SECTION 1

REVIEW OF THE LITERATURE

1.1 INTRODUCTION

Growth is a biologically complex character that expresses a co-ordinated development of various parts and organs of the body, and so it is a composite trait. It is the end product of many different physiological processes, easy to measure and because variation in body weight has a large additive genetic component, it is easy to manipulate by selective breeding. However, the precise effects of genetic manipulation of growth on the physiological and developmental processes are difficult to define.

Selection for growth rate or body weight may result in various types of changes in the carcass components giving rise to the increase of body weight. Results of some long term experiments with mice have indicated that selection to increase or decrease growth rate has little effect on the shape of the growth curve (Gall and Kyle, 1968; Eisen *et al.*, 1969; Timon and Eisen, 1969; Bakker, 1974), but it can alter the chemical composition of the body (Fowler, 1958; Hull, 1960; Clarke, 1969; Timon *et al.*, 1970; Dawson *et al.*, 1972; Bakker, 1974; Sutherland *et al.*, 1974; Hayes and McCarthy, 1976; McPhee and Neill, 1976; Eisen and Bandy, 1977; Eisen *et al.*, 1977, Kownacki *et al.*, 1977; McPhee *et al.*, 1980).

Another dimension in an analysis of growth rate is food intake utilisation. Animals need energy for growth which they obtain from food. Food is broken down in the gastro-intestinal tract and is then converted into body substance by means of constructive or assimilatory synthesis. In growing animals a major portion of food intake is used for maintenance (Stephenson and Malik, 1984), while some also is used for synthesising new tissues. Although energy requirements per unit of protein and fat deposition are known (Fuller and Webster, 1977), the partitioning of the total feed intake of growing animals into maintenance and growth components can not easily be done because of the problems associated with their measurement. In addition, little information is available about the genetic

control of this partitioning. Whereas constancy of maintenance requirement in mature animals is well documented, the maintenance requirement in growing animals is poorly understood (Kibler and Brody, 1944; Fowler, 1962; McCarthy, 1980).

Genetic differences in growth rate, voluntary feed intake and feed utilisation, are often associated with differences in body composition. The fact that the differences in body composition, particularly in carcass fat percentage, are generated by selection for body weight, for feed intake (Sharp *et al.*, 1984) or for feed efficiency (Yuksel *et al.*, 1981) indicates the existence of genetic variation for body composition and demonstrates some of the physiological interactions in phenotypic expression of these characters.

A number of studies in mice have shown significant between-line genetic variation in body weight and weight gain (Eisen, 1973; Bakker *et al.*, 1976; Nagai *et al.*, 1976; Bandy and Eisen, 1984), body composition, feed intake and feed efficiency (Eisen *et al.*, 1977; Bandy and Eisen, 1984). The two major sources of between-line genetic variation are genetic effects of progeny and dam and these may be partitioned further into such parameters as additive, heterotic and recombination effects. Knowledge of these genetic sources of variation is required for comparing phenotypically different populations and for planning of future breeding programmes.

1.2 GROWTH PATTERN OF THE MOUSE

Before discussing any particular aspect of growth in the mouse, it will be useful to determine the normal postnatal growth pattern. The usual life span of the mouse is about 2.5 years. From birth, given adequate nutrition, a mouse will grow in body weight along a sigmoid curve showing acceleration until about puberty and slowing as maturity is reached between 5 and 6 weeks of age in unselected mice (Falconer, 1984). On the basis of its growth curve, the mouse's growth period can be divided into four phases (Silberman and Kedar, 1977).

1. A post-embryonic development phase extending up to three weeks postnatally until the weaning period. This phase is characterised by a steady but submaximal growth. This growth period functions as a preparatory stage to the rapid growth of adolescence.

2. A phase of very active growth extending from the 3rd to 6th week. During this phase, normal mice experience their highest rates of growth and attain sexual maturity.

3. The phase of skeletal maturation extending from the 7th to the 20th week. This phase is characterised by slow but continual growth rate until skeletal maturation is accomplished.

