Differences in body compositions, growth and food intakes between mice which have been selected for a small and large body size

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1. Q-strain mice selected for high (QLF) or low (QSC) body-weight at 6 weeks of age were compared with respect to their body-weight increases, gross body compositions and food intakes.

2. DNA, RNA, protein and hydroxyproline contents were measured.

3. QLF animals were larger at all stages of development but ate more food and gained more body-weight per unit food intake with an apparently improved efficiency of utilization compared with QSC mice.

4. The efficiency of deposition of dietary energy in Q-strain mice was found to be significantly lower than that of other growing mammals receiving similar energy intakes.

5. Body water, protein and fat of both strains were similar at birth and at 42 d of age but the contribution of fat to body-weight in the preweaning phase was greater for QLF while QSC accreted more fat per unit weight gain in the postweaning period.

6. An increase in cell number made a greater contribution to the growth post partum of the QLF mice, but by 42 d of age little difference between the number of cells per unit weight in the two strains was evident.

7. Despite increases in RNA concentrations at all stages of development, of QLF mice compared with QSC, measurements of body composition do not indicate any accompanying increases of protein concentration in these animals.

From a base population of random-bred Q-strain mice, genetic selection has been performed on the basis of large or small body-weight at 6 weeks of age (Falconer, 1973). Mice other than Q-strain have been selected on the basis of differences in their rates of growth during either the pre-or postweaning period (Brown & Frahm, 1975; Kownacki *et al.* 1975). However, selection for large size at 6 weeks produces a correlated response of rapid growth before and after weaning. It is therefore reasonable to regard information about animals selected under one regimen as having some relevance to the corresponding line from the other set, e.g. small 6 week body-weight animals compared with animals with a slow rate of growth during the postweaning period.

In order to define differences in body compositions between mice selected for fast or slow growth, as opposed to those selected for large or small body size, previous studies have concentrated largely on comparisons of 'cell sizes' and cell numbers in individual organs (Robinson & Bradford, 1969; Eisen *et al.* 1978) and in particular the skeletal muscle from these mice has been well characterized (Luff & Goldspink, 1967; Ezekwe & Martin, 1975). To estimate efficiency of food utilization, the ratio, weight gain: food consumed, (FCR) food intake has to be measured. This has been done by Brown & Frahm (1975) and Brown *et al.* (1977) who found that the FCR was increased by selection for rapid postweaning growth. Kownacki *et al.* (1975) and Kownacki & Keller (1978) have shown that the basal metabolic rate is lower in mice selected for rapid growth compared to unselected controls.

Deoxyribonucleic acid (DNA), ribonucleic acid (RNA) and protein contents of brain, liver, kidney, heart, skeletal muscle, spleen and lung have been compared in Q-strain mice selected for large and small body size (Priestley & Robertson, 1973; Falconer *et al.* 1978). Skeletal muscle has been shown to contain more fibres of an increased length in the Q-strain mice selected for large body size (Hanrahan *et al.* 1973). Some results regarding food intake of Q-strain mice have been published (Falconer, 1977) but these do not illustrate differences between selected lines in terms of efficiency of food utilization.

Table 1. *Diet composition (g/kg)*

Ingredient	
Casein	223·0
Maize starch	443·0
Glucose	112·0
Salt mixture*	60·0
Cellulose	110·0
Maize oil	50·0
Vitamin mixture*	2·0
Chemical composition	
Total nitrogen	31·7
Fat	47·1
Dry matter	915
Gross energy (MJ/kg dry matter)	18·88
Apparently digestible N	28·2
Apparently digestible energy (MJ/kg dry matter)	17·18

* Miller & Bender (1955).

There is little information about the contribution of body fat to differences in efficiency defined as gain in weight per unit food intake between the selected lines of Q-strain mice and in general the chemical composition of the whole body of these mice has not been well defined, particularly at an early age. It seemed desirable to examine the whole-body composition of the different lines of Q-strain mice at different stages of development from birth to 42 d of age. These findings and differences in the efficiencies of utilization of food between large and small selected Q-strain mice are reported in the present paper.

