Maximum herd efficiency in meat production
IV. Crossbred reproduction and constant slaughter mass

C.Z. Roux*

Department of Genetics, University of Pretoria, Pretoria, 0002 Republic of South Africa

M.M. Scholtz

Animal and Dairy Science Research Institute, Private Bag X2, Irene, 1675 Republic of South Africa

Higher reproduction and lower replacement rates lead to a higher proportion of terminally crossbred offspring to sell. Substantial improvement in herd efficiency can be achieved by improvement in the ratio of replacement rate to reproduction rate by selection or crossbreeding. In crossbreeding for surplus reproduction, reproduction from F_1 dams may do better than rotational crossbreeding, especially in pigs. Evidence is presented that a strong enough maternal limitation on offspring size sometimes exists in small enough dams in primiparous animals so that fetal dystocia can be avoided. With a constant slaughter mass, a decrease in breeder limit mass or an increase in feeder limit mass will lead to gain in herd efficiency; if, furthermore, an optimal or maximal feeder-breeder limit mass ratio exists, an optimal feeder limit mass can be calculated for the maximization of herd efficiency.

Hoër reproduksie- en laer vervangingstempo's lei daartoe dat 'n hoër proporsie kruisgeteelde nageslag vir bemarking beskikbaar is. Merkbare verbeterings in kuddedoeltreffendheid kan verkry word met 'n verbetering van die verhouding van vervangingstempo tot reproduksietempo deur seleksie of kruisteelt. Met kruisteelt vir surplus reproduksie, mag produksie vanaf F_1-moeders beter wees as rotasiekruisteelt, veral by varke. Getuienis word gegee dat daar somtyds 'n sterk genoeg moederlike beperking op nageslagsgrootte is, sodat fetale distokie vermy kan word. In die geval van 'n konstante slagmassa sal 'n vermindering in teeldierlimietmassa of 'n vermeerdering in slagdierlimietmassa tot vordering in kuddedoeltreffendheid lei. Voorts, as 'n optimum of maksimum verhouding van slagdier- tot teeldier-limietmassa bestaan, kan 'n optimum slagdierlimietmassa bereken word wat kuddedoeltreffendheid sal maksimiseer.

Keywords: Constant slaughter mass, crossbred reproduction, herd efficiency, meat production.

* To whom correspondence should be addressed at present address: Animal and Dairy Science Research Institute, Private Bag X2, Irene, 1675 Republic of South Africa.

Introduction

In the previous paper (Roux, 1992b), predictive theory was developed and the experimental and modelling evidence was analysed for the advantage in herd cost efficiency of feeder–breeder dimorphism. Two topics, however, remain to be dealt with. The first is the evaluation of the degree of improvement possible in herd efficiency by increased reproduction from crossbred females in the utilization of feeder–breeder dimorphism, as well as the possibility of fetal dystocia from crossbred offspring in primiparous animals. The material for the second topic consists of necessary modifications in the conceptual framework, to deal with the requirement of constant slaughter mass.

Reproduction and replacement in terminal cross-breeding

Define $\Delta e_h(\text{sys}) = e_h(\text{sys}) - e_h(\text{br})$ and $\Delta e_h(\text{fe}) = e_h(\text{fe}) - e_h(\text{br})$, where $e_h(\text{sys})$, $e_h(\text{fe})$ en $e_h(\text{br})$ are the herd efficiencies for the whole system, the feeders and the breeders, respectively. It follows immediately from (18) in Roux (1992b) that:

$$\Delta e_h(\text{sys}) = q \, \Delta e_h(\text{fe}). \tag{27}$$

It follows from (18) and (27) that the ratio of actual gain to potential gain = $\Delta e_h(\text{sys})/\Delta e_h(\text{fe})$ is determined by q, the proportion of terminally crossbred offspring sold.

