Reducing body fat in broiler chickens and some physiological consequences

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Five experiments were conducted to devise a feeding strategy to reduce fat deposition in broiler chickens. From these experiments it was determined that early feed restrictions, beginning at 7 days of age, decreased body fat, improved FCE, and had little effect on body mass. The severity of feed restriction had the greatest influence on body fat whereas the duration of the feed restriction phase ultimately affected compensatory growth and final body mass. The optimum level of severity was that which provided only the maintenance requirement of the bird. Optimum duration varied with the strain of bird. Feed restriction by dietary dilution was shown to have similar effects to quantitative feed restriction. Metabolic consequences of feed restrictions were determined by adipocyte measurements and respiration calorimetry. Extreme feed restrictions reduced adipocyte volume but milder restrictions affected adipocyte number. Calorimetric measurements showed that when birds, aged 7 days, were restricted-fed for 4 days, subsequent heat production was higher than *ad libitum* fed birds even after 30 days of age.

Vyf eksperimente is uitgevoer om 'n voedingstrategie te beplan om vetneerslae in roosterkuikens (jong slaghoenders, jong braaihoenders) te verminder. Daar is gevind dat 'n beperkte voedselinname by kuikens vanaf die vroeë ouderdom van 7 dae gelei het tot verminderde liggaamsvet en verbeterde voeromsetdoeltreffendheid (FCE), terwyl dit min effek op ligaamsmassa gehad het. Die felheid van voedingrantsoenering het die grootste invloed op liggaamsvet getoon, terwyl die tydperk van die voedselbeperkingsfase uiteindelik die kompenserende groei en finale liggaamsmassa beïnvloed het. Die optimale strawwe vlak van voedselweerhouding was slegs dít wat die voëls benodig het vir lewensonderhoud. Die optimale tydperk het gewissel volgens die voëlstam. Voedselbeperking deur 'n verdunningsdieet het dieselfde effek as kwantitatiewe voedselrantsoenering getoon. Die metaboliese gevolge van voedingbeperkings is deur vetselmetings en asemhalingskalorimetrie bepaal. Uiterste voedingbeperkings het vetsel-volume laat afneem, maar minder strawwe rantsoenering het die aantal vetselle geaffekteer. Kalorimetriese bepalings het getoon dat voëls, op die ouderdom van 7 dae, wat op beperkte voedingsinname van 4 dae was, se daaropvolgende hitteproduksie hoër was as voëls wat *ad libitum* gevoed is, selfs na die ouderdom van 30 dae.

Keywords: Abdominal fat pad, adipocytes, body fat, broilers, energy metabolism, feed restriction

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Introduction

There is increasing pressure in the broiler industry to reduce the fat content of its meat products. Traditionally, chicken meat has been considered to be low in fat but recent studies have suggested that the fat content of chicken meat is comparable to pork and some beef cuts (Hutchinson, Thomas & Truswell, 1987).

Many factors influence the level of fat in the chicken, such as the genotype, environment, nutrition, age, and sex of the bird. Selection for a lean bird is the most likely long-term solution to reduce excess fat, but such programmes can introduce undesirable traits (Gous, 1986) which may offset any positive benefits, particularly in breeder hens (R.A.E. Pym, pers. communication). The use of nutritional manipulation techniques offers a rapid solution to the problem of excess fat without undesirable consequences.

Previous nutritional work has considered the influence of dietary density and concentration as well as the alteration of the protein : energy ratio of the diet. Carcass fat can be reduced by manipulating these factors but the growth rate of the bird may be adversely affected or the cost of the diet increased so as not to warrant commercial acceptance.

The use of feed restrictions is well known in the layer and broiler breeder industries. Their use in broiler production, however, is relatively new. Research initiated in Israel (Plavnik & Hurwitz, 1985) indicated that feed restrictions, when applied to young chicks, reduced the fat content of the bird whilst improving feed conversion efficiency. Their results were inconsistent and final body mass was often less than that for unrestricted birds.

In this paper the use is described of feed restrictions imposed by two methods, during the early growth of the broiler chicken to reduce body fat. Some physiological and metabolical consequences of these manipulations are presented.

Materials and Methods

Birds and management

One-day-old unsexed experimental broiler chicks, selected for low or high body fat (R.A.E. Pym, University of Queensland; Experiments 1 & 2), unsexed commercial broiler chicks (Experiment 3), or sexed commercial broiler chicks (Experiments 4 & 5) were placed in electrically heated brooders until 6 days of age. They were then individually weighed, wing-tagged, and allocated to groups of eight in small, wire-mesh cages. At 14 days, they were transferred to larger cages where they were kept until slaughter. The birds were fed a commercial starter crumble (220 g/kg crude protein) until 28 days and then a commercial finisher feed (190 g/kg crude protein) in all experiments.