MATERIALS AND METHODS

Experimental animals were obtained from the Unit of Animal Genetics, Edinburgh. The breeding stock of large mice was designated QLF (Q-strain, large line (L), replicate (F)) and that of the small mice QSC (Q-strain, small line (S), replicate (C); Falconer, 1973). The stocks of the Unit of Animal Genetics had been maintained with normal precautions to prevent infection; on arrival at this Institute they were tested and found free of *Toxoplasma*.

Once the female was confirmed to be pregnant, the male was removed before parturition to prevent post-partum mating. Litters were culled to eight pups on the day of birth to standardize litter size. The pups were weighed daily from birth until 19 d when they were removed and the mother mated again.

At 19 d post partum, two mice (one male, one female) were placed in a metabolism cage (Rucklidge & McKenzie, 1980) and their combined intake of a powdered, semi-synthetic diet, the composition of which is given in Table 1, was measured. The room temperature was held at 25° and the mice had free access to water. Urine and faeces were collected daily and their nitrogen contents estimated by the Kjeldahl method as modified by Davidson *et al.* (1970). The remaining mice in the litter were killed at 19 d post partum. At 42 d of age the mice used in the metabolism trial were weighed and killed. All mice whether killed at 19 or 42 d were treated similarly. The abdominal cavity was opened, gut contents were flushed with distilled water to remove digesta, and the digesta-free carcass was reweighed, frozen and freeze-dried. The dried carcass was weighed and finely ground and representative homogeneous samples were removed for the various estimations, each of which was performed in duplicate.

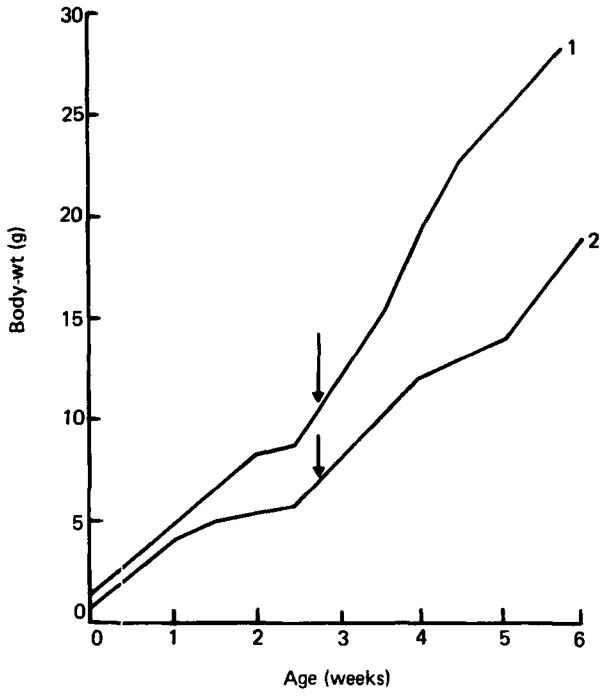

Fig. 1. Growth curves of selected mice from birth to 6 weeks of age. (1) Large line (QLF) mice, (2) small line (QSC) mice, 19 d of age (weaning).

Body protein was measured by the Kjeldahl method as described previously (Davidson *et al.* 1970). Fat was estimated by chloroform–methanol extraction (Atkinson *et al.* 1972). Ash was measured by complete combustion of the dried carcass.

RNA and DNA were measured by a modification of the Schmidt-Thannhauser method as recommended by Munro & Fleck (1969). A sample of the dried carcass was hydrolysed for 18 h in 5·7 M-hydrochloric acid at 108° and the hydroxyproline content of the hydrolysate was estimated by the method of Firschein & Shill (1966).

