An investigation into the consequences of selection for growth, size and efficiency*

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The effect of selecting for growth, size and efficiency on fitness (fertility and survival rate) and body composition was investigated by surveying a number of selection experiments which have appeared in *Animal Breeding Abstracts* since 1938. In the case of rodents and poultry, selection for body mass, growth rate and feed efficiency was studied in 26, 21 and 13 experiments respectively. Much less information on the relationship between growth, size or efficiency and fitness is available for beef cattle and mutton sheep. When selecting for increased body mass or growth rate in rodents and poultry, almost 90% of the experiments yielded data which demonstrated an increase in body fat, or a decrease in fitness, or both in the offspring. When selecting for increased feed efficiency, only 15% of the experiments surveyed reported unfavourable results. In general, the relationship between growth rate or body mass and fertility in beef cattle tends to be negative. Animal breeding for meat should therefore not be based on selection for growth or size alone. Other selection criteria should be investigated and the principle of utilizing sire and dam lines in beef cattle should receive attention.

'n Ondersoek na die invloed van seleksie vir groei, grootte en voerdoeltreffendheid op fiksheid (vrugbaarheid en oorlewing) en liggaamsamestelling is uitgevoer deur seleksie-eksperimente te bestudeer wat sedert 1938 in *Animal Breeding Abstracts* verskyn het. By knaagdiere en pluimvee is 26, 21 en 13 seleksie-eksperimente vir onderskeidelik massa, groeitempo en voerdoeltreffendheid bestudeer. Baie minder inligting oor die verwantskap tussen groei, grootte of voerdoeltreffendheid en fiksheid is vir vleisbeeste en -skape beskikbaar. Met seleksie vir 'n hoër liggaamsmassa of groeitempo by knaagdiere en pluimvee het ongeveer 90% van die eksperimente 'n toename in liggaamsvet of 'n afname in fiksheid of beide getoon, in vergelyking met 15% wanneer vir 'n beter voerdoeltreffendheid geselekteer is. Oor die algemeen neig die verwantskap tussen groeitempo of liggaamsmassa en vrugbaarheid by vleisbeeste om negatief te wees. Vleisdierteelt kan dus nie net op seleksie vir groei of grootte gefundeer word nie. Ander seleksie-kriteria behoort ondersoek te word en die beginsel van die gebruik van vader- en moederlyne by vleisbeeste behoort oorweeg te word.

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A recent experiment (Scholtz, Roux, de Bruin & Schoeman, 1990) which selected for parameters of growth and efficiency reduced reproductive fitness. In order to determine whether these results were anomalous, the literature was reviewed for experiments selecting for growth and efficiency in animals. The investigation was not limited to fertility alone, but was extended to include survival rate, body composition and feed intake. All the experiments investigated were performed on rodents (rats and mice) and poultry (chickens, turkeys and quails).

Materials and Methods

The correlated responses in fitness, body composition and feed intake were investigated by using selection experiments which have appeared in *Animal Breeding Abstracts* since 1938. Experiments were chosen where selection was for body mass, and traits related to growth rate or efficiency. The number of experiments for each trait (body mass, growth rate, feed efficiency) and species (rodents, poultry) involved in this study are summarized in Table 1.

Components of fitness, such as litter size, fertility, survival rate, etc. were all referred to as fitness.

The results of 26 selection experiments for body mass were obtained. Traits such as rate of live mass-gain, lean growth and protein gain were all considered as selection experiments for growth rate, of which 21 were found. Results reflecting selection for feed efficiency *per se* were not often found. This is probably due to the necessity for measuring individual feed intakes. Experiments reflecting selection for traits related to feed efficiency, e.g. growth at constant feed intake and minimum intake for constant gain, were included with experiments in which efficiency was selected for directly. There was a total of 13 experiments.

Results

The correlated responses in body fat, mature mass, fitness and feed intake with selection for increased body mass, growth rate and feed efficiency are summarized separately for rodents and poultry in Table 2. Only correlated responses mentioned explicitly were considered in this Table. Consequently, the data in Table 2 probably underestimate the correlated responses.