The experiments were conducted in environmentally controlled rooms maintained at 32°C, with gradual reductions in temperature to 20°C by 28 days. Continuous lighting was provided.

Feed restrictions were based on the metabolizable energy (ME) content of the diet (~13 MJ/kg) and the body mass of the birds, using the observations of Plavnik & Hurwitz (1985), where 6,3 kJ/g $W^{0,67}$/day was calculated to support maintenance. Feed restriction treatments began at 7 days and were applied continuously for various durations (see below). The birds were fed *ad libitum* otherwise.

The birds were weighed and fed daily during the feed restriction phases. The birds were weighed and feed intake was recorded at weekly intervals otherwise. Prior to slaughter, the birds were starved for 24 h but with continued access to water. After slaughter by cervical dislocation, the abdominal fat pads were removed, weighed, and stored in polythene bags at –20°C. Birds used for carcass fat analysis were frozen in polythene bags at –20°C, cut into small pieces, and finely ground twice by an electrically powered mincer. Carcass fat was determined by measuring the density of a fat/tetrachloroethylene extract, as described by Usher, Green & Smith (1973).

Experimental design

The first five experiments used a factorial, randomized block design. Experiment 1 used five treatments, two lines of experimental broiler chicks (described above), and was replicated twice. The five treatments were an *ad libitum* control and feed restriction to 6,3 kJ/g $W^{0,67}$/day for 6 or 10 days or 8,4 kJ/g $W^{0,67}$/day for 6 or 10 days, where W = mean body weight of each treatment group. Birds were slaughtered at 56 days and six pairs of male and female birds from each treatment were used for carcass fat analysis.

Five treatments, two lines of experimental broiler chicks, and two replicates were used in Experiment 2. The five treatments were an *ad libitum* control and feed restriction to 4,2 kJ/g $W^{0,67}$/day for 6 days; 5,2 kJ/g $W^{0,67}$/day for 6 or 10 days or 6,3 kJ/g $W^{0,67}$/day for 10 days. The birds were slaughtered at 56 days and six pairs of male and female birds from each treatment were used for carcass fat analysis.

In Experiment 3 the use was examined of feed restrictions on two lines of unsexed commercial broiler chicks (Strains 1 & 2). Three treatments were used with three replicates. The three treatments were an *ad libitum* control and feed restriction to 3,1 kJ/g $W^{0,67}$/day for 4 days or 4,2 kJ/g $W^{0,67}$/day for 6 days. The birds were slaughtered at 49 days and nine pairs of birds from each treatment were used for carcass fat determinations.

Two lines of sexed commercial broiler chicks (Strains 3 & 4) were used in Experiment 4. The experiment comprised four treatments with three replicates. The treatments were an *ad libitum* control and feed restriction to 1,0 kJ/g $W^{0,67}$/day for 1 d; 2,0 kJ/g $W^{0,67}$/day for 2 days or 3,1 kJ/g $W^{0,67}$/day for 3 days. The birds were slaughtered at 49 days and nine pairs of birds from each treatment were used for carcass fat determinations.

In the fifth experiment commercial male broiler chicks from one line (Strain 1) and female commercial broiler chicks from another line (Strain 3) were examined. Five treatments and three replicates were used. The birds were fed *ad libitum,* feed restricted to 3,1 kJ/g $W^{0,67}$/day for 4 days or fed a commercial starter diet diluted with 65, 60, or 55% rice hulls for 4, 5, or 6 days, respectively, commencing at 7 days. The birds were slaughtered at 49 days and nine pairs of birds from each treatment were analysed for carcass fat.

The cellular characteristics of the adipose tissues were determined with tissue slices from the abdominal fat pads of fully fed or feed restricted birds in Experiments 2—5 by the procedures of Hood & Allen (1977). The tissue slices were fixed using OsO_4 and the adipocytes counted using a Coulter Counter, Model B.

Respiration calorimetry was conducted using the methods of Farrell (1972) and Pym & Farrell (1977) on two groups each of seven commercial female broiler chicks (Strain 3) from 4—13 days of age. The groups were fed either *ad libitum* or feed restricted to 3,1 kJ/g $W^{0,67}$ for 4 days from 7 days of age. Measurements were again made on two birds from each group from 30—32 days. The experiment was repeated four times.