RESULTS

The body-weights of QLF and QSC mice were measured daily from birth until 42 d and the growth curves are shown in Fig. 1. At all ages QLF mice were heavier than QSC ($P < 0{\cdot}001$ at birth, 19 and 42 d; Table 2).

The compositions of the QLF and QSC mice at birth, 19 and 42 d were measured and are shown in Table 2. The concentration (g/kg body-weight) of body water in large mice was lower ($P < 0{\cdot}05$) than in small mice at 19 d but was not different at birth or 42 d. There were no differences between the lines in concentration body protein or ash at 19 or 42 d of age. The concentration of body fat was higher in QLF mice at 19 d ($P < 0{\cdot}05$) but at 42 d was similar to that of the QSC mice. Estimates of body composition of the mouse pups at birth are included in Tables 2 and 4; these were made on a single pooled sample. The composition of weight gains between birth and weaning and between weaning and 42 d for both lines are shown in Table 3.

As one might expect from the values for body composition in Table 2, the contribution

Table 2. *The composition of digesta-free carcass of QLF and QSC mice at birth, 19 and 42 d of age*

(Values are means ± 1 SE; no. of mice given in parentheses)

	Live body-wt (g)				Body water (g/kg)				Body protein (g/kg)			
	QLF		QSC		QLF		QSC		QLF		QSC	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Birth	1·78	0·02***	1·49	0·03	82·63		81·75		12·90		11·70	0·17
	(64)		(32)		(pooled sample of 14)		(pooled sample of 7)		(pooled sample of 14)		(18)	
19 d	9·66	0·21***	6·84	0·20	71·59	0·96*	74·00	0·41	18·34	0·51 NS	18·03	0·21
	(96)		(34)		(8)		(9)		(8)		(9)	
42 d	29·94	0·80***	19·39	0·62	66·03	0·90 NS	66·09	0·69	19·35	0·52 NS	19·45	0·26
	(17)		(22)		(6)		(14)		(6)		(14)	

	Body fat (g/kg)				Ash (g/kg)				Hydroxyproline (mmol/g body-wt)			
	QLF		QSC		QLF		QSC		QLF		QSC	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Birth	3·36		3·00		1·96		†		7·04	0·13 NS	7·21	0·28
	(pooled sample of 14)		(pooled sample of 14)		(pooled sample of 14)				(4)		(6)	
19 d	6·44	0·76*	4·42	0·36	3·23	0·10 NS	3·13	0·17	16·01	1·03 NS	19·74	0·50
	(8)		(9)		(8)		(8)		(7)		(8)	
42 d	7·43	1·43 NS	9·85	0·84	3·22	0·12 NS	3·31	0·09	19·16	1·55 NS	20·05	1·51
	(6)		(7)		(6)		(8)		(8)		(9)	

NS, not significant; † value not available.

QLF, mice selected for large body size at six weeks of age; QSC, mice selected for small body size at 6 weeks of age.

Mean values were statistically significantly different from those for QSC mice: * $P < 0·05$, *** $P < 0·001$.

Table 3. *The composition of weight gains (protein, fat, water, ash, DNA and RNA) between birth and weaning and between weaning and 42 d for QLF and QSC mice*

Gain from ...	QLF				QSC			
	Birth to weaning		Weaning to 42 d		Birth to weaning		Weaning to 42 d	
	Total	% of gain	Total	% of gain	Total	% of gain	Total	% of gain
Body-wt (g)	7·88	100	20·28	100	5·35	100	12·55	100
Body protein (g)	1·55	19·63	4·01	19·80	1·00	18·69	2·59	20·66
Body fat (g)	0·56	7·11	1·60	7·89	0·26	4·82	1·61	12·79
Body water (g)	5·44	69·10	13·45	66·33	3·84	71·78	7·75	61·78
Ash (g)	0·28	3·52	0·65	3·21	ND	ND	0·43	3·41
DNA (mg)	5·93	0·075	34·02	0·17	3·50	0·065	19·37	0·15
RNA (mg)	40·52	0·51	165·80	0·82	13·02	0·24	73·41	0·58

QLF, mice selected for large body size at 6 weeks of age; QSC, mice selected for small body size at 6 weeks of age; ND, not determined.