Differences between species across traits and between traits across species for the different correlated responses are summarized in Table 2. These differences were tested for significance (χ^2) and the results are given in Table 3. In most cases there were no differences between species in the percentage of experiments showing a certain correlated

Table 1 Summary of the number of experiments involved for each trait and species

	Species		
Trait	Rodents	Poultry	Total number
Body mass	18	8	26
Growth rate	18	3	21
Feed efficiency	9	4	13
Total	45	15	60

response. The only differences between species were found between increased body fat and feed intake. Owing to the general similarity of the correlated responses between species, these responses were combined in Table 2. In all cases there were significant differences between traits, indicating that the correlated responses were significantly different for the different traits.

From Table 2 it is clear that selection for increased body mass or growth rate led to an increase in the percentage of body fat in 42% and 67% of the experiments, respectively, while fitness decreased in 65% and 43% of the experiments, respectively. When selecting for feed efficiency, on the other hand, body fat increased and fitness decreased in only a small percentage of the experiments (8% and 15%, respectively). In fact, there was a decrease in body fat in 31% of the experiments. When selecting for increased body mass or growth rate, body fat increase or fitness decrease or both occurred in almost 90% of the experiments. When selecting for increased feed efficiency, this figure dropped to 15%.

When selecting for increased body mass and growth rate, feed intake increased in 23% and 33% of the experiments, respectively. Where feed efficiency was the selected trait, an increase in feed intake was found in 15% of the experiments. Mature mass increased in 27%, 24% and 31% of the experiments when selecting for body mass, growth rate and feed efficiency respectively. Only recent experiments, however, considered mature mass as a possible correlated response.

The number of generations involved in selecting for feed efficiency was much smaller than the number when selecting for body mass or growth rate. One may, therefore, reason that the more frequent deleterious effects encountered with selection for body mass or growth rate result from more generations of selection. It was, therefore, decided to investigate the correlated responses where selection was practised for 10 to 15 generations. These results are summarized in Table 4.

The same conclusions can be drawn from Table 4 as from Table 2. For instance, in almost 90% of the experiments in which the trait selected for was body mass or growth rate, deleterious effects on body fat or fitness or both were encountered, compared with 25% with selection for efficiency. This supports the conclusions drawn from Table 2.

Discussion

The results investigated indicate that selection for increased body mass or growth rate may have an adverse effect on body composition, fertility and survival rate. Selection for increased feed efficiency, on the other hand, may lead to fewer adverse effects.

For example, mice selected for body mass or growth rate became obese with age (Roberts, 1965; Timon & Eisen, 1970; Bradford, 1971; Eisen, 1976). A further consequence of selecting for body mass or growth rate in mice may be a reduced fitness (Bradford, 1971; Eisen, 1974; Roberts, 1974; Baker & Chapman, 1975; Barria & Bradford, 1981). Litter size was usually larger in mice selected for body mass but there were more infertile matings and their reproductive life was shorter (Roberts, 1961; Bradford, 1971; Eisen, Hanrahan & Legates, 1973). Roberts (1980) concluded that selection for increased body mass or growth rate in laboratory animals generally has two undesirable consequences, viz. obesity, especially with age, and a reduced fertility to the point where population numbers decrease.

The same conclusion may be drawn for poultry. In fast-growing lines, obesity was encountered with age (Edwards, Denham, Abou-Ashour & Nugara, 1973). This led to infertil-

Table 2 Correlated responses to selection for body mass, growth rate or feed efficiency in terms of the percentage experiments exhibiting effects on body fat, mature mass, fitness and feed intake

			Correlated response (% of experiments)					
Selection for increased:	Species	Average number of generations	Increased fat	Decreased fat	Decreased fitness	Increased feed intake	Increased mature mass	Deleterious effect on fat or fitness
Body mass	Rats / mice	20	56	0	61	0	11	89
	Poultry	10	12	0	75	33	63	88
	Combined	17	42	0	65	23	27	89
Growth rate	Rats / mice	16	67	0	44	39	28	89
	Poultry	7	66	0	33	0	0	66
	Combined	15	67	0	43	33	24	86
Feed efficiency	Rats / mice	8	11	33	11	22	33	11
	Poultry	4	0	25	25	0	25	25
	Combined	7	8	31	15	15	31	15