4. The phase of full maturation from the 26th to the 52nd week.

The period of growth between birth and puberty is one during which there is a major interaction between growing animal and its environment. Therefore, this phase of growth is particularly important in studies of body composition and efficiency of feed utilisation.

The time sequence of maximal growth activity of different tissues indicates that the peak rates do not coincide. Sequentially, bone is an early developing tissue as compared with muscle and in turn muscle develops earlier than fat (Palsson, 1955), and within fat there are early and late maturing sites (Leat and Cox, 1980; Allen and McCarthy, 1980).

1.3 GENETIC VARIATION IN GROWTH RATE AND BODY WEIGHT

Over the past 30 years growth rate and body weight have been extensively used as characters for studying the responses to genetic selection in mice. Selection has usually been effective in bringing about marked changes in weight and the limits to selection response are usually not reached for about 20 generations with a range of 11 to 45 generations (Eisen, 1980). The realised heritability estimates ranged from

0.08 ± 0.004 to 0.17 ± 0.01 for preweaning litter weight and weaning weight (Eisen *et al.*, 1970; Robinson *et al.*, 1974; Frahm and Brown, 1975), 0.17 ± 0.01 to 0.52 ± 0.07 for post-weaning body weights at different ages (Falconer, 1953; Legates, 1969; Wilson *et al.*, 1971; Rutledge *et al.*, 1973; McCarthy and Doolittle, 1977; Butler *et al.*, 1984; Sharp *et al.*, 1984) and 0.21 ± 0.03 to 0.43 ± 0.02 for postweaning gains (Sutherland *et al.*, 1970; Bradford, 1971; Wilson, 1973; Frahm and Brown, 1975). Realised heritability estimates for the postweaning gain were higher and ranged from 0.20 ± 0.02 to 0.40 ± 0.02 in generations 0-14 as compared to -0.10 ± 0.06 to 0.17 ± 0.05 for 15-27 generations of selection (Eisen, 1975). The estimates of the realised genetic correlations of 0.9 for 5 and 10 week body weights (McCarthy and Doolittle, 1977); 0.17 to 0.89 for early and late postweaning gain and 0.20 to 0.73 for postweaning gain and weights (Wilson, 1973) have been reported. The disagreement between the reported results for realised estimates of genetic parameters can be explained on the basis of different base populations from which selection lines were derived, age at selection, method of selection, number of generations of selection, level of inbreeding and variability of environmental conditions between experiments. The selection responses in phenotypic and genetic standard deviations in body weight and postweaning weight gain in a number of studies reviewed by Eisen (1980) ranged from 1.3σ_p to 6.9σ_p and 2.3σ_A to 16.0σ_A. A particular feature of the selection responses was that they tended to increase with the increase in effective population size. Given the observed magnitude and cumulative nature of selection responses and the desired direction of change in the phenotypic means of the selected populations over a number of generations in many studies reported in the literature, it is clear that the genetic variation in the growth rate and body weight is of additive genetic nature.

Between line genetic differences involve both additive and non-additive genetic effects. A number of diallel crossing experiments using laboratory mice to examine the relative importance of these sources of variation have been

reported (Carmon, 1963; Kidwell and Howard, 1969; Jamison *et al.*, 1975; Raymond, 1978). Carmon's diallel analysis involved four lines of mice, one of which was highly inbred, two lines were slightly inbred and another outbred. Significant heterosis for weight at 21 and 45 days of age was observed. General combining ability reflecting additive genetic effects was highly significant at both these ages. A similar design and analysis were used by Kidwell and Howard (1969) in their study involving four inbred lines and examined body weight at birth and at weekly intervals through to ten weeks. Heterosis was significant at all ages. Differences between lines for general combining ability were not significant at any age. Specific combining ability indicating non-additive genetic variation was significant from one to seven weeks but generally accounted for a lower proportion of the total variance than did general combining ability effects. Mean squares for general combining ability were tested against those of specific combining ability. Insufficient degrees of freedom for general and specific combining abilities (3 and 2, respectively) appears to be the likely reason for non-significance of general combining ability.