The increased reproduction of F_1-crossbred females under favourable conditions prompts an investigation of systems where small F_1 females are terminally crossbred to large males of a sire breed. Let P_p be the proportion of purebred dams in the herd, and P_f the proportion of F_1 dams from sires of another dam line/breed, which will be mated to sires from a sire line/breed. Let R_p, R_f and r_p, r_f be the replacement and reproduction rates of purebred and F_1 dams respectively. For constant herd size, reproduction must be equal to replacement:

$$r_p P_p / 2 = R_f P_f + R_p P_p.$$

Hence,

$$P_p = R_f / (r_p/2 + R_f - R_p) \tag{28a}$$

and

$$P_f = (r_p/2 - R_p)/(r_p/2 + R_f - R_p). \tag{28b}$$

Hence,

$$\begin{aligned} q &= r_f P_f / (r_f P_f + r_p P_p / 2) \\ &= (r_p - 2R_p)/(r_p - 2R_p + r_p R_f / r_f). \end{aligned} \tag{29}$$

For purpose of comparison, consider systems of purebred dam lines with $R = R_p$ and $r = r_p$, so that (19d) becomes:

$$q_p = (r_p - 2R_p)/(r_p - R_p), \tag{30}$$

or, with $R = R_f$ and $r = r_f$, so that (19d) becomes

$$q'_p = (r_f - 2R_f)/(r_f - R_f). \tag{31}$$

It is important to note that if, in the comparison of different systems,

$$R_f/r_f < R_p/r_p \qquad (32)$$

then

$$q'_p > q > q_p. \qquad (33)$$

Note furthermore that reproduction must always exceed replacement in the female herd. Hence $r/2 > R$ and $0 < R/r \leq 1/2$.

For cattle and sheep, the relationship between q'_p, q and q_p can be tabled as follows:

R_f/r_f	R_p/r_p	0,1	0,2	0,3	0,4
0,1		0,89	0,85	0,80	0,67
0,2			0,75	0,67	0,50
0,3				0,57	0,40
0,4					0,33

On the diagonal the values of q_p or q'_p for (30) or (31) can be read, whereas the values of q from (29) are off the diagonal. For example, consider $R_p/r_p = 0,25/0,83 = 0,30$. From the q – table $q_p = 0,57$. If the crossbred cows have a value of $R_f/r_f = 0,20$, a value of $q = 0,67$ for the crossbred cow system would be obtained. If, however, purebred cows were available with $R_p/r_p = 0,20$, then $q_p = 0,75$. Thus the inequalities, (32) and (33), indicate that substantial improvements in terminal crossbreeding systems are achievable for decreases in the R/r ratio. The values $q = 0,67$ versus $q_p = 0,75$ indicate that selection for reproduction and longevity may be worthwhile. For reasons why progress can often be expected in selection for reproduction, see Scholtz & Roux (1984).

In pigs, $R_p/r_p = 0,20/8 = 0,025$, from Large (1976). Hence, the relationship between q'_p, q and q_p can be tabled as follows:

R_f/r_f	R_p/r_p	0,01	0,02	0,03
0,01		0,99	0,99	0,99
0,02			0,98	0,98
0,03				0,97

It is clear that in pigs, only restricted possibilities exist for the improvements of system efficiency by improvement of the R/r ratio.

Crossbreeding for surplus reproduction

Rotational crossbreeding is a generally accepted way to take advantage of hybrid vigour from breed or line crosses. Carmon et al. (1956) developed equations to predict gains due to rotational crossbreeding. Let $r_s(n)$ be the mean reproduction rate in a n-line rotational crossbreeding system, with $r_p(n)$ the mean of the parental lines and $r_f(n)$ the mean of all F$_1$-s or single crosses. Then, under the assumption of no epistatic interactions between loci, Carmon et al. (1956) proved that:

$$r_s(n) - r_p(n) = [(2^n - 2)/(2^n - 1)] [r_f(n) - r_p(n)], \qquad (34a)$$

exactly for $n \leq 3$, and approximately for $n > 3$. Equation (34a) can also be used for replacement rate (R). Defining:

$$\Delta(r_s - R_s) = (r_s - R_s) - (r_p - R_p) \quad \text{and}$$
$$\Delta(r_f - R_f) = (r_f - R_f) - (r_p - R_p),$$

it follows that (34a) can be written for surplus reproduction rate ($r - R$) as:

$$\Delta[r_s(n) - R_s(n)] = [(2^n - 2)/(2^n - 1)] \Delta[r_f(n) - R_f(n)]. \qquad (34b)$$

Equations (34a) and (34b) define a system where feeder–breeder dimorphism can be obtained from small rotationally crossbred females mated to a large sire line. This system can be compared to a system where only small F$_1$ females are mated to a large sire line. With P_f defined in (28a), the analog of (34b) is,

$$\Delta(r_s - R_s) = P_f \Delta(r_f - R_f), \qquad (35a)$$

where

$$\Delta(r_s - R_s) = (r_s - R_s) - (r_p - R_p) \quad \text{and}$$
$$\Delta(r_f - R_f) = (r_f - R_f) - (r_p - R_p).$$

Equation (35a) gives the improvement in surplus reproduction in a self-sustaining system in relation to the improvement of crossbreds (F$_1$-s) above purebreds.