Table 3 χ^2 Values for differences between species across traits and between traits across species

	Increased fat	Decreased fat	Decreased fitness	Increased feed intake	Increased mature mass	Deleterious effect on fat or fitness
Between species	14,79***	1,16	1,10	8,34***	1,60	0,27
Between traits	105,40***	60,80***	116,20***	4,74*	20,46***	93,79***

* Significant at 10% level.
*** Significant at 1% level.

ity, since excessive fat may interfere with the laying ability of hens (McCarthy, 1977). Selection for increased egg production in chickens showed a negative genetic correlation between body mass and egg production. The same was found in turkeys, where selection for egg production led to a decrease in body mass (Nestor & Bachev, 1970). An excellent example of the negative correlation between growth rate and fitness was cited by Pym (1981), who reported a 26% decrease in hatchability and a 46% decrease in the number of chickens produced after nine generations of selection for growth rate. This finding supports the general conclusion that a negative genetic correlation between body mass or growth rate and egg production may cause changes in fitness without the involvement of inbreeding (McCarthy, 1977).

Possible reasons why selection for body mass or growth rate may negatively influence fitness can be postulated as follows:

1. Eisen *et al.* (1973) suggested that the dramatically increased infertility results from the deviation from an optimum body mass associated with an optimum degree of fitness.
2. Barria & Bradford (1981) suggested that pleiotropic genes with opposite effects on growth rate and fertility may become important after prolonged selection.
3. Berg & Walters (1983) and Scholtz *et al.* (1990) believe that major changes in body mass or growth rate may upset homeostasis and endocrine balance, which has developed in each species over its evolutionary history.
4. Selection for increased growth rate may result in indirectly selecting for feed intake and this may lead to the breeding of gluttons. Such gluttons will become obese at maturity which may influence fertility.

Selecting for feed intake implies that gluttons will result from the breeding programme. This was demonstrated by two selection experiments (summarized in Table 5); one with mice (Sutherland, Biondini, Haverland, Pettus & Owen, 1970) and the other with chickens (Pym, 1981). The results of Pym's experiment (1981) clearly illustrate the deleterious effects on body composition and fitness when selecting for feed intake. The data reflected a 25% increase in total body fat, a 44% increase in abdominal fat, a 10% decrease in hatchability and a 46% decrease in the number of chickens produced.

A higher growth rate is usually associated with leaner animals. Thus, the increased body fat resulting from selection for a higher growth rate was unexpected. This can be explained, however, by evidence that shows that selection for increased growth rate tends to increase feed intake (Sutherland *et al.*, 1970; Hetzel & Nicholas, 1978; Kownacki & Jezierski, 1980) and decrease activity and maintenance requirements (Kennedy & Mitra, 1963; Owens, Siegel & van Krey, 1971; Masic, Wood-Gush, Duncan, McCorquodale & Savory, 1974; Kuenzel & Kuenzel, 1977). The nett result is that more energy is available for fat deposition, because the rate of lean tissue deposition slows down with age.

Information on the effect of selection for body mass or growth rate on fitness in cattle and sheep is limited. The results of Cundiff, Gregory & Koch (1974), Koch, Gregory & Cundiff (1974) and Muggli & Hohenboken (1983) indicated that calves from lines selected for heavier body masses showed a higher incidence of dystocia and calf mortality than calves from unselected control lines. The results of Laster, Smith & Gregory (1976), however, suggested that there was an optimum growth rate for optimum reproduction in heifers.

Table 4 Correlated responses after 10 to 15 generations of selection for body mass, growth rate or feed efficiency in terms of the percentage experiments exhibiting effects on body fat, mature mass, fitness and feed intake

		Correlated response (% of experiments)					
Selection for increased:	No. of experiments	Increased fat	Decreased fat	Decreased fitness	Increased feed intake	Increased mature mass	Deleterious effect on fat or fitness
Body mass	9	22	0	67	33	33	89
Growth rate	10	60	0	60	30	20	90
Efficiency	4	0	50	25	50	25	25

