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Maximum herd efficiency in meat production
II. The influence of growth and reproduction

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A general method is developed for the evaluation of herd efficiency in terms of efficiencies for growth and reproduction. Almost the only requisite knowledge for the application of this method is the value of the allometric slope between the cost of cumulate feed intake and body mass for a target population. The evaluation of reproduction efficiency involves reproduction and replacement rates, early fertility, and degree of fertility at first mating. Growth efficiency is discussed in terms of cumulate *vs.* constant period efficiency and the influence of a likely negative genetic relationship, induced by selection, between components like preweaning and postweaning efficiencies. Finally, some consequences are derived for the effect of constant costs per time unit on total efficiency.

'n Algemene metode is ontwikkel vir die evaluasie van kuddedoeltreffendheid in terme van doeltreffendhede vir groei en reproduksie. Omtrent die enigste vooraf-kennis wat nodig is vir die toepassing van hierdie metode is die allometriese helling tussen geakkumuleerde voedselinname en liggaamsmassa vir 'n toepassingsbevolking. By die evaluasie van reproduksiedoeltreffendheid is reproduksie- en vervangingstempo's, vroeë vrugbaarheid en graad van vrugbaarheid by eerste paring, betrek. Groeidoeltreffendheid is bespreek in terme van geakkumuleerde *vs.* konstante periode doeltreffendhede en die invloed van 'n moontlike negatiewe genetiese verwantskap tussen voorspeense en naspeense doeltreffendhede wat deur seleksie geïnduseer mag word. Laastens word sommige afleidings oor totale doeltreffendheid gemaak vir die geval van konstante kostes per tydseenheid.

Keywords: Growth, herd efficiency, meat production, reproduction.

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Introduction

In a comparison of selection gains for different traits or methods, $h^2\sigma_p$ (h^2 = heritability; σ_p = phenotypic standard deviation) is often used, since it is proportional to the selection gains for a given selection intensity (Falconer, 1981). For purposes of comparison of the importance in selection of multiple traits, Dickerson (1976) proposes consideration of $h^2\sigma_p\beta$, where β is the partial regression coefficient of the trait under consideration on total herd efficiency. In situations where management and biotechnological gains are under consideration, the term $h^2\sigma_p$ is clearly inappropriate and only β remains relevant.

In contrast to Dickerson's (1976) regression approach, the approach of Taylor *et al.* (1985) is to study the whole response surface in terms of plots of total efficiency against percentages of mature body mass. In this paper, a response surface approach is employed whenever convenient or appropriate. For purposes of comparison between different traits, an approach akin to that of Dickerson (1976) is also employed. This procedure consists of an evaluation of the concomitant increase in herd efficiency for a given increase in a certain component, while the other components are assumed constant. The kinship between the procedures follows since a partial regression coefficient can be interpreted as the regression between two variables for constant values of the others.

Maximum herd efficiency [e_h (max)] in (6b) of Roux (1992a) can, at optimal slaughter mass [m (opt)], be written as:

$$e_h\,(\max) = [be_g]^b\,[(1-b)e_r]^{1-b}, \tag{6e}$$

with e_g equal to the cumulate growth cost efficiency at maximum body mass (α_m), and e_r equal to the reproduction cost efficiency at that point. The parameter b is the allometric slope between cumulate feed cost and body mass, from (3).

Let $\Delta b/b$, $\Delta e_h/e_h$, $\Delta e_g/e_g$ and $\Delta e_r/e_r$ be relative gains, respectively, in the allometric slope, and in herd, growth and reproduction efficiencies. Under the assumption that the gains are small enough that their squares and cross products can be ignored, it follows from (6e) that:

$$\Delta e_h/e_h = [m(\text{opt})/\alpha_m]^{\Delta b/b}\,[1+\Delta e_g/e_g]^b\,[1+\Delta e_r/e_r]^{1-b} - 1, \tag{13a}$$

as $m(\text{opt})/\alpha_m = [be_g/(1-b)e_r]^b$, from (5). Since it seems that only restricted possibilities may exist (Roux, 1992a) for genetic change in b, $\Delta b = 0$ is assumed as a first approximation for present purposes. If $\Delta b = 0$,