Statistical analysis

The data were subjected to analysis of variance or regression analysis procedures. Paired-sample *t* tests were used to determine differences between treatments in the respiration calorimetry experiment.

Results

The initial experiment was designed to examine the influence of feed restrictions, commencing at 7 days of age, on two lines of experimental broilers that had been selected for high or low body fat. No interactions were evident between the two lines to the treatments imposed and the results obtained, regardless of line, are shown in Table 1. The maintenance restriction (6,3 kJ/g $W^{0,67}$/day; Plavnik & Hurwitz, 1985) produced similar results to the above maintenance restriction (8,4 kJ/g $W^{0,67}$/day). The duration of the restrictions had the greatest

Table 1 Effect of the severity and duration of feed restrictions on the 8-week body mass, feed conversion efficiency (FCE), abdominal fat pad (AFP), and carcass fat of experimental broiler chickens (Experiment 1)

Treatment	Mass (g)	FCE	AFP (%)	Carcass fat (%)
Ad libitum	1563	0,44	3,37	14,2
6,3 kJ/g $W^{0,67}$/d : 6 d	1509	0,44	2,92	13,7
6,3 kJ/g $W^{0,67}$/d : 10 d	1436	0,47	2,41	12,8
8,4 kJ/g $W^{0,67}$/d : 6 d	1415	0,43	2,96	13,5
8,4 kJ/g $W^{0,67}$/d : 10 d	1460	0,45	2,87	13,5
LSD (P = 0,05)	107	0,02	0,49	1,2

effect on body mass and body fat. Birds on the maintenance restriction for 6 days had a similar 8-week body mass to the *ad libitum* fed birds with no improvement in feed conversion efficiency (FCE). The abdominal fat pad (AFP) and carcass fat were reduced, but not significantly ($P > 0{,}05$). When subjected to a 10-day period of restriction, the birds fed the maintenance ration had a decreased 8-week body mass but an improved FCE (7% above *ad libitum* fed birds) and decreased fat levels. The AFP was reduced by 28% and carcass fat by 10%. The 8-week body mass and FCE were improved and the AFP was reduced by increasing the duration of the restriction phase from 6 days to 10 days in the 8,4 kJ / g $W^{0,67}$ / day treatment but not significantly ($P > 0{,}05$).

The first experiment indicated that feed restrictions above the maintenance level suggested by Plavnik & Hurwitz (1985) were ineffective in reducing body fat deposition. Experiment 2 considered increased feed restriction severities and compared these to the most successful restriction from Experiment 1 (6,3 kJ/g $W^{0,67}$/day : 10 days). Three treatments gave similar results (4,2 kJ / g $W^{0,67}$ / day : 6 days; 5,2 kJ / g $W^{0,67}$ / day :10 days; 6,3 kJ / g $W^{0,67}$ / day : 10 days) where the 8-week body mass was not decreased significantly. The AFP was significantly decreased ($P < 0{,}05$) in two treatments (4,2 kJ / g $W^{0,67}$ / day : 6 days; 6,3 kJ / g $W^{0,67}$ / day : 10 days) whilst the FCE and carcass fat were decreased by the longer durations of feed restriction (Table 2). The two experimental lines of broilers again responded similarly to feed restriction and no interactions were apparent. From both experiments, the 6,3 kJ/g $W^{0,67}$/day : 10 days treatment produced a decrease in body fat, an improvement in FCE with an inconsistent effect on 8-week body mass.

Table 2 Effect of the severity and duration of feed restrictions on the 8-week body mass, feed conversion efficiency (FCE), abdominal fat pad (AFP), and carcass fat of experimental broiler chickens (Experiment 2)

Treatment	Mass (g)	FCE	AFP (%)	Carcass fat (%)
Ad libitum	1525	0,44	2,70	14,7
4,2 kJ/g $W^{0,67}$/d : 6 d	1459	0,45	1,90	13,4
5,2 kJ/g $W^{0,67}$/d : 6 d	1500	0,45	2,58	14,4
5,2 kJ/g $W^{0,67}$/d : 10 d	1482	0,46	1,90	12,8
6,3 kJ/g $W^{0,67}$/d : 10 d	1457	0,46	1,90	12,7
LSD ($P = 0{,}05$)	99	0,01	0,47	1,4