Equation (28b) can be rewritten as:

$$P_f = 1 - 2R_f/r_p/(1 - 2R_p/r_p + 2R_f/r_p), \qquad (35b)$$

which makes it natural to table P_f in terms of R_f/r_p and R_p/r_p for cattle and sheep as follows:

R_f/r_p	R_p/r_p	0,1	0,2	0,3	0,4
0,1		0,80	0,75	0,67	0,50
0,2			0,60	0,50	0,33
0,3				0,40	0,25
0,4					0,20

The importance of a low replacement rate (longevity) in the utilization of F$_1$ heterosis is apparent. For example, improving R_f/r_p from 0,2 to 0,1 for $R_p/r_p = 0,3$, will increase P_f in (35a) from 0,50 to 0,67. The increase in herd efficiency then follows from (15) and (13b).

For pigs, it is clear from the following table of (35b) that F$_1$ heterosis can be efficiently utilized:

R_f/r_p	R_p/r_p	0,01	0,02	0,03
0,01		0,98	0,98	0,98
0,02			0,96	0,96
0,03				0,94

The tables enumerating (35b) allow interesting comparisons between (34b) and (35a). In general, $\Delta(r_f - R_f) > \Delta[r_f(n) - R_f(n)]$, simply because it is possible to choose an F$_1$ better than average. Assume $n = 2$. Then $(2^n - 2)/(2^n - 1) = 2/3$, a value equal to P_f for $R_f/r_p = 0,1$ and $R_p/r_p = 0,3$. Therefore it seems possible to equal rotational crossbreeding with a self-sustaining F$_1$ system in cattle and sheep. The table from (35b) for pigs shows that a F$_1$ system can be expected superior to rotational cross-breeding for $n = 2, 3, 4$ and R_f/r_f, $R_p/r_p \geq 0,03$; $[P_f > (2^n - 2)/(2^n - 1)]$.

Fetal dystocia

The classical experiment showing the effect of the prenatal maternal environment on birth body size, was that of Walton & Hammond (Hammond et al., 1971), in which reciprocal crosses were made between the large Shire horse and the small

Shetland pony. It was found that the size of the offspring in each case was considerably affected by the size of the dam. In horses, maternal effects persist up to adult life because length growth below the knee and hock is completed at birth. In cattle and sheep there is hope for negative maternal effects to be cancelled to some degree on the way to maturity (Hammond *et al.*, 1971).

There is a considerable amount of evidence that an increase in body mass by selection may often lead to fetal dystocia in primiparous animals (Baker & Morris, 1984; Roux & Scholtz, 1984). It is, therefore, a question of considerable importance whether fetal dystocia can be avoided in terminal crossbreeding by a strong maternal limitation on fetal size, curtailing the genetic effect of the sire breed at birth, while allowing adequate expression of the genetic growth potential later in life.

Confirming evidence for a significant maternal effect on birth body mass comes from a diallel crossbreeding experiment on European cattle breeds (Gregory *et al.*, 1978). In Table 1, reciprocal differences in heterosis (deviation from the midparental value) in birth mass for the different crosses are given, together with the birth body masses of the purebreds on the main diagonal. The main feature of Table 1 worthy of note is the significant reciprocal differences between the upper right-hand and lower left-hand corners, indicating the most divergent matings. This means that Angus and Hereford cows significantly limited calf birth size when mated to male breeds with extreme birth sizes.

Table 1 Reciprocal differences in heterosis of birth body mass, computed from Gregory *et al.* (1978); birth body masses of purebreds are on the main diagonal

Dam breeds	Sire breeds			
	Angus	Hereford	Red Poll	Brown Swiss
Angus	33,4	1,5	–0,7**	0,0*
Hereford	1,2	37,7	–0,1	–0,7**
Red Poll	1,7**	1,3	38,5	0,8
Brown Swiss	2,1*	3,4**	0,2	44,8

** Reciprocal effects significantly different at 1% level.

* Reciprocal effects significantly different at 5% level.