$$\Delta e_h/e_h = [1+\Delta e_g/e_g]^b\,[1+\Delta e_r/e_r]^{1-b} - 1, \tag{13b}$$

exactly. Under the assumption that all relative gains are small enough that their products can be ignored, binomial approximations of the form $(1+x)^b = 1 + bx$ for $|x| < 1$ then give:

$$\Delta e_h/e_h = b\,\Delta e_g/e_g + (1-b)\,\Delta e_r/e_r. \tag{13c}$$

It follows from (13c) that a 20% improvement in growth efficiency, e_g, while reproduction efficiency remains constant, would result in approximately

$$\Delta e_h/e_h = 20\,b\%$$

improvement in total herd efficiency, e_h. Similarly, a 20% improvement in reproduction efficiency, e_r, while growth efficiency remains constant, would result in approximately

$$\Delta e_h/e_h = 20\,(1-b)\,\%$$

improvement in herd efficiency.

For cattle (steers), Roux & Meissner (1984) found that b tends to vary with mature body mass, from $b = 0{,}5$ to $b = 0{,}6$, with a reasonably strong concentration of values for South African cattle around $b = 0{,}55$. For sheep, the average value of b over two breeds and sexes obtained by Meissner *et al.* (1975), is 0,54. Hence, for sheep and cattle a value of $b = 0{,}55$ will be used in this article. In a comparison between lean and obese Landrace pigs, Siebrits *et al.* (1986) found b to be constant within sexes between the two types of pigs, with an average of $b = 0{,}72$ across sexes. Hence, a value of $b = 0{,}72$ will be assumed for present purposes.

Reproduction efficiency

Replacement rate

In Roux (1992a), the optimal values for replacement rate have been given as extreme values, i.e. as small or as large as possible. This nevertheless allows room for the application of (13c). Let e'_r be the reproduction efficiency associated with replacement rate R', and likewise for e_r and R. To simplify a complicated expression, assume equal reproduction rates, $r_1 = r_2$. It then follows from (8) that:

$$e'_r/e_r = (r-R')\,(1+kR)/(r-R)\,(1+kR')\,, \qquad (14a)$$

with $k = (w + x - y - z)/y$. The component terms of k were defined in (1a) (Roux, 1992a), but in abbreviated form are: w = cost of a replacement female, x = feed and other costs of a first parity female, y = feed and other costs for older females from one weaning to the next, and z = value of a mature female. This (14a) is still somewhat unwieldy. Consider therefore, the expedient of obtaining boundary values for k. A convenient and perhaps biologically realistic upper boundary can be obtainded from the following argument. Assume $x = y$ and $z = 0$. It follows then, from Dickerson (1978), that $k = 1$ approximately for cattle while $k = 1/4$ for pigs, from Tess *et al.* (1983). From the definition of w, x, y and z in (1), it is clear that the assumption of $k = 0$, when $w = z$ and $x = y$, would often be a convenient and realistic lower boundary. For $k = 0$, it follows that (14a) simplifies to:

$$(-\Delta R/R)\,R/(r-R) = \Delta e_r/e_r\,, \qquad (14b)$$

from which the relationship between $\Delta R/R$ and $\Delta e_h/e_h$ follows from (13b).

For cattle it follows from (14a), (14b) and (13b) that a 20% improvement of $R = 0{,}25$ to $R' = 0{,}20$ with $r = 0{,}80$ and $b = 0{,}55$ gives an improvement in total herd efficiency $\Delta e_h/e_h = 4\%$ for $k = 0$ and $\Delta e_h/e_h = 6\%$ for $k = 1$. An improvement from $R = 0{,}10$ to $R' = 0{,}08$ gives values of 2 and 4% in $\Delta e_h/e_h$ for $k = 0$ and $k = 1$, respectively. The same percentage improvement in $R = 0{,}25$ gives a value of 2% in $\Delta e_h/e_h$ for $k = 0$ and 4% for $k = 1$ for sheep with $r = 1{,}5$. For pigs, an improvement from $R = 0{,}20$ to $R' = 0{,}16$, $b = 0{,}72$ and $r = 8$ gives improvements of $\Delta e_h/e_h = 0{,}1\%$ and $\Delta e_h/e_h = 0{,}4\%$ for $k = 0$ and $k = 1/4$, respectively. It is clear that the importance of replacement rate in herd efficiency depends on the level of the reproduction rate.