Jamison *et al.* (1975) used inbred lines derived from a single outbred base in their diallel experiment. Individual body weights were recorded at 12, 21, 42 and 56 days of age and weight gain betewen 12-21, 21-42 and 42-56 days. Heterosis was significant for all traits except for 21-day weight; specific combining ability for 21-day weight, 12-21 and 42-56 day gain and general combining ability for 12 and 56 day weights and 21-42 day gain.

Another diallel experiment using the lines derived from a single large population base was that of Raymond (1978). Two of the three lines used in this study had been selected over ten generations for high and low eight week body weight, whereas the third line was an unselected control. These lines showed large differences in weaning weight and were very diverse at eight weeks. General combining ability was

significant for body weight at both these ages. Specific combining ability effects were important only at eight weeks.

In summary, the diallel crosses between inbred lines showed heterosis in body weight at pre- and postweaning ages, which is expected in F_1 crosses due to dominance and gene frequency differences between inbred lines. Specific combining ability effects in 8 week body weight in a diallel cross between the lines selected for body weight and the control line also indicates the presence of interaction variance.

In addition to the diallel experiments, there are other reports indicating the presence of non-additive genetic variation in body weight. Butler (1958) demonstrated that the heterosis for body weight increased with increase in age up to 60 days in a cross between two inbred strains. McCarthy (1965) and McLaren (1967) reported heterosis in fetal weight at 17.5 days and birth weight in crosses of highly inbred lines. Nagai *et al.* (1976) observed significant heterosis for 12-day litter weight. A number of workers have reported significant heterosis for pre- and postweaning body weights and weight gains (Morton, 1970; White *et al.*, 1970; Eisen, 1973; Nagai *et al.*, 1976; Bakker *et al.*, 1976). Williams *et al.* (1978) observed significant heterosis for degree of maturity, absolute maturing rate and relative maturing rate at various pre- and postweaning ages.

Some other reports indicate little evidence of non-additive genetic variation and heterosis in the body weight of the mouse. Miller *et al.* (1963) in a detailed study did not find significant non-additive genetic variance for three and six week weight. Vinson *et al.* (1969) reported reciprocal recurrent selection to be the least effective of the three methods of selection used by them to increase genetic gain in body weight. Earlier, Newman (1960) and Hansson and Lindkvist (1962) were unable to make progress under a scheme of

recurrent selection. Comstock *et al.* (1963) observed that the increased growth of F_1 crosses between the selected and inbred line at each generation of selection was all due to general combining ability associated with additive genetic variance. Nagai *et al.* (1980) found no evidence of heterosis in body weight at a number of ages with the exception of 21-day weight in only one of 16 reciprocal F_1 crosses.

Therefore, from the experimental evidence available so far, it appears that the between-line differences in body weight of mice are due primarily to additive genetic effects. The presence of non-additive genetic variance has been reported in a number of studies, but it is not an invariable feature of the mouse data.

1.4 BODY COMPOSITION

Weight increments in growing animals are accompanied by changes in their chemical body composition. Chemical components of the body of the mouse exhibit differential growth from birth to maturity. During the active growth period, the percentage of protein and fat increases while that of water and ash decreases. As the asymptote weight is reached, percentages of protein, water and ash reach more or less constant proportions of the fat-free body. Fat is deposited at an exponential rate but relatively late in the life cycle. The increments in weight after maturity are largely due to gain in fat.

The constancy of the fat-free body weight was referred to as 'chemical maturity' by Moulton (1923). Moulton proposed that the chemical composition of different animals should be compared on a fat-free basis. Based on the decreasing proportion of protein up to the age of chemical maturity, Brody (1945) suggested that the ratio of protein to water should serve as an indicator of 'physiological aging'. On this basis, age and weight at chemical maturity should then coincide with the age and weight at which the ratio of protein to water is maximum.