Table 5 Correlated responses with selection for higher feed intake

Selection for:	Species	Generation	Correlated response	Source
1. Feed intake	Mice	12	Moderate increase in rate of gain and efficiency; drastic increase in body size and % fat; decreased fitness.	Biondini, Sutherland & Haverland (1968); Sutherland, Biondini, Haverland, Pettus & Owen (1970)
2. Increased feed consumption	Chicken	9	Increased % total body fat (24,6%) and abdominal fat (44,3%); decreased hatchability (10,2%) and chickens produced (46,2%).	Pym (1981)

A number of researchers (Monteiro, 1969; Bar-Anan, 1971; Gaillard, 1974; Soller & Bar-Anan, 1974; Taylor, Monteiro & Perreau, 1975) reported a positive correlation between increased growth rate and the incidence of dystocia or calf mortality. More recently, Scholtz & Roux (1984) demonstrated a negative relationship between body mass and fitness in beef cattle in South Africa. Selection experiments for growth rate in beef cattle in the USA showed that calving problems and calf mortalities increased. The same problems, however, were not encountered in similar experiments in Australia, Canada and New Zealand (Baker & Morris, 1984).

In an earlier literature review, Roux & Scholtz (1984) found that the global relationship between growth rate or body mass and fertility with between-breed correlations in beef cattle is uniformly negative (varies from −0,3 to −0,9). By contrast, MacNeil (1988) found a positive between-breed correlation of 0,2 in cattle. However, he also found a rather strong negative between-breed correlation of −0,4 in sheep.

The contradictions illustrated above may be explained by Sewall Wright's presentation of the genetic landscape as elucidated by Lush (1945). This genetic landscape interlinks with Fisher's (1930) fundamental theorem of natural selection which implies that in natural populations, reproductive fitness and body mass will be near to a peak of maximum fitness.

The nature of any particular relationship will depend on the position of the population studied on the genetic landscape. If the position of the population is to the left of a peak, the relationship will be positive, while it will be negative if it is to the right-hand side of a peak (Scholtz, 1988).

Conclusions

In this study it has clearly been shown that selecting for body mass or growth rate may adversely affect reproductive performance and body composition. Selecting for efficiency may be a solution, but it is not always practical since it is labour-intensive and expensive. Some form of index selection, restricting feed intake or mature mass, may therefore provide a partial solution to the antagonism which exists between growth rate or body mass and reproductive performance or body composition. Some of the alternatives are listed below, although they are as yet unproven.

Firstly, selection may be practised for growth rate on restricted feeding, which might imply selection on roughage in beef cattle. Hetzel & Nicholas (1978) found that selecting for growth rate when mice are fed either *ad libitum* or on a restricted basis (82% of *ad libitum*) acts on different genetic components. When mice were fed *ad libitum*, correlated increases in feed intake, mature mass and fatness at maturity were found. When feeding was restricted, feed intake, mature mass and fatness at maturity were reduced. Feed efficiency, however, was improved in both cases.

Secondly, restricted index selection aimed at achieving a high body mass at an early age of the animal's life, but keeping body mass constant at a later age, can be practised (Wilson, 1973). In essence, this represents a change in the growth curve of animals.

Thirdly, a partial solution may be to select for growth rate, accompanied by a change in current feeding regimes. This implies a movement towards restricted feeding practices in breeding animals, as is the case with pigs and poultry (Siegel & Dunnington, 1988). Hence, a solution may lie in the use of growth models, such as the allometric-autoregressive model of Roux (1980) or Parks' model (1982), to predict feed intake for required growth rates and rates of protein and fat deposition. The feasibility of using this method in beef cattle is limited at this stage, since it is difficult to restrict feeding of breeding cows.

The use of sire and dam lines in terminal cross-breeding may be the ideal solution for beef cattle to overcome the problems of the antagonism between growth and reproductive performance. In such a system of terminal cross-breeding it would be possible to combine growth and fertility, which are likely to be two antagonistic traits.

References

BAKER, R.L. & CHAPMAN, A.B., 1975. Correlated responses to selection for postweaning gain in the rat. *Genetics* 80, 191.