That (14a) is also a measure of the importance of the length of reproduction life follows from (12b), since the number of age classes in a herd will depend on the reproductive life of females.

Reproduction rate

Assume, for the moment, that a change in reproduction rate does not change the values of x and y in (1a, 14a). The effect of an increase in surplus reproduction, defined to be reproduction rate (r) minus replacement rate (R), is therefore:

$$\begin{aligned}\Delta(r-R)/(r-R) &= \Delta r/(r-R)\\ &= \Delta e_r/e_r \qquad (15)\end{aligned}$$

since $e_r = \alpha_m/Q$ and under the assumption of constant values of R and α_m.

Cattle and sheep

Dickerson (1978) shows that, for cattle and sheep, the energy cost of lactation is small in relation to the energy cost of maintenance and replacement. It follows that the stage of reproductive loss may not be important in a first approximation of the effect of improvement of reproduction efficiency on herd efficiency. Therefore, Q in (1c) will probably change mainly as a result of the change in $(r-R)$.

In the case of cattle, Roux & Meissner (1984) found the value of b to be between 0,5 and 0,6. Hence from (15) and (13b), an increase of 8—10% in herd efficiency for a 20% increase in surplus reproduction seems reasonable. This is in good agreement with a value of 8% calculated by Dickerson (1983) and a value of 8—10% by Taylor *et al.* (1985). Similar values can be accepted for sheep as their values of b seem similar to those of cattle (Meissner *et al.*, 1975).

Dickerson *et al.* (1988) predicted, without subtracting replacements, a value of 0,97 for $\Delta r/r$ for twinning in cattle. Assuming A approximately constant in (1), it follows from (15) and (13b) that $\Delta e_h/e_h = (1{,}97)^{0{,}45} - 1 = 0{,}36$. The experimentally obtained $\Delta e_h/e_h$ values from Table 1 of Dickerson *et al.* (1988), are $1/0{,}74 - 1 = 0{,}35$ and $1/0{,}76 - 1 = 0{,}32$ for feed and total cost efficiency, respectively.

Ignoring replacement rates, (13b) predicts $\Delta e_h/e_h = 2^{0{,}45} - 1 = 0{,}37$ and $\Delta e_h/e_h = 3^{0{,}45} - 1 = 0{,}64$ for herd efficiency of twins and triplets relative to singles. Arranged according to ewe mass, the experimentally obtained percentage values (± standard errors) for $\Delta e_h/e_h$ from Large (1970), are:

	Ewe mass (kg)	Twins	Triplets
Heavy ewes	79	38 ± 4	64 ± 7
Kerry Hill	58	27 ± 6	–
Welsh Mountain	33	23 ± 6	–

The heavy ewes were Scottish Halfbred and Devon Longwool sheep. For heavy ewes the agreement between theory and experiment is exceptionally good. For the lighter ewes (Kerry, Welsh) the agreement is poor, presumably because their milk production is inadequate to allow twin lambs to grow to their full potential, and equal limit masses for singles and twins are implicit in (15). Indirect evidence for this supposition comes from Roux (1992b), where a correction for lamb carcass mass gave experimental observations in agreement to theory. Such a correction is impossible in the present comparison, since carcass masses of singles, twins and triplets are not listed separately by Large (1970).

Early fertility

For cattle and sheep, an estimate of the effect of early breeding on herd efficiency is important. Let $e_r(r_1)$ be the reproduction efficiency with a reproduction rate of r_1 for first parity females, and let $e_r(0)$ be the reproduction efficiency in a herd with $r_1 = 0$. Then, from (8):

$$\Delta e_r / e_r(0) = r_1 R / [r_2 - R(1 + r_2)], \qquad (16a)$$

where $\Delta e_r = e_r(r_1) - r_r(0)$, under the same assumptions as in the derivation of (15).