It should furthermore be noted that Gregory *et al.* (1978) reported highly significant total heterosis for birth mass in the Angus × Hereford reciprocal crosses, i.e. an increase in birth mass of all crossbred offspring occurred, without a significant reciprocal difference in Table 1. This is an indication that maternal restriction of offspring birth size may be evident only when the difference between sire and dam breeds is large enough. It is of considerable interest to note that Gregory *et al.* (1978) report less prenatal mortality and greater weaning percentages for the smaller Angus and Hereford cows averaged over all sire breeds, than the larger Red Poll and Brown Swiss cows.

In a crossbreeding experiment by the Animal and Dairy Science Research Institute (ADSRI) between the largest and smallest cattle breeds in the South African performance testing scheme (Charolais and Nguni, a Sanga type), no calving difficulties or prenatal deaths were found in 23 Charolais × Nguni crossbred calves, compared to the same situation for 127 comparable purebred Nguni calves. If a 10% chance of calving difficulty or death exists, the probability of observing one or more cases from a sample of 23 would be $100 \ (1 - 0.9^{23}) = 91\%$. Therefore, with a considerable probability of birth problems, there would be a high chance of observing them from 23 births.

The Nguni calves had an average body mass of 27.3 ± 0.29 kg at birth and Charolais × Nguni calves an average of 34.1 ± 0.59 kg. In related stock, Els (1988) recorded an average of 46.8 ± 0.94 kg for birth body mass of Charolais calves. The Nguni cows, therefore, restricted the birth mass of the crossbred calves well below the mid-parental value of 37,1 kg.

Els (1988) reported birth body masses of 34.5 ± 0.75 kg for Afrikaner, 46.8 ± 0.94 kg for Charolais and 41.5 ± 1.07 kg for Charolais × Afrikaner crossbreds; slightly above the mid-parental value of 40,7 kg. The heifers grew to mature body masses at partus of 435 kg (Afrikaners), 502 kg (Charolais), and 497 kg (Charolais × Afrikaner). It follows, therefore, that the possibility exists for maternal birth size restrictions to be eliminated later in the life cycle. In terms of muscle growth, this probably means that the crossbred calves had the same potential for growth as the purebred Charolais, with a restriction in birth mass due to muscle cell size rather than number. This conclusion follows since most of the muscle cells of an animal are already present at birth (Beitz, 1985), and catch-up growth can only occur in cell length or diameter.

Constant slaughter mass

All previous comparisons between different breeding systems have been at maximum herd efficiencies obtained under the assumption of optimal slaughter masses. In pigs and chickens, the market often dictates fixed constant slaughter masses (Tess *et al.*, 1983; Siegel & Dunnington, 1988), which may, of course, be different from the optimal value associated with maximal herd cost efficiency. The consequences for herd efficiency of feeder–breeder dimorphism need, therefore, to be explored in the situation of constant slaughter masses.

Consider the herd efficiency (e_h) of the feeders from (4a), where all quantities are properties of the feeders, except for Q, which is mainly a property of the breeders. Then, if it is assumed that Q depends on the breeder limit mass, $[\alpha_m \text{(br)}]$:

$$Q = a\alpha^d_m \text{(br)}, \tag{36}$$

where a, d are the allometric intercept and slope, respectively. From Roux (1986) one would expect $d = 1$. Consequently, if it is assumed that growth efficiency ($e_g = \alpha_m/\alpha_f$, 4.b) and slaughter mass (m) as well as the allometric slope (b) remain constant, it follows from (4a) and (36) that $\alpha'_m \text{(fe)} \geq \alpha_m \text{(fe)}$ and $\alpha'_m \text{(br)} \leq \alpha_m \text{(br)}$ imply that $e'_h \geq e_h$, with $e'_h = e_h$ only if both limit mass equalities hold. In words this statement means that an increase in feeder limit mass, coupled with either constancy or a decrease in breeder limit mass, will always cause an increase in feeder herd efficiency. Likewise, a decrease in breeder limit mass, coupled with either constancy or increase in feeder limit mass, also will always cause an increase in feeder herd efficiency, provided that the constancy

assumptions of the foregoing mathematical formulation hold. It should be noted that an increase in α_m (fe) and a decrease in α_m (br) will lead to an increase in feeder–breeder dimorphism [the ratio α_m (fe)/α_m (br)], but that the converse of this statement is not necessarily true.

An increase in growth rate implies an increase in limit mass (Taylor & Murray, 1987). In chickens and pigs, it is general practice to control breeder body mass by restricted feeding (Siegel & Dunnington, 1988; Thornton, 1978), while the dwarf gene is also employed in chicken breeding (Gous, 1986). The principle of increasing herd efficiency due to increasing feeder limit mass together with constancy or decreasing breeder limit mass, derived from (4a), confirms the importance attached to growth rate as a selection criterion in chickens for feeders, with constant slaughter mass (Shalev & Pasternak, 1983). This is in agreement with the economic weights based on an optimal slaughter mass, derived in Roux (1992b).