The growth rate of the experimental lines was below that of commercial broilers. The validity of the feed restriction techniques was tested, therefore, on two strains of commercial broiler chickens in Experiment 3. One of these was a lean (Strain 1) and the other a fat (Strain 2) strain. The restrictions imposed were more severe than previously but for shorter durations. The two feed restrictions used (3,1 kJ / g $W^{0,67}$ / day : 4 days; 4,2 kJ / g $W^{0,67}$ / day : 6 days) had no effect on body fat in Strain 1 although 7-week body mass and FCE were influenced by the 4,2 kJ / g $W^{0,67}$ / day : 6-day treatment (Table 3). The 3,1 kJ / g $W^{0,67}$ / day : 4-day treatment was most effective on Strain 2. The 7-week body mass was not significantly reduced ($P > 0{,}05$), FCE was improved and carcass fat reduced by 16%. The loss of body mass (60 g) due to this restriction was accounted for by a loss of 67 g of fat tissue. The feed restrictions had no influence on the AFP of either strain, although interactions were apparent. Strain 1 males showed a decrease in AFP when subjected to feed restriction, whereas female birds did not. Strain 2 birds exhibited the reverse effect.

Table 3 Effect of the severity and duration of feed restrictions on the 7-week body mass, feed conversion efficiency (FCE), abdominal fat pad (AFP), and carcass fat of two strains of commercial broiler chickens (Experiment 3)

Treatment	Mass (g)	FCE	AFP (%)	Carcass fat (%)
Strain 1				
Ad libitum	2268	0,52	1,34	11,7
3,1 kJ/g $W^{0,67}$/d : 4 d	2143	0,52	1,18	11,7
4,2 kJ/g $W^{0,67}$/d : 6 d	2109	0,55	1,17	11,4
Strain 2				
Ad libitum	2241	0,47	2,01	15,1
3,1 kJ/g $W^{0,67}$/d : 4 d	2181	0,50	1,78	12,7
4,2 kJ/g $W^{0,67}$/d : 6 d	2032	0,50	1,78	13,9
LSD ($P = 0{,}05$)	120	0,03	0,34	1,5

When very severe feed restrictions were applied for short durations to two further strains of commercial broiler chickens (Experiment 4), no benefits were obtained (Table 4). In some cases, the size of the AFP tended to increase.

Table 4 Effect of the severity and duration of feed restrictions on the 7-week body mass, feed conversion efficiency (FCE), abdominal fat pad (AFP), and carcass fat of two strains of commercial broiler chickens (Experiment 4)

Treatment	Mass (g)	FCE	AFP (%)	Carcass fat (%)
Strain 3				
Ad libitum	2307	0,50	2,84	15,0
1,0 kJ/g $W^{0,67}$/d : 1 d	2230	0,50	2,93	15,2
2,0 kJ/g $W^{0,67}$/d : 2 d	2193	0,49	2,38	14,8
3,1 kJ/g $W^{0,67}$/d : 3 d	2221	0,50	2,70	15,4
Strain 4				
Ad libitum	2300	0,50	1,95	14,5
1,0 kJ/g $W^{0,67}$/d : 1 d	2274	0,50	2,02	14,4
2,0 kJ/g $W^{0,67}$/d : 2 d	2218	0,49	2,09	15,1
3,1 kJ/g $W^{0,67}$/d : 3 d	2205	0,50	1,90	14,7
LSD ($P = 0{,}05$)	89	0,02	0,07	0,9

The first four experiments indicated the possibility of feed restriction techniques being successful in reducing body fat. However, three problems were apparent with the techniques being employed. These were an increase in wet droppings from birds subjected to the restrictions, the increased excitability of these birds and the impracticality of these feeding methods in commercial practice. The fifth experiment, therefore, considered feed restrictions by dietary dilution with rice hulls (a relatively indigestible diluent) and compared these to the most successful quantitative restriction (3,1 kJ/g $W^{0,67}$/day : 4 days).

The quantitative restriction had a non-significant effect on the 7-week body mass, no effect on FCE, but decreased the AFP and carcass fat level (Table 5). The 35 : 65 (starter crumble : rice hull) treatment, designed to produce intakes of starter crumble equivalent to the 3,1 kJ/g $W^{0,67}$/day : 4-day treatment, decreased body fat but also depressed the 7-week body mass. The two other treatments, less severe but for longer durations, decreased body fat but had more pronounced effects on body mass.