Assume $R = 0{,}2$ or $R = 0{,}1$ and $r_2 = 0{,}8$ for cattle. Then (16a) and (13b) give increases in relative herd efficiency ($\Delta e_h / e_h$ %) for various values of r_1:

r_1	0,2	0,4	0,6	0,8	1,0
$R = 0{,}2$	4	8	11	15	18
$R = 0{,}1$	1	3	4	6	7

For sheep, assume $r_2 = 1{,}5$ and $R = 0{,}2$. Then (16a) and (13b) predict for $\Delta e_h / e_h$ %:

r_1	0,2	0,4	0,6	0,8	1,0	1,2
$R = 0{,}2$	2	4	5	7	9	10

In the light of the agreement between experimental observations on large ewes and cattle and (15), one would expect that predictions based on (16a) would be equally valid, if the implicit assumption of equal limit masses for offspring of first parity and more mature females is valid. If this assumption does not hold, an adjustment for differences in limit mass is possible.

Pigs

In the case of pigs, the cost of gestation and lactation is probably not a negligible part of the cost of the total amount of feed of the breeding herd (Dickerson, 1978). If the costs involved in housing and management is taken into account in A (eqn. 1) it may, however, be approximately true that $Q = A/(r - R)$ will change mainly as a result of the change in surplus reproduction rate for changes in fertility and viability. From Siebrits *et al.* (1986), an average $b = 0{,}72$ seems acceptable for pigs. Hence, from (13b) and (15), an increase of 5—6% in herd cost efficiency for a 20% increase in surplus reproduction rate seems acceptable. Tess *et al.* (1983) predicted a comparable 5% increase in herd cost efficiency for number of offspring born alive. Equation (13b) predicts an increase of 4% for an increase of 15% in e_r. The increase in herd cost efficiency is 2% for a 15% increase in conception rate and 5% for a 15% increase in offspring viability, by Tess *et al.* (1983). Thus it seems that increases in herd efficiency predicted from (13b) and (15) by increases in reproduction efficiency are in line with more or less equivalent estimates in the literature, for both cattle and pigs.

Degree of fertility at first mating

From (8) the relationship between the relative increase in the reproduction rate of first parity females and the relative increase in reproduction efficiency is:

$$(\Delta r_1 / r_1)(r_1 R)/[r_2 - R(1 - r_1 + r_2)] = \Delta e_r / e_r, \qquad (16b)$$

under the same assumption as noted for (15).

Consider $\Delta r_1 / r_1 = 20\%$ and $R = 0{,}20$. Then, for cattle with $r_1 = 0{,}67$ and $r_2 = 0{,}8$, (16b) and (13b) give $\Delta e_h / e_h = 2\%$. For sheep $r_1 = 1{,}25$ and $r_2 = 1{,}50$, give $\Delta e_h / e_h = 2\%$. For pigs $r_1 = 6{,}7$ and $r_2 = 8{,}0$, give $\Delta e_h / e_h = 1\%$. With the same assumptions as above, but $R = 0{,}1$, $\Delta e_h / e_h = 1\%$, for cattle.

Growth efficiency

The effect of variable b in (13a) can be ignored in the case of cattle and sheep since the term $b^b(1 - b)^{1-b}$ in (6b) is virtually constant for b between 0,4 and 0,6. It follows, for $b = 0{,}55$ from Roux & Meissner (1984) and Meissner *et al.* (1975), that (13b) predicts an 11% increase in herd efficiency for a 20% increase in cumulate growth efficiency, for cattle and sheep.

In the comparison between efficient (lean) and less efficient (obese) pigs of the same breed, Siebrits *et al.* (1986) found b constant within sexes between the two types of pigs, with only a shift in the α_m / α_f ratios. Hence, for an average $b = 0{,}72$, a gain in herd efficiency of 14% is predicted from (13b), for a 20% increase in cumulate growth efficiency.

As a rough generalization, Taylor (1987) states that 75% or more of the variation in growth traits is typically associated with mature size and 25% or less with atypical genetic adaptations and variations of interest to animal breeders. It follows that cumulate efficiency to a constant degree of maturity, which is uncorrelated to mature size, can be expected to have a much lower heritability than the conventional constant period efficiency, which is in general strongly related to mature size. Potential selection gains in cumulate growth efficiency (e_g) can, therefore, be expected to be correspondingly less than in the case of constant period efficiency.

