlots on concentrate feeds. This suggests selecting for growth rate or body mass under favourable (feedlot) conditions in the expectation that gains will not be carried over to pasture conditions. In this way, feeder-breeder dimorphism can be obtained merely by the exposure of animals to a suitable diet.

In cattle, evidence favourable to the dietary induction of feeder-breeder dimorphism follows from the observation by Scheltz & Roux (1991) that continued gains in average daily gain and body mass at end of test, at central testing stations on concentrate diets, did not materialize in on-farm testing under extensive conditions for the major beef breeds. Under some circumstances it may even be advantageous to select for large body size on concentrate feeds, and small body size on pasture, since it seems to be difficult to obtain market finish on large-framed cattle on pasture in some regions of South Africa.

In the situation of chickens and pigs it is general practice to restrict the size of breeders by restricted feeding. The gain from feeder-breeder dimorphism can be predicted from (19a), whatever the method of dietary induction of the dimorphism. In many situations $q = 1$, since only animals on a feeder diet will be marketed.

Economic weights

The generally accepted way of dealing with multiple objectives in animal breeding is by the application of selection indices. For the calculation of selection indices, economic weights, defined as the value of a unit improvement in a trait, are necessary. After considerable confusion, agreement seems to have been reached that economic weights should be calculated from savings in cost per unit of value (Smith *et al.*, 1986), i.e. from herd cost efficiency (2a, 2b) when $\Delta v/v$ is negligible.

Under the assumption of small enough changes in efficiencies so that products of changes can be ignored, it follows that:

total relative improvement = relative improvement due to terminal crossbreeding or dietary induction of feeder-breeder dimorphism + the relative improvement of the breeding herd. Hence,

$$\begin{aligned} \Delta e_h(\text{tot})/e_h(\text{br}) &= \Delta e_h(\text{sys})/e_h(\text{br}) + \Delta e_h(\text{br})/e_h(\text{br}) \\ &= q \{ [\alpha_m(\text{fe})/\alpha_m(\text{br})]^{1-b} - 1 \} \\ &\quad + \{ [1 + \Delta(r-R)/(r-R)]^{1-b} - 1 \}, \end{aligned} \quad (26a)$$

from (13b), (15) and (19a) under the assumption that total herd reproduction cost $[A$ in (1)] changes negligibly for a change in R , or that R remain constant, and by the argument of the section on Growth efficiency (Roux, 1992b) on the limited possibilities for change in growth efficiency, together with the same assumption for A in (1).

Similar to the derivation of (13c) from (13b), the linearized form of (26a) becomes:

$$\Delta e_h(\text{tot})/e_h(\text{br}) = q(1-b)\Delta\alpha_m/\alpha_m + (1-b)\Delta(r-R)/(r-R), \quad (26b)$$

where $\Delta\alpha_m$ is the difference in limit body mass between feeders and breeders, while α_m pertains to either $\alpha_m(\text{fe})$ or $\alpha_m(\text{br})$.

Equation (26b) is of special interest in the development of selection criteria for dam lines in terminal crossbreeding systems, showing that the economic weights pertaining to body mass and surplus reproduction are $q(1-b)$ and $(1-b)$ respectively. To accommodate different reproduction rates, it may be desirable to extend (19b) to:

$$q = r_s P_s / (r_s P_s + r_d P_d / 2), \quad (26c)$$

similar to the derivation of (29) and to define:

$$r = r_s P_s + r_d P_d \quad (26d)$$

for the calculation of economic gains by (26a) or (26b). The subscripts, s and d, refer to sire and dam respectively.

Discussion

The calculation, in Table 6, of the gain in herd cost efficiency for a 20% gain in a component, represents an attempt at comparison and integration of the value of improvement of given components of herd efficiency.

Perhaps an attempt to arrive at an intuitive understanding of the underlying causes of the results in Table 6 would be worthwhile. The arguments are based on interpretations of growth phenomena by Taylor (1987) and Taylor & Murray (1987) as well as Roux & Scholtz (1984) and Roux (1986).

Animals can be tested over constant time intervals or over the same physiological interval, e.g. from birth to maturity or a certain percentage of mature body mass. Constant time

Table 6 Gain in herd cost efficiency for a 20% gain in a component

Component	% Gain cattle, sheep	% Gain pigs	Achievability	Eqn. No.
Replacement rate	3—5	—	Medium	(14a, b)
Surplus reproduction rate	8—10	5—6	Medium	(13c; 15)
Fertility at first mating:				
5 Matings	2	1	Medium	(16b)
10 Matings	1	—	Medium	(16b)
Sire / dam line mature mass:				
Favourable complete dominance	6—7	5—6	Easy	(25a)
Additive gene action	3—4	3	Easy	(25b)
Sexual dimorphism	6	3	Medium	(22)
Feeder-breeder growth manipulation	9	5—6	Easy	(22)
Growth feed efficiency conception to given % of maximum size	11	14	Hard	(13c)
Maintenance and lactation feed efficiency in female herd	8—10	5—6	Hard	(13c)

interval tests favour large types, lines or breeds, while tests of feed efficiency over corresponding physiological intervals do not show an association with mature body mass.

The explanation is as follows. At similar sizes, animals with large mature body masses generally eat and grow more per day than smaller animals. In relative terms (i.e. per kg body mass), however, large animals eat and grow less than animals with small mature body masses. Consequently large animals take longer to grow to a given percentage of mature body mass. The smaller amount of feed per day per kg body mass is equivalent to the better constant interval feed efficiency of larger animals. This greater efficiency per day is lost over the total period because it takes longer for larger animals to reach a certain percentage of mature body mass. The longer feeding period thus cancels the better constant period feed efficiency.

Probably as a consequence of the longer developmental periods of large animals, their inter-birth periods tend to be longer, and hence their reproduction rates tend to be lower. This effect is again cancelled in reproductive efficiency because larger dams eat less per unit body mass per day than smaller dams. It follows, when the growth and reproductive efficiencies of the whole production system are taken into account, that total life cycle or herd feed efficiency shows no association with mature body size.

In genetic terms, the negative physiological relationships between rates and efficiency ratios associated with the same and different developmental periods will be manifested as negative genetic correlations. Such negative correlations would probably cause total period growth and reproductive feed efficiencies to have very low heritabilities, even though it is known that constant interval feed efficiency and growth rate generally have high heritabilities.

If this argument is correct, it follows that there are at present only two ways of appreciably improving herd feed or cost efficiency:

- (i) increasing fertility and viability, and
- (ii) feeder-breeder dimorphism.

Feeder-breeder dimorphism can be achieved in two ways: (i) by terminal crossbreeding and (ii) by manipulating growth either biotechnologically or by other means. The achievable gains in herd efficiency by the different approaches are given in Table 6. The advantage to growth manipulation depends on the mode of inheritance and the size of the feeder-breeder dimorphism. Growth manipulation by gene transfer might have an advantage over crossbreeding, if the transferred genes could be activated in feeders and kept inactive in breeders.

If growth efficiency could be improved by uncoupling protein synthesis and degradation, Table 6 indicates substantial gains in herd efficiency by improvement of growth efficiency. This may be difficult to achieve in terms of present knowledge.

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