Constant feeder–breeder mass ratios

Instead of assuming a given limit mass and obtaining an optimal slaughter mass, the procedure can be reversed to obtain an optimal limit mass for a required slaughter mass in situations where a maximum or optimum α_m (fe)/α_m (br) ratio exists. For example, the dwarfing gene in chickens causes a 30% decline in body mass in females (Gous, 1986). If carriers are mated to normal males, normal progeny will result. These facts can be used to obtain optimal limit masses in a terminal cross-breeding system with α_m (fe)/α_m (br) = 1/0,7 = 1,43 for females, under the assumption of a fixed slaughter mass (m).

From Dexter $\times$ South Devon crosses in cattle, Joubert & Hammond (1958) concluded that the size of the crossbred calf is limited in the large mother by heredity and in the small mother by nutrition. The effect of such maternal inhibition of offspring size is likely to persist to maturity if it is severe and early enough to inhibit the number of cells instead of only cell size (Winick & Noble, 1966). With cell number inhibition it is possible that a maximal ratio between feeder and breeder limit masses may exist.

From these examples on chickens and cattle, it is clear that a given maximal or optimal ratio between feeder and breeder limit masses may exist. Denote such a ratio between the limit masses α_m (fe)/α_m (br) by D. In situations where the market demands a fixed slaughter mass (m), and such a value D exists, it is possible to solve for a value for α_m (fe) that will maximize herd efficiency. Such a limit mass can then be obtained by appropriate selection procedures or choice of a sire line.

In the situation where α_m (fe)/α_m (br) = D, it is advantageous for further development of theory to rewrite (4b) as:

$$e_h(fe) = 1/[\{m/\alpha_m(fe)\}^{1/b-1} e_g^{-1}(fe) + \{mD/\alpha_m(fe)\}^{-1} e_r^{-1}(br)] \tag{37}$$

From Roux (1992a; 1992b) it is reasonable to assume e_g and e_r constant. Then, by differentiation of (37) and putting de_h (fe)/$d\alpha_m$ (fe) = 0, the value of α_m (fe) can be obtained that will give a maximum value of e_h (fe) for a constant slaughter mass m(const). It turns out that the answer is identical to (5):

$$m(const)/\alpha_m(fe) = [bQ(br)/(1-b)\alpha_f(fe)]^b. \tag{38}$$

From Roux (1992a; 1992b) it is possible to assume α_f proportional to α_m. Hence,

$$m(const)/\alpha_m(fe) = [bQ(br)/(1-b)\alpha_f(br)D]^b. \tag{39}$$

Equations (38) and (39) can be used to solve for α_m (fe), given m(const), to obtain the limit mass maximizing herd efficiency. From (39) and (37) it also follows that:

$$e_h(fe) = e_h(br) D^{1-b}, \tag{40}$$

in agreement to (19a), as one would expect from the identity of (5) and (38).

Discussion

Perhaps the most important theoretical results from this paper are:

(i) the delineation of the circumstances where reproduction from F_1 dams may do better than rotational cross-breeding,

(ii) that with a constant slaughter mass a decrease in breeder limit mass or an increase in feeder limit mass will necessarily lead to gains in herd efficiency, and

(iii) that an optimal feeder limit mass can be calculated for breeding purposes in the situation of a desired (constant) slaughter mass and an optimal or maximal ratio in feeder–breeder limit masses.

In discussions with producers, the most important practical objection to the utilization of the advantages of feeder–breeder dimorphism in terminal crossbreeding is always felt to be the possibility of serious fetal dystocia. It is, therefore, welcome that evidence for the maternal restriction of birth mass exists in crosses between animals of widely divergent mature mass, and that some breeds may possess this ability as a special feature.

Parthian shot

This series of articles is part of an attempt to incorporate comparative physiology into breeding theory. Reliable indications of possible gains in efficiency of production are only possible on the basis of scientific theory. Without such a separation of the plausible from the probable, the danger exists that animal breeding may become an infinite regress of experiments, necessarily involving large numbers, in a vain attempt to accommodate or exploit biological variation.