Table 4. *The concentrations of DNA, RNA and protein, and protein: DNA, RNA: DNA and protein: RNA in digesta-free carcases of QLF and QSC mice at birth, 19 and 42 d of age*

(Values are means ± 1 SE; no. of mice in parentheses)

	DNA (mg/g body-wt)				RNA (mg/g body-wt)			
	QLF		QSC		QLF		QSC	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Birth	3·29 (8)	0·04	4·95 (18)	0·25***	4·86 (8)	0·10	5·63 (18)	0·13***
19 d	1·22 (7)	0·10	1·59 (8)	0·13*	5·08 (7)	0·46	3·13 (8)	0·12***
42 d	1·53 (8)	0·05	1·56 (10)	0·12 NS	7·18 (8)	0·63	4·89 (8)	0·30***

	Protein: DNA (mg:mg)		RNA: DNA (mg:mg)		Protein: RNA (mg:mg)	
	QLF	QSC	QLF	QSC	QLF	QSC
Birth	39·21	23·64	1·48	1·14	26·54	20·78
19 d	150·33	113·40	4·17	1·96	36·03	57·60
42 d	126·47	124·47	4·69	3·13	26·94	39·78

NS, not significant; QLF, mice selected for large body size at 6 weeks of age; QSC, mice selected for small body size at 6 weeks of age.

Mean values were statistically different from those for QLF mice: * $P < 0·05$, *** $P < 0·001$.

of protein to the weight gain was similar in the two lines at the same stage of development (Table 3). In the QLF mice however, body fat contributed more to weight gains before weaning than in the QSC mice whereas after weaning it contributed more in the QSC mice. Differences in body fat between lines at 19 d appeared to be made at the expense of body water rather than body protein (Table 2).

The DNA concentration (mg/g body-weight) in the QLF animals was significantly less at birth ($P < 0·001$) and at 19 d of age ($P < 0·05$) than in the small animals (Table 4). As

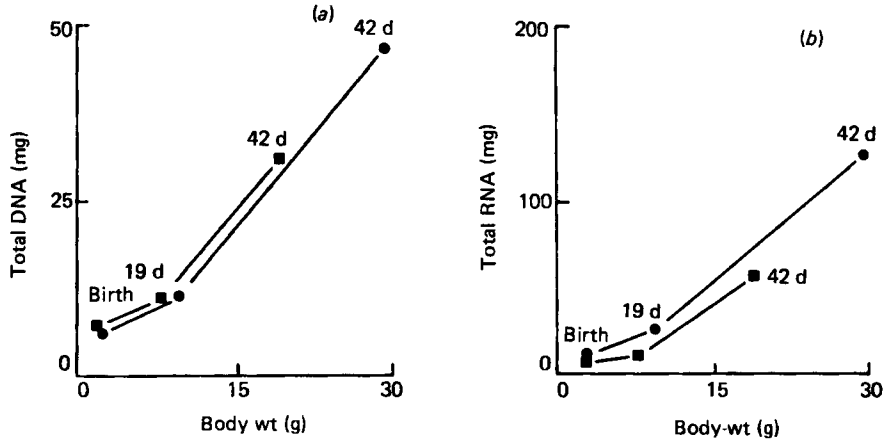

Fig. 2. The rate of accretion of total (*a*) DNA and (*b*) RNA with respect to body-weight. Slope of line of best fit: DNA for QLF mice (●) 1·33 ± 0·20 (mg/g body-wt) and for QSC mice (■) 1·47 ± 0·20 (mg/g body-wt); RNA for QLF mice (●) 7·50 ± 0·67 (mg/g body-wt) and for QSC mice (■) 5·01 ± 0·78 (mg/g body-wt).