The above considerations suggest that the knowledge of body composition can be helpful in understanding the physiology of growth and in making genetic comparisons at equivalent physiological or chronological ages or at equivalent body or carcass weights. A number of workers have traced changes in the body composition of growing mice and expressed these in different ways (Eisen, 1974; McCarthy, 1979; Roberts, 1979). In a large majority of cases the lines of mice used were selected for a number of generations for body weight or growth rate and body composition was studied as a correlated response to selection for these traits.

1.4.1 SELECTION RESPONSES IN BODY COMPOSITION

Body composition can be altered by genetic and/or nutritional means. McLellan and Frahm (1973) reported that seven generations of sib selection for high and low hind leg muscle weight at 12 weeks of age produced changes in muscle weight by changing the body weight. Changes in fat were not reported. They recorded realised heritability estimates of 0.24 ± 0.06 and 0.70 ± 0.17 for hind leg muscle weight in the high and low lines. More recently Sharp *et al.* (1984) discussed a selection experiment in which mice were selected for a high and low ratio of gonadal fat to body weight, and for total lean mass using an index. Selection was done for 11 generations on male mice and replicated lines were maintained. Selection for the ratio of gonadal fat weight to body weight produced changes in total fat percentage, but little change in percentage protein, food intake or gross efficiency. Selection for lean mass increased body weight, food intake and 4 to 6 week gross efficiency. Realised heritabilities for the ratio and for the lean mass were 0.44 ± 0.06 and 0.51 ± 0.01. The studies by McLellan and Frahm (1973)

and Sharp *et al.* (1984) provide evidence for the presence of additive genetic variability between individual mice for body composition traits which can be utilised by selective breeding to maximize change in body weight without a change in the proportion of body fat.

A number of reports of indirect effects on body composition as a consequence of direct selection for weight or weight gain on full or restricted feeding are available in the literature. Interest in body composition has mainly related to the proportion of body fat which is indeed the major variant of all the body tissues. The majority of reports (Fowler, 1958; Biondini *et al.*, 1968; Clark, 1969; Timon and Eisen, 1970; Hayes and McCarthy, 1976; Eisen *et al.*, 1977; Hetzel, 1978, Allen and McCarthy, 1980; McPhee *et al.*, 1980) have indicated that at equal ages and on *ad libitum* feeding the lines selected for high body weight tend to be fatter as compared to unselected lines or low body weight selection lines. Some other reports do not support this trend. Lang and Legates (1969), Dawson *et al.* (1972) and Brown *et al.* (1977) did not observe significant differences in the fat percentage between their high, low and control lines. Similar results were found by Fowler (1958) in the lines derived from 'C' strain of Falconer's mice.

The age at selection appears to be a significant factor in determining the stage of rapid fat development in mice. A general view emerging from a number of studies (Fowler, 1958; Hull, 1960; Clarke, 1969; McPhee and Neill, 1976; Hayes and McCarthy, 1976; Allen and McCarthy, 1980), in which fat was measured over a range of ages is that, prior to the age of selection, the lines selected for increased body weight will be leaner on weight basis with a tendency to rapidly grow fatter at later ages. Selection for increased weight at an early age would appear to result in a greater increase in carcass fat compared to selection at a later age. A biological explanation to this was given by Hayes and McCarthy (1976). The model presented by them and its interpretation to their

set of lines suggests that the mice selected for increased weight at older ages would consume more food and divert less metabolisable energy to fat production at younger ages or up to the age of selection. The reason is that the deposition of lean tissue is energetically more efficient than the deposition of the same weight of fat because muscle contains 5 to 6 times as much water as the fatty tissue. Therefore, although the cost of depositing one gram of fat and one gram of protein is the same (Pullar and Webster, 1977), a mouse depositing a particular weight of protein would weigh more as compared to another mouse depositing the same amount of fat. This is the idea behind the concept of the lines selected for faster growth being relatively leaner up to the age of selection than the unselected lines on a body weight basis. By the same analogy the selection for low body weight should favour fatter animals. On the contrary, in a majority of experiments, selection has been shown to produce lean mice by reducing appetite. In two studies (McPhee *et al.*, 1980 and Yuksel *et al.*, 1981) selection for gain has resulted in an increase in body weight on restricted intake with an increase in the proportion of fat. In terms of metabolic energetics these results may be explained if the unselected mice were inefficient in the use of their dietary energy and the selected lines can redirect that loss into tissue synthesis (Stephenson and Malik, 1984).