References

BAKER, R.L. & MORRIS, C.A., 1984. A review of correlated responses to weight selection in beef cattle under different management and climatic conditions. In: Proc. 2nd World Congress on Sheep and Beef Cattle Breeding. Eds. Hofmeyr, J.H. & Meyer, E.H.H., South African Stud Book and Livestock Improvement Association, Bloemfontein. p. 236.

BEITZ, D.L., 1985. Physiological and metabolic systems important to animal growth – an overview. J. Anim. Sci. 61, Suppl. 2, p. 1.

CARMON, J.L., STEWARD, H.A., COCKERHAM, C.C. & COMSTOCK, R.E., 1956. Prediction equations for rotational crossbreeding. J. Anim. Sci. 15, 930.

ELS, D.L., 1988. Kruisteling vir vleisproduksie. Ph.D thesis, Univ. of the Orange Free State, Bloemfontein.

GOUS, R.M., 1986. Genetic progress in the poultry industry. S. Afr. J. Anim. Sci. 16, 127.

20

GREGORY, K.E., CUNDIFF, L.V., KOCH, R.M., LASTER, D.B. & SMITH, G.M., 1978. Heterosis and breed maternal and transmitted effects in beef cattle. 1. Preweaning traits. *J. Anim. Sci.* 47, 1031.

HAMMOND, J., MASON, I.L. & ROBINSON, T.J., 1971. Hammond's farm animals. Edward Arnold, London.

JOUBERT, D.M. & HAMMOND, J., 1958. A crossbreeding experiment with cattle, with special reference to the maternal effect in South Devon — Dexter crosses. *J. Agric. Sci. Camb.* 51, 325.

LARGE, R.V., 1976. The influence of reproductive rate on the efficiency of meat production in animal populations. In: Meat animals – growth and productivity. Eds. Lister, D., Rhodes, D.N., Fowler, V.R. & Fuller, M.F., Plenum Press, New York. p. 43.

ROUX, C.Z., 1986. A comparison of between and within species reproductive and total life cycle efficiencies. In: 3rd World Congress on Genetics Applied to Livestock Production. XI. Genetics of Reproduction, Lactation, Growth, Adaptation, Disease and Parasite Resistance. Eds. Dickerson, G.E. & Johnson, R.K., University of Nebraska, Lincoln. p. 55.

ROUX, C.Z., 1992a. Maximum herd efficiency in meat production. II. The influence of growth and reproduction. *S. Afr. J. Anim. Sci.* 22, 6.

ROUX, C.Z., 1992b. Maximum herd efficiency in meat production. III. Feeder–breeder dimorphism. *S. Afr. J. Anim. Sci.* 22, 11.

ROUX, C.Z. & SCHOLTZ, M.M., 1984. Breeding goals for optimal total life cycle production systems. In: Proc. 2nd World Congress on Sheep and Beef Cattle Breeding. Eds. Hofmeyr, J.H. & Meyer, E.H.H.,

South African Stud Book and Livestock Improvement Association, Bloemfontein. p. 444.

SCHOLTZ, M.M. & ROUX, C.Z., 1984. Improving fertility by emulating natural selection. In: Proc. 2nd World Congress on Sheep and Beef Cattle Breeding. Eds. Hofmeyr, J.H. & Meyer, E.H.H., South African Stud Book and Livestock Improvement Association, Bloemfontein. p. 743.

SHALEV, B.A. & PASTERNAK, H., 1983. Genetic–economic evaluation of traits in a broiler enterprise: the relative economic values. *Brit. Poult. Sci.* 24, 521.

SIEGEL, P.B. & DUNNINGTON, E.A., 1988. Long-term selection for meat production in poultry. In: Animal breeding opportunities. Occ. Publ. Br. Soc. Anim. Prod., No. 12. p. 238.

TAYLOR, St C.S. & MURRAY, J.I., 1987. Genetic aspects of mammalian survival and growth in relation to body size. In: Nutrition of herbivores. Prod. 2nd International Symp., Academic Press, Australia. p. 487.

TESS, M.W., BENNETT, G.L. & DICKERSON, G.E., 1983. Simulation of genetic changes in life cycle efficiency of pork production. 1. A bio-economic model. 2. Effects of components on efficiency. 3. Effects of management systems and feed prices on importance of genetic components. *J. Anim. Sci.* 56, 336.

THORNTON, K., 1978. Practical pig production. Farming Press, Ipswich.

WINICK, M. & NOBLE, A., 1966. Cellular response in rats during malnutrition at various ages. *J. Nutr.* 89, 300.