Table 5. *Food intake, nitrogen excretion, weight gains and gross food efficiency of QSC and QLF mice between 19 and 42 d of age on the feeding trials*

(Values are means ± 1 SE for two mice per cage)

No. of pairs of mice...	QLF 6		QSC 4	
	Mean	SE	Mean	SE
Food intake (g/mouse)	107·30	2·90	84·45	3·68***
Wt increase (g/mouse)	17·74	0·59	10·37	1·04***
Gross food efficiency (g food intake/g wt gain)	6·06	0·12	8·23	0·64**
Urinary N excretion (% of N intake)	74·72	2·55	75·28	3·26 NS
Faecal N excretion (% of N intake)	8·72	0·25	10·42	0·72*

NS, not significant; QLF, mice selected for large body size at 6 weeks of age; QSC, mice selected for small body size at 6 weeks of age.

Mean values were statistically significantly different from those for QLF mice: * $P < 0·05$, ** $P < 0·01$, *** $P < 0·001$.

growth continued the DNA concentration declined in both lines. The rate of DNA accretion with respect to body-weight showed a similar pattern in the two lines Fig. 2(*a*). With respect to age however total DNA was lower in QLF animals at birth but was higher at 19 and 42 d.

RNA concentration (mg/g body-weight) was higher ($P < 0·01$) for QSC animals at birth but was lower ($P < 0·001$) at 19 and 42 d (Table 4). With respect to body-weight rather than age the rate of accretion of RNA was not significantly different between lines but total RNA was higher in QLF animals at birth, 19 and 42 d (Fig. 2(*b*)).

The whole body hydroxyproline concentration which may be taken as an index of

Table 6. *The utilization of apparently digestible energy and apparently digestible nitrogen by QLF and QSC mice between 19 and 42 d of age*

(Values are mean ± 1 SE)

No. of pairs of mice...	QLF 6		QSC 4	
	Mean	SE	Mean	SE
Percentage digestible energy deposited as protein and fat†	7·26	0·75	8·31	0·54 NS
Percentage digestible energy deposited as fat	2·79	0·72	4·86	0·33*
Percentage digestible energy deposited as protein	4·42	0·27	3·44	0·32*
Percentage digestible N deposited as protein	18·09	1·15	14·08	1·30*

NS, not significant.

QLF, mice selected for large body size at 6 weeks of age; QSC, mice selected for small body size at 6 weeks of age.

Mean values were statistically significantly different from those for QLF mice: * $P < 0·05$.

† Assuming the heats of combustion of body protein and fat to be 23·7 and 39·6 kJ/g respectively.

collagenous protein concentration did not differ between the lines at any of the ages studied (Table 2).

Food intake, measured from 19 to 42 d, was higher ($P < 0·001$) for the QLF mice. These mice also gained more in the same period ($P < 0·001$) (Table 5). The food intake on a per g body-weight increase basis was lower ($P < 0·01$) for the QLF animals. The mice in metabolism cages grew less well than those in the study of growth from birth to 42 d which were kept in standard mouse cages (weight gains (g) from 19–42 d in standard cages: QSC 12·55; QLF 20·28; corresponding values in metabolism cages: QSC 10·37; QLF 17·74).

Expressed as a percentage of N intake, urinary N did not differ between lines but faecal N was lower ($P < 0·05$) for QLF mice (Table 5).

The lines did not differ significantly in the percentage of apparently digestible energy which was deposited as the sum of protein and fat between 19 and 42 d (Table 6). However the partition of the retained energy was different between the strains. In terms of percentage digestible energy QLF animals deposited 2·79 as fat and 4·42 as protein while QSC mice deposited 4·86 as fat and 3·44 as protein between 19 and 42 d (Table 6). QLF animals deposited 18% of their digestible N as protein compared to 14% by QSC (Table 6).