More evidence of the effect of selection on fat deposition in mice is available from the study of fat distribution by Allen and McCarthy (1980). They studied mesenteric, forelimb, hind limb, kidney and gonadal sites of fat deposition and found that the fat depots did not contribute equally to the increases in the fat content of the carcass of a growing mouse. For example, it was noticed that the kidney and gonadal fat depots were late developing but fastest maturing of all the depots and correlated effects of selection were more pronounced in these locations. Their findings add another dimension to the experimental approaches in seeking

solution to the problem of between-line differences in tissue deposition. These results not only confirm the effect of selection in a general way but they also indicate the importance of various regions of the body in contributing to the differences in body composition among lines.

In two studies, continued selection for increased body weight appeared to reduce the age and weight at which fat deposition was accelerated (Fowler, 1958; McPhee and Neill, 1976). Fowler's explanation was that if the genes causing rapid growth, that is, protein and water deposition, are fixed during the course of selection before those causing fat deposition, selection in earlier generations would result in increased protein deposition, while selection in later generations would accelerate earlier fat deposition. On a fat-free basis, selection for body weight in mice has been ineffective in changing the percentage composition of protein, water and ash in mice carcasses (Robinson and Bradford, 1969; Timon *et al.*, 1970; Sutherland *et al.*, 1974). These results suggest that it may be difficult to alter chemical composition of the fat-free body.

1.5 MATERNAL EFFECTS ON GROWTH AND BODY COMPOSITION

A dam influences the traits of her progeny in at least three ways. Firstly, she contributes to each offspring a sample half of her genes. Secondly, through genetic maternal effects she conditions the expression of phenotype in her progeny. Usually these two contributions of the dam are confounded among themselves and with the genetic effects of the progeny and consequently the estimation of maternal effects is difficult. Thirdly, the environmental maternal influences are often implicated as causes of observed variation in growth of her progeny. Knowledge of the extent of maternal effects on growth traits is important for three reasons, (1) as a source of bias in estimating genetic parameters, (2) the repercussion on selection responses of the relationship of maternal effects with the direct effects, and (3) the

influence of maternal heterosis on growth of crossbred progeny, thus signifying the importance of F_1 dams in crossbreeding programmes.

Evidence of significant maternal effects on body weight of mice has been demonstrated by experiments which utilised procedures such as (a) estimation of milk secretion by weighing pups before and after suckling, (b) crossfostering, (c) estimating maternal and paternal covariances between relatives, and (d) reciprocal crossing.

Maternal effects on growth can be partitioned into prenatal and postnatal components. The former are associated with uterine influences, whereas the latter are mainly associated with milk yield of the dam. Several crossfostering studies with mice have shown that prenatal effects on early postnatal growth were small and were normally not detectable beyond two weeks of age. The postnatal effects are large in the preweaning growth period and decrease in relative importance at later ages (Young *et al.*, 1965; El Oksh *et al.*, 1967; Nagai, 1971; Rutledge *et al.*, 1972; Brandsch and Kadry, 1977). As the direct genetic effects are normally confounded with the prenatal or uterine effects, some workers (Brumby, 1960; Moore *et al.*, 1970) have used ova transfer techniques to separate these effects.

Rutledge *et al.* (1972) found a small positive covariance between direct genetic and maternal genetic effects on body weights in a random mating stock of mice. However, a high positive correlation of 0.56 between maternal genetic effects for body weight at 12 days and direct genetic effect for body weight at 42 days was reported by Nagai (1978) in a random-bred line of mice. Robinson *et al.* (1974) and Hanrahan and Eisen (1974) observed a negative correlation between direct and maternal genetic effects for 12-day body weight in an unselected population of mice. A positive correlation between

direct and maternal genetic effects in one randombred line and a negative correlation in another randombred line suggests a real difference between two populations for maternal genetic effects. Poor maternal genetic effects will tend to impede selection response. Willham (1972) postulated that if a negative correlation exists between the direct and maternal effects, it could result either from the dam giving to her progeny a 'plus' set of genes for direct effect and a poor maternal effect, or vice versa. Therefore, improvement by selection on phenotypic values would be slow.