Table 5 Influence of feed restriction and dietary dilution by rice hulls on the 7-week body mass, feed conversion efficiency (FCE), abdominal fat pad (AFP), and carcass fat of commercial broiler chickens (Experiment 5)

Treatment	Mass (g)	FCE	AFP (%)	Carcass fat (%)
Ad libitum	2157	0,48	2,26	12,1
3,1 kJ/g $W^{0,67}$/d : 4 d	2082	0,48	2,02	10,7
Dilution [a]				
35 : 65 4 d	2024	0,48	1,84	10,2
40 : 60 5 d	2004	0,50	1,94	10,4
45 : 55 6 d	1971	0,47	2,02	10,7
LSD (P = 0,05)	78	0,02	0,24	0,5

[a] Starter crumble : rice hull.

The effects of feed restrictions on the cellularity of the adipose tissues were examined using abdominal fat pads from birds in Experiments 2, 3, and 5. Effects of the sex of the bird on adipose cellularity were examined in birds (Strain 3) from Experiment 4. The mean volume of the adipocytes from the abdominal fat pad was highly variable, however, a significant reduction ($P < 0,05$) in volume was observed in the low fat line used in Experiment 2 and the male birds examined from Experiment 4 (Table 6). No differences between the treatments were observed in Experiments 3 and 5. However, adipocyte volume was linearly related to the size of the abdominal fat pad in Experiment 2 (Y = 10,4 + 113X; r^2 = 0,51***), Experiment 3 (Y = –6,13 + 235X; r^2 = 0,71***) and in the male birds examined from Experiment 4 (Y = 18,9 + 167X; r^2 = 0,23*).

Table 6 Mean adipocyte volume (nl) determined from the abdominal fat pads of chickens from selected treatments in Experiments 2 and 4

Treatment		Experiment 2 Fat	Experiment 2 Lean	Experiment 4 Male	Experiment 4 Female
Ad libitum		0,244	0,226	0,276	0,239
1,0 kJ/g $W^{0,67}$/d :	1 d			0,233	0,240
2,0 kJ/g $W^{0,67}$/d :	2 d			0,174	0,254
3,1 kJ/g $W^{0,67}$/d :	3 d			0,193	0,248
4,2 kJ/g $W^{0,67}$/d :	4 d	0,200	0,130		
LSD (P = 0,05)		0,090		0,080	

Respiration calorimetry (Experiment 7) indicated that the effects of feed restrictions (3,1 kJ/g $W^{0,67}$/day : 4 days) imposed at 7 days of age were still apparent at 30 days of age (Table 7). During the restriction phase (days 7—10), the metabolizability of the diet and feed intake were depressed, with subsequent effects on the energy and nitrogen balances of the birds. Some of these effects were maintained immediately after the restrictions were lifted. However, heat production and energy retention were still affected at 30 days of age (Table 7). Heat production was higher, and hence energy balance lower, in birds previously subjected to feed restrictions. The maintenance energy requirement of these birds was 60% lower (803 kJ/kg $W^{0,75}$) than the birds fed *ad libitum*. No effects on the nitrogen economy were observed at 30 days of age.

Table 7 Diet metabolizability, feed intake, and energy and nitrogen balances of female commercial broiler chickens fed either *ad libitum* (C) or feed restricted (R) to 3,1 kJ/g $W^{0,67}$/day : 4 days

Phase		Pre-restriction	Restriction	Post-restriction	
Age (d)		4–6	7–10	11–13	30–32
Metabolizability	C	75,8	75,4	75,1	74,3
(%)	R	74,0	67,3***	74,2	73,0
Feed intake	C	498	767	847	593
(g)	R	494	174***	848	561
ME intake	C	2478	2377	2263	1463
(kJ/kg $W^{0,75}$/d)	R	2462	540***	2926***	1539
Heat production	C	1188	1183	1223	839
(kJ/kg $W^{0,75}$/d)	R	1176	851**	1291**	908*
Energy retention	C	40,4	35,5	34,5	33,7
(%)	R	39,9	–40,2***	42,5**	30,1**
Nitrogen intake	C	6,78	6,46	6,13	3,96
(g/kg $W^{0,75}$/d)	R	6,76	1,63**	8,02**	4,38
Nitrogen retention	C	57,7	55,3	51,3	47,8
(%)	R	57,5	38,2**	50,8	46,0

* $P < 0,05$; ** $P < 0,01$; *** $P < 0,001$.