DISCUSSION

The criteria for selection of Q-strain mice have been for an increased (QLF) or decreased (QSC) body-weight at 42 d. It is clear that selection for this trait has produced a correlated response in that the two lines of mice differ with respect to body-weight at all ages between birth and 42 d. Although absolute weight gains were different, the relative rates of growth (g body-weight gain/g body-weight per d) were similar between 19 and 42 d (0·044 and 0·042 for QLF and QSC respectively).

The experiments described in this paper set out to investigate whether selection: (*a*) had altered the body composition, particularly with respect to changes in the rates of deposition

of fat and protein and the efficiency with which food is deposited; (*b*) had altered the cell size and number of cells in these animals.

As would be expected the QLF mice consumed more food than QSC mice but expressed per unit metabolic body-weight (kg body-weight $(W)^{0.75}$) QLF mice consumed a similar amount of food to QSC mice (g/kg $W^{0.75}$ per d; QLF 94·75; QSC 92·30). The efficiency with which food consumed was utilized for gain of body-weight was higher in QLF animals and this is consistent with the fact that protein deposition contributed a higher proportion of the energy deposition between 19 and 42 d in these animals. The apparent anomaly that body composition, with respect to protein, fat and water was little different at 42 d of age is explained by the fact that between birth and weaning the QLF mice deposited proportionaltely more fat than the QSC line.

One of the most striking observations in the present work was the low efficiency with which dietary energy was deposited. In both lines, between 19 and 42 d, approximately 8% of the total digestible energy was deposited as protein and fat, a value which is significantly lower than the gross efficiency of energy deposition in growing rats (200 g rats deposit approximately 24% of their digestible energy; Pullar & Webster, 1977) and pigs (30 kg pigs deposit approximately 30% of their digestible energy; Reeds *et al.* 1980) receiving a similar intake of energy per unit metabolic weight (1400 KJ/kg $W^{0.75}$ per d). A similarly low gross efficiency of energy deposition in mice both unselected and selected for rapid rates of growth can be calculated from the results of Brown *et al.* (1977) but this does not appear to be a universal finding in selected mice (Van der Wal *et al.* 1976). Although a contributory factor in this may be the high contribution of protein deposition to the weight gain, FCR (g weight gain:g food intake) is also low.

Two questions arise from these observations. First, is the low efficiency of energy deposition associated with a high requirement of energy for maintenance and second, are the present findings characteristic of mice or due to selection for differences in weight gain? It is impossible to answer the first of these questions unequivocally using the results presented in the present paper because assumptions as to the efficiency with which energy above maintenance is deposited have to be made. However, adoption of the values for the partial energetic efficiencies of protein and fat deposition (Kielanowski, 1972) imply a maintenance heat production (kJ/kg $W^{0.75}$ per d) of 1150 for QLF mice and 1250 for QSC mice, much higher than most estimates for other mammals (see Blaxter, 1972). Similar calculations from the results of Brown *et al.* (1977) also indicate a high maintenance heat production (WWL and ADGL mice selected for rapid rates of growth, and CL, control line, 950 kJ/kg $W^{0.75}$ per d). This calculation is of course entirely dependent on the assumption that selection for high weight gains does not affect partial energetic efficiencies of either protein or fat deposition. Nevertheless there is some support for the view that maintenance heat production is elevated from measurements of basal metabolic rates (BMR) in mice selected for rapid rates of growth between 19 and 42 d (Kownacki & Keller, 1978). Although their measurements were made using mice which were 5 months old, their results suggest a BMR (i.e. under fasting conditions) of approximately 600 kJ/kg $W^{0.75}$ per d.