Selection gains in cumulate growth efficiency can also be inhibited by negative genetic correlations between the efficiencies of different growth phases. Evidence for such a negative genetic relationship follows from the discovery of a negative genetic correlation between preweaning and postweaning average daily gain in mice, by Riska *et al.* (1984), and in cattle by MacNeil *et al.* (1984). If, in both phases, average daily gain and feed efficiency show the usual positive genetic relationship, a negative genetic relationship between the feed efficiencies of the two phases is indicated.

In cattle, Thiessen & Taylor (1986) found negative between-breed correlations between the feed efficiencies for different time intervals. The near-zero correlation between 12—24 week efficiency and 12—72 week efficiency indicates the potential strength of the effect of preweaning efficiency on total period efficiency.

In an examination of the effect of the gene for halothane sensitivity by Simpson *et al.* (1986) and by Webb & Simpson (1986), it was found that piglets from the halothane positive selection line were significantly lighter at birth and 42 days (weaning) than piglets from the halothane negative line, whereas halothane positive pigs had significantly better feed conversion between 25 and 85 kg than halothane negative pigs. It seems plausible that the gene for halothane sensitivity has a negative effect on feed conversion before weaning at 42 days, whereas after 42 days it has a positive effect on feed conversion.

Since post-mortem rates of calcium efflux from the mitochondria have been shown to be closely related to the halothane phenotype (Cheah & Cheah, 1982), it is clear that an alteration of the permeability of cell membranes must be a primary effect of the halothane gene. It is now generally known that water-filled pores, or channels, regulate ion flow across cell membranes. Furthermore, ion channels generally couple extracellular events to cytoplasmic biochemical pathways and this mediates glandular secretion, hormonal control, immunity to disease as well as normal development and growth (Schauf, 1987). Ion channel distribution also varies during development, with calcium channels appearing first, followed by potassium channels. Recent evidence implicates the calcium ion as one factor controlling gene expression. Thus, calcium channels could modify growth and development (Schauf, 1987).

Genes code for 50—100 chemically unique ion channels, so that, simply by changing the specific channels they synthesize, cells are able to alter their responses (Schauf, 1987). It follows that the differential effects of the halothane gene on preweaning and postweaning growth may be explained by differential effects on the availability of ion channels during these stages.

Results from a rat selection experiment (experimental details are available in Scholtz *et al.*, 1990) involving two-way selection for the allometric slope and intercept, associated with the relationship between feed intake and body mass, indicate that the relationship between the efficiencies of different growth phases can change as a result of selection. In the unselected founder population, the correlation between feed efficiencies of phase I (24—36 days) and phase II (36—60 days) was significantly positive, $r = 0{,}47$ ($n = 80$, $P \leqslant 0{,}001$). In contrast to this, the average within selection line correlation in generation 19 (peak selection progress) was equal to zero ($r = 0{,}00$; $n = 133$).

Recently, Siebrits & Barnes (1989) found that a break in the growth curve of rats at 30—31 days, characterizing the transition from one phase to the next, was also observed in muscle protein metabolism. It follows, therefore, that there may be metabolic reasons behind a change in statistical relationship between different growth phases due to selection.

Negative genetic relationships between components of performance, such as a negative relationship between preweaning and postweaning efficiency, may make selection progress with specialized sire and dam lines greater than in the case of unitary populations (Smith, 1964). This fits into the pattern showing the advantage of terminal crossbreeding with feeder–breeder dimorphism that will be developed in the next paper of this series.

Constant costs per time unit

Assume that costs per animal per time unit is constant or constant over appropriate intervals, so that costs per animal for a given period can be expressed in the form:

$$c = g + ht, \tag{17a}$$

where h is the cost per time unit and g is the initial cost, say to buy the animal. Two situations nay be important in this respect, viz. feeding animals a constant amount of feed per day irrespective of size, and secondly, where housing costs are important and h represents the cost of housing per animal. Such a situation would obtain when a fixed amount of floor space is allotted to an animal irrespective of size, which is a common management procedure in poultry. In such a situation total efficiency (e_t) can be defined as:

$$e_t = m/(g + ht), \tag{17b}$$

where m is body mass as before. The magnitude of m where e_t is a maximum, is obtained by differentiation and equating to zero:

$$de_t/dt = dm/dt[g + ht]^{-1} - hm[g + ht]^{-2} = 0,$$

which implies that e_t will be a maximum when

$$am/dt = hm\,(g + ht)^{-1} \tag{17c}$$

and that

$$e_t\,(\max) = h^{-1}dm/dt, \tag{17d}$$

at the maximum given by (17c).