BAKER, R.L. & MORRIS, C.A., 1984. A review of correlated responses to weight selection in beef cattle under different management and climate conditions. *Prov. 2nd Wrld. Congr. Sheep Beef Cattle Breed.* (Pretoria, South Africa) 236.

BAR-ANAN, R., 1971. Einige probleme bei der zucht des zweinutzungsrindes. *Zuchtungskunde* 43, 74.

BARRIA, N. & BRADFORD, G.E., 1981. Long-term selection for rapid gain in mice. I. Genetic analysis at the limit of response. *J. Anim. Sci.* 52, 729.

BERG, R.T. & WALTERS, L.E., 1983. The meat animal: Changes and challenges. *J. Anim. Sci.* 47, Suppl. 2, 133.

BIONDINI, P.E., SUTHERLAND, T.M. & HAVERLAND, L.H.,

1968. Body composition of mice selected for rapid growth rate. *J. Anim. Sci.* 27, 5.

BRADFORD, G.E., 1971. Growth and reproduction in mice selected for rapid body weight gain. *Genetics* 69, 499.

CUNDIFF, L.V., GREGORY, K.E. & KOCH, R.M., 1974. Effects of heterosis on reproduction in Herefords, Angus and Shorthorn cattle. *J. Anim. Sci.* 38, 711.

EDWARDS, H.M., DENHAM, F., ABOU-ASHOUR, A. & NUGARA, D., 1973. Carcass composition studies. 1. Influence of age, sex and type of dietary fat supplementation on total carcass and fatty acid composition. *Poultry Sci.* 42, 934.

EISEN, E.J., 1974. The laboratory mouse as a mammalian model for the genetics of growth. *Proc. 1st Wrld. Congr. Genet. Appl. Livestock Prod.* (Madrid, Spain) 1, 467.

EISEN, E.J., 1976. Results of growth curve analysis in mice and rats. *J. Anim. Sci.* 42, 1008.

EISEN, E.J., HANRAHAN, J.P. & LEGATES, J.E., 1973. Effects of population size and selection intensity on correlated responses to selection for postweaning gain in mice. *Genetics* 74, 157.

FISHER, R.A., 1930. The genetical theory of natural selection. Clarendon press, Oxford.

GAILLARD, C., 1974. Genetishe korrelationen zwischen verschiedenen merkmalen beim rindvieh. *Schweizerishe Landwirtschaftliche Monatshefte* 53, 381.

HETZEL, D.J.S. & NICHOLAS, F.W., 1978. Growth and body composition of mice selected for growth rate under *ad libitum* or restricted feed. *Proc. Aust. Soc. Anim. Prod.* (Melbourne, Australia) 12, 194.

KENNEDY, G.C. & MITRA, J., 1963. Hypothalamic control of energy balance and the reproductive cycle in the rat. *J. Physiol.* 166, 395.

KOCH, R.M., GREGORY, K.E. & CUNDIFF, L.V., 1974. Selection in beef cattle. II. Selection response. *J. Anim. Sci.* 39, 459.

KOWNACKI, M. & JEZIERSKI, T., 1980. Effects of selection on some physiological and biochemical traits in mice. *31st Ann. Meet. Eur. Ass. Anim. Prod.* G1, 12, 7.

KUENZEL, W.J. & KUENZEL, N.T., 1977. Basal metabolic rate in growing chick *Gallus domesticus*. *Poult. Sci.* 56, 619.

LASTER, D.B., SMITH, G.M. & GREGORY, K.E., 1976. Characterization of biological types of cattle. IV. Postweaning growth and puberty of heifers. *J. Anim. Sci.* 43, 63.

LUSH, J.L., 1945. Animal breeding plan. Iowa State College Press, Ames.

MACNEIL, M.D., 1988. Consequences of selection for growth and tissue development on maternal qualities. *Proc. 3rd Wrld. Congr. Sheep Beef Cattle Breed.* (Paris, France) 1, 415.

MASIC, B., WOOD-GUSH, D.G.M., DUNCAN, I.J.H., McCORQUODALE, D. & SAVORY, C.J., 1974. A comparison of the feeding behaviour of young broiler and layer males. *Br. Poult. Sci.* 15, 499.