Discussion

The recovery from a period of undernutrition, induced here by feed restrictions, is influenced by a number of factors (Wilson & Osbourn, 1960), the two most critical being the severity of the undernutrition and its duration. As these increase, the recuperative ability of the animal diminishes. If a feed restriction is too mild or of too short a duration, over-compensation may arise (Clarke & Smith, 1938) and fat levels may increase. If the feed restriction is too severe or of too long a duration, bone growth will be retarded (Brody, 1945) and body mass will not fully recover.

The influence of the severity of a feed restriction, as determined in the experiments conducted here, can be summarized as follows. If the animal loses weight during the restriction phase, body mass will not, or will be slow to recover and fat levels will be depressed. If the animal gains body mass, then recovery will be complete and fat levels may rise. If the animal maintains body mass, the recovery will be generally complete and fat levels depressed. Hence, the optimum level of severity will be constant between strains. However, the ideal duration is largely determined by the growth rate of the bird.

To maintain body mass during the restriction phase, the restriction regime must provide the maintenance requirement only. The experimental broilers gained body mass during the restriction phase. Therefore, the severity of the feed restrictions was decreased when applied to commercial broilers. In Experiments 3 and 5, only when the amount of feed provided during restriction was decreased by 50% (3,1 kJ/g $W^{0,67}$/day) maintenance was achieved. This restriction, when applied for 4 days, decreased body fat whilst generally improving FCE and maintaining body mass. When applied for a shorter duration (3 days; Experiment 4), this restriction had no effect on body fat.

The use of rice hulls to dilute commercial starter diets has some potential, although this was not fully realized in the experiment conducted. The rice-hull diets were less palatable than the commercial diet and hence produced more severe restrictions than intended, which was reflected in the final body mass. Fat levels were depressed but without full body mass recovery, the results are unsatisfactory. A 40 : 60 (starter crumble : rice hull) dilution applied for 4 days may have produced more favourable results.

It is possible that under extreme nutritional restriction, both cell hyperplasia and cell hypertrophy are affected and, in less extreme restrictions, only cell number is affected. The birds in Experiment 2 were subject to the most extreme restriction and the male birds of Experiment 4 would have been more extremely restricted than the females due to greater growth rates under normal conditions. In both cases, cell volume was affected. In the two other experiments, cell volume was not influenced and hence the success of the restrictions imposed is possibly due to cell number differences. The methods used here give no independent estimate of cell number, although, if the size of the abdominal fat pad is reduced and cell volume unaffected by feed restriction, it can be deduced that cell number has been depressed by the feed restriction.

The results of the respiration calorimetry study indicate that the effects of feed restriction on heat production were still apparent three weeks after they were lifted. This increase may be a reflection of either compensatory growth or the younger physiological age of the treated birds which would give a higher heat production. The initial decrease in growth rate causes a shift in the growth curve. However, the slope of this curve is increased.

Reducing the feed intake of broilers at 7 days of age has been shown to be a viable method of reducing body fat. It may be necessary to 'fine tune' the restrictions to suit particular strains of broilers. In the experiments presented here, the birds were grown to age rather than mass. Again, adjustment to the restrictions would be necessary for birds grown to a set body mass.

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References

BRODY, S., 1945. Bioenergetics and growth. Reinhold, New York.

CLARKE, M.F. & SMITH, A.H., 1938. Recovery following suppression of growth in the rat. *Br. J. Nutr.* 15, 245.

FARRELL, D.J., 1972. An indirect closed circuit respiration chamber suitable for fowl. *Poult. Sci.* 51, 683.

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

HOOD, R.L. & ALLEN, C.E., 1977. Cellularity of procine adipose tissue : effects of growth and adiposity. *J. Lipid Res.* 18, 275.

HUTCHINSON, G.I., THOMAS, D.E. & TRUSWELL, A.S., 1987. Nutrient composition of Australian chicken. *Food Technol. Aust.* 39, 196.

PLAVNIK, I. & HURWITZ, S., 1985. The performance of broiler chicks during and following a severe feed restriction at an early age. *Poult. Sci.* 64, 348.

PYM, R.A.E. & FARRELL, D.J., 1977. A comparison of the energy and nitrogen metabolism of broilers selected for increased growth rate, food consumption and conversion of food to gain. *Br. Poult. Sci.* 18, 411.

USHER, C.D., GREEN, C.J. & SMITH, C.A., 1973. The rapid estimation of fat in various foods using the Foss-Let density apparatus. *J. Fd. Technol.* 8, 429.

WILSON, P.N. & OSBOURN, D.F., 1960. Compensatory growth after undernutrition in mammals and birds. *Biol. Rev.* 35, 324.