Regarding the second of these questions, there are available in the literature two sets of measurements of BMR in mice which have not been specifically selected for rapid rates of growth (Benedict, 1938; Usinger, 1957). Both sets of measurements suggest values of between 250 and 300 kJ/kg $W^{0.75}$ per d, which are compatible with many similar measurements in adult mammals (Blaxter, 1972). In both these reports no mention was made of the strain of mice used and it is reasonable to presume that they were genetically-outbred mice. Brown *et al.* (1977) and Kownacki & Keller (1978) also provided information on their control (unselected) or foundation stock. Both sets of measurements suggest that the growth

of the foundation lines is as inefficient and the BMR is as high as the selected mice. It would appear therefore that the inbred strains from which the experimental animals had been selected possessed a trait associated with a low energetic efficiency of growth and that further selection on the basis of growth rate (both increased and decreased) has not altered the manifestation of this trait. Without further information it is impossible to say whether this is a common finding in inbred strains of mice or whether it is confined to CL (Brown *et al.* 1977) Q, (Falconer, 1973) or the unspecified strains used by Kownacki & Keller (1978).

Cell size and cell number

The two strains showed similar patterns of development with respect to the changes in cell number (DNA per unit weight) and 'cell size' (protein per unit DNA) (Table 4). In both lines there was a marked increase in the value for protein:DNA before weaning indicating an increase in the 'cell size' rather than cell number during this phase of development i.e. a hypertrophic growth phase (Table 4) although there was some increase in the absolute amount of DNA in the preweaning period (Fig. 2(*a*)). After weaning the protein:DNA value changed much less (Table 4) but total DNA increased with body-weight (Table 3, Fig. 2(*a*)), indicating that cell numbers were increasing i.e. a hyperplastic growth phase. The pattern of growth observed here appears to be different from that reported by Winick & Noble (1966) for the rat where preweaning growth is almost exclusively hyperplastic. Immediately after weaning the growth of the rat is a combination of hyperplasia and hypertrophy, gradually becoming exclusively hypertrophic until adult body size is attained.

Differences do exist between QLF and QSC lines despite a similar over-all pattern of development. At birth and 19 d DNA:body-weight was lower and protein:DNA was higher in the QLF mice. Protein:DNA increased less between birth and 19 d in QLF mice compared to QSC with respect to the value at birth (QLF 3·8-fold, QSC 4·7-fold) indicating that an increase in cell numbers (rather than cell size) contributed more to over-all growth in the preweaning period. These results support the measurements of protein:DNA in a range of defined skeletal muscles from mice selected for rapid and slow rates of growth (Aberle & Doolittle, 1976; Martin *et al.* 1979). There is contradictory evidence for an increase in cell size in QL mice reported by Falconer *et al.* (1978) where absolute cell mass was estimated in lung, liver, spleen, kidney and skeletal muscle and compared with an unselected control line. However this increase in cell size was not sufficient to account for the total increase in the weight of the organs examined and it was shown that the major contribution to increased weight was an increase in cell number.

RNA:DNA of the QLF mice was higher than that of the QSC at birth, 19 and 42 d, indicating a higher RNA content per cell. An increase in RNA content per cell often is assumed to reflect a greater capacity of that cell for protein synthesis (Needham, 1964). However, total protein:total RNA was lower in the large strain mice at 19 and 42 d and was higher only at birth. There are many factors which can influence protein synthesis and the results available from this experiment do not permit speculation about alterations in protein metabolism between the two strains although Priestley & Robertson (1973) failed to demonstrate differences in either protein synthesis or turnover between different lines of Q-strain mice using isolated ribosomes.

The Q-strain and other selected mice appear to be ideally suited to the study of changes in tissue components or metabolism brought about by selection for body size. Despite much endeavour by many workers, no major contributing factor to the cause of the increase in body size, apart from increased appetite, has yet come to light. The large animals do eat more but it is impossible to say if this is the cause or the effect of larger body size. In summary, the two strains of mice exhibit somewhat different patterns of development, but

by maturity have a similar body composition. An increase in body size due to genetic selection may be due to a multiplicity of factors and it would appear that no one component of growth will suffer an easily detectable aberration from the normal.

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