McCARTHY, J.C., 1977. Quantitative aspects of the genetics of growth. In: Growth and poultry meat production. British Poultry Science Ltd. Edinburgh, p. 117.

MONTEIRO, L.S., 1969. The relative size of calf and dam and the frequency of calving difficulties. *Anim. Prod.* 11, 293.

MUGGLI, N. & HOHENBOKEN, W., 1983. Inheritance of maternal immunoglobin G1 concentration by the bovine neonate. *Proc. XV Int. Congr. Genet.* (New Delhi, India) 1, 36.

NESTOR, K.E. & BACHEV, W.D., 1970. Breeding for increased body weight and egg production in turkeys. *Proc. 14th Wrld. Poult. Congr.* 147.

OWENS, C.A., SIEGEL, P.B. & VAN KREY, H.P., 1971. Selection for body weight at eight weeks of age. Growth and metabolism in two environments. *Poult. Sci.* 50, 584.

PARKS, J.R., 1982. A theory of feeding and growth of animals. Springer-Verlag, Berlin.

PYM, R.A.E., 1981. Growth, food conversion and body composition in broilers: Genetic and physiological interrelationships. In: Recent advances in animal nutrition in Australia. Univ. New England Publishing Unit, Armidale, p. 219.

ROBERTS, R.C, 1961. The lifetime growth and reproduction of selected strains of mice. *Heredity* 16, 369.

ROBERTS, R.C., 1965. Some contributions of the laboratory mouse to animal breeding research. *Anim. Breed. Abstr.* 33, 339.

ROBERTS, R.C., 1974. Selection limits in the mouse and their relevance to animal breeding. *Proc. 1st Wrld. Congr. Genet. Appl. Livestock Prod.* (Madrid, Spain) 1, 493.

ROBERTS, R.C., 1980. Lessons to be drawn from selection experiments with laboratory animals. *Proc. 1st Wrld. Congr. Sheep Beef Cattle Breed.* (Palmerston North, New Zealand) 253.

ROUX, C.Z., 1980. A dynamic model for animal growth. In: Lecture notes in Biomathematics. Springer-Verlag, Berlin, Heidelberg, New York, 33, 117.

ROUX, C.Z. & SCHOLTZ, M.M., 1984. Breeding goals for optimal total life cycle production systems. *Proc. 2nd Wrld. Congr. Sheep Beef Cattle Breed.* (Pretoria, South Africa) 444.

SCHOLTZ, M.M., 1988. Selection possibilities of hardy beef breeds in Africa: The Nguni example. *Proc. 3rd Wrld. Congr. Sheep Beef Cattle Breed.* (Paris, France) 2, 303.

SCHOLTZ, M.M. & ROUX, C.Z., 1984. Correlated responses in selection for growth, size and efficiency. *Proc. 2nd Wrld. Congr. Sheep Beef Cattle Breed.* (Pretoria, South Africa) 433.

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

SIEGEL, P.B. & DUNNINGTON, E.A., 1988. Long-term selection for meat production in poultry. *Anim. Breed. Opportunities* 12, 238.

SOLLER, M. & BAR-ANAN, R., 1974. Correlated effects of selection for rate-of-gain in dairy cattle. *Proc. 1st Wrld Congr. Genet. Appl. Livestock Prod.* (Madrid, Spain) 3, 689.

SUTHERLAND, T.M., BIONDINI, P.E., HAVERLAND, L.H., PETTUS, D. & OWEN, W.B., 1970. Selection for rate of gain, appetite and efficiency of feed utilization in mice. *J. Anim. Sci.* 31, 1049.

TAYLOR, ST. C.S., MONTEIRO, L.S. & PERREAU, B., 1975. Possibilities of reducing calving difficulties by selection III. A note on pelvic size in relation to body weight of cattle. *Ann. Génet. Sélection Anim.* 7, 49.

TIMON, V.M. & EISEN, E.J., 1970. Comparisons of *ad libitum* and restricted feeding of mice selected and unselected for postweaning gain. I. Growth, feed consumption and feed efficiency. *Genetics* 64, 41.

WILSON, S.P., 1973. Selection for a ratio of body weight gain in mice. *J. Anim. Sci.* 37, 1098.