If a Gompertz growth curve is assumed for the description of growth, then:

$$e_t\,(\max) = -h^{-1}\gamma\alpha_m\,(m/\alpha_m)\,ln\,(m/\alpha_m)\,, \tag{17e}$$

from Roux & Meissner (1984), where γ is a relative growth rate constant. The maximum value of the function: $-(m/\alpha_m)\,ln\,(m/\alpha_m)$ for $0 \leqslant m/\alpha_m \leqslant 1$ is equal to $1/e$ (= 0,37, approximately). Hence,

$$e_t\,(\max) \leqslant (0{,}37)\,\gamma h^{-1}\alpha_m\,. \tag{17f}$$

If housing cost is proportional to floor space, then h would be proportional to the square of linear dimensions ($\alpha_m{}^{1/3}$) or to $\alpha_m{}^{2/3}$, if animals are kept to the same values of m/α_m. Taylor & Murray (1987) quote evidence that growth rate is proportional to $\alpha_m{}^{0,73}$, so that (17d) gives advantage (proportional to $\alpha_m{}^{0,06}$) to larger animals. Furthermore, Feldman & McMahon (1983) found a detectable difference in the relationship between basal metabolism and body mass between and within species, with exponents of 3/4 and 2/3 respectively. If this would also be true for growth rate, there would be no advantage to larger animals in (17d) within species.

The effect of cost per animal per time unit on total efficiency is clear from (17d, 17e). The effect of initial cost (g) is much more difficult to quantify than that of Q in (2), and nothing comparable to (13c) seems possible, as g plays an indirect role in e_t (max) by influencing the value for dm/dt for which (17c) holds.

The ideal approach would be to combine e_t from (17b) and e_h from (2) or (13a). On its own, e_t is mathematically intractable, so that no useful explicit algebraic formulations on a combined cost function seems possible. However, it seems highly possible that most practical cost functions will result in efficiency functions with an optimal slaughter mass associated with maximum efficiency.

Discussion

Almost the only requisite knowledge for the evaluation of efficiency components in terms of herd efficiency is the value of the allometric slope between the cost of cumulate feed intake and body mass for a target population. That the allometric slope *b* is a scale-free parameter is convenient and important in the comparison of breeding strategies. Thus, comparisons of cost and energetic efficiencies based on allometric slopes would lead to the same conclusions as long as the same or comparable items are included in the analyses.

Perhaps the most interesting aspect of the present results is the possibility to predict the increase in herd efficiency due to increased reproduction. Thus, it is possible to calculate for sheep that four (4) surviving offspring per parity is necessary to double herd efficiency in comparison to survivors from single births, if replacement rate is equal to 0,25 : $(1 + 3/0,75)^{0,45} - 1 = 1,1$; from equations 13b, 15. A complete comparison between the gains in herd efficiency due to improvement in its components will be delayed to the next article (Roux, 1992b), when the inclusion of the gains due to feeder–breeder dimorphism in terminal crossbreeding becomes possible.

Rererences

CHEAH, K.S. & CHEAH, A.M., 1982. In: Membrane Fluidity. Eds. Kates, M. & Manson, L.A., Plenum Press, New York.

DICKERSON, G.E., 1976. The choice of selection objectives in meat-producing animals. In: Meat Animals. Growth and productivity. Eds. Lister, D., Rhodes, D.N., Fowler, V.R. & Fuller, M.F., Plenum Press, New York. p. 449.

DICKERSON, G.E., 1978. Animal size and efficiency: Basic concepts. *Anim. Prod.* 27, 367.

DICKERSON, G.E., 1983. Potential genetic improvements in the efficiency of beef production. In: Strategies for the most efficient beef production. Kyoto University, Kyoto.

DICKERSON, G.E., GUERRA-MARTINEZ, P., ANDERSON, G.B. & GREEN, R.D., 1988. Twinning and performance efficiency in beef production. In: Proc. of 3rd World Congress on Sheep and Beef Cattle Breeding. Vol. 1. INRA Publ., Paris.

FALCONER, D.S., 1981. Introduction to quantitative genetics. Longmans, New York.

FELDMAN, M.A. & McMAHON, T.A., 1983. The 3/4 mass exponent for energy metabolism is not a statistical artifact. *Respir. Physiol.* 52, 149.

LARGE, R.V., 1970. The biological efficiency of meat production in sheep. *Anim. Prod.* 12, 393.

MacNEIL, M.D., CUNDIFF, L.V., DINKEL, C.A. & KOCH, R.M., 1984. Genetic correlations among sex-limited traits in beef cattle. *J. Anim. Sci.* 58, 1171.

MEISSNER, H.H., ROUX, C.Z. & HOFMEYR, H.S., 1975. Voluntary feed intake, growth, body composition and efficiency in the sheep: breed and sex differences. *Agroanimalia* 7, 105.

RISKA, B., ATCHLEY, W.R. & RUTLEDGE, J.J., 1984. A genetic analysis of targeted growth in mice. *Genetics* 107, 79.

ROUX, C.Z., 1992a. Maximum herd efficiency in meat production. I. Optima for slaughter mass and replacement rate *S. Afr. J. Anim. Sci.* 22, 1.

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

ROUX, C.Z. & MEISSNER, H.H., 1984. Growth and feed intake patterns. 1. The derived theory. In: Herbivore nutrition in the subtropics and tropics. Eds. Gilchrist, F.M.C. & Mackie, R.I., The Science Press, Craighall. p. 672.

SCHAUF, C.L., 1987. Ion channel diversity: A revolution in biology? *Sci. Prog. Oxf.* 71, 459.

SCHOLTZ, M.M., ROUX, C.Z., DE BRUIN, D.S. & SCHOEMAN, S.J., 1990. Medium-term responses to and changes in fitness with selection for parameters of the allometric-autoregressive model. *S. Afr. J. Anim. Sci.* 20, 65.

SIEBRITS, F.K. & BARNES, P.M., 1989. The change in the rate of muscle protein metabolism of rats from weaning to 90 days of age. *Comp. Biochem. Physiol.* 92A, 485.

SIEBRITS, F.K., KEMM, E.H., RAS, M.N. & BARNES, P.M., 1986. Protein deposition in pigs as influenced by sex, type and livemass. 1. The pattern and composition of protein deposition. *S. Afr. J. Anim. Sci.* 16, 23.

SIMPSON, S.P., WEBB, A.J. & WILMUT, I., 1986. Performance of British Landrace pigs selected for high and low incidence of halothane sensitivity. 1. Reproduction. *Anim. Prod.* 43, 485.

SMITH, C., 1964. The use of specialized sire and dam lines in selection for meat production. *Anim. Prod.* 6, 337.

TAYLOR, St C.S., 1987. An evaluation of genetic size-scaling in breed and sex comparisons of growth, food efficiency and body composition. Proc. 6th Conf. Australian Assoc. Anim. Breeding and Genet. Perth.

TAYLOR, St C.S., MOORE, A.J., THIESSEN, R.B. & BAILEY, C.M., 1985. Efficiency of food utilization in traditional and sex-controlled systems of beef production. *Anim. Prod.* 40, 401.

TAYLOR, St C.S. & MURRAY, J.I., 1987. Genetic aspects of mammalian survival and growth in relation to body size. In: Nutrition of Herbivores. Proc. 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.

THIESSEN, R.B. & TAYLOR, St C.S., 1986. Inter-age correlation of food conversion efficiency with body weight, growth rate and food intake within and between British breeds of cattle. *Anim. Prod.* 43, 91.

WEBB, A.J. & SIMPSON, S.P., 1986. Performance of British Landrace pigs selected for high and low incidence of halothane sensitivity. 2. Growth and carcass traits. *Anim. Prod.* 43, 493.