There are reports indicating the importance of postnatal environmental influences on body weight and body composition in mice. Hayes and Eisen (1979a) studied body weights and weights of ether extract, water, ash and protein in mice reared in litters of three, six or nine. The mice of the three lines studied differed widely in growth rate. Body weights and weights of body constituents at 3, 6, 9 and 12 weeks were larger for mice reared in litters of three than for those reared in litters of nine. Mice reared in litters of six were intermediate in body weight and weights of some of the body constituents between those reared in litters of three and nine. Differences in body weight and weight of body components due to postnatal maternal environment were small by comparison with differences due to genetic line. Significant line by maternal environment interactions in body weight at 21 days and in ether extract weight at 21 and 63 days were reported in their study. Smaller effect of maternal environment on body weight in comparison to genetic line differences in body weight have been reported by Eisen and Leatherwood (1976) in comparing a polygenic obese and control strain of mice. In another study, Eisen and Durrant (1980) observed no important effects of varying postnatal litter size (maternal environment effect) or line x postnatal litter size interaction on litter weight and litter feed efficiency at various ages up to 6 weeks.

Maternal effects on body weights of the individual progeny were not examined.

Some workers (White *et al.*, 1968; Nagai *et al.*, 1971; Eisen, 1973; Lasalle and White, 1975; Raymond, 1978; Hayes and Eisen, 1979b) have compared the performance of two or three lines of mice for direct and postnatal maternal genetic effects on weights and weight gains at different ages. A few attempts were made to partition the direct or correlated responses into direct and maternal genetic effects and direct and maternal heterosis (Eisen, 1973; Nagai *et al.*, 1976; Bakker *et al.*, 1976; Williams *et al.*, 1978). In general, the results of these studies indicate that, although maternal genetic effects were significant at preweaning ages, the direct genetic effects were more important at all ages. Maternal heterosis was significant for weight gain at early ages and for body weight, degree of maturity, absolute maturing rate, and relative maturing rates at most preweaning and postweaning ages. Nagai *et al.* (1976) observed that the level of maternal heterosis was more among F_2 crosses between two selected lines as compared to the F_2 crosses between two control lines and the difference was significantly greater than the direct heterosis. Since maternal effects are part of the reproductive complex, evidence of maternal heterosis even in the absence of individual heterosis for growth traits is not surprising.

More evidence of between-line variation for maternal effects was available from diallel experiments using inbred or selected lines of mice (Carmon, 1963; Kidwell and Howard, 1969; White *et al.*, 1970; Jamison *et al.*, 1975; Raymond, 1978). These studies indicate that, in general, the maternal effects account for an increasing proportion of the total variance in body weight from birth to three or four weeks of age and steadily decrease thereafter.

In summary, the foregoing studies suggest that the growth traits of young mice are influenced not only by their own

genotypes, but also to a varying degree by maternal effects. The maternal sources of variation are important in the studies of both within- and between-line variation. Whereas, the genetic analysis of within-line variation is necessary for selective breeding, the components of between-line differences can be used in analysing responses from crossbreeding.

1.6 FEED EFFICIENCY

There is a good deal of confusion regarding the terminology of feed efficiency. Various measures of efficiency have been frequently used interchangeably in the literature. Therefore, it is essential that feed efficiency be clearly defined prior to discussion of any of its aspects. The terms feed efficiency and feed conversion ratio, are synonymous and refer to the ratio gain/feed (or its reciprocal). Energetic efficiency is the ratio of the increment of energy stored in body tissues to the increment of metabolisable energy input. The term biological efficiency is used for efficiency of absorption of nutrients from the food stuffs ingested. Metabolic efficiency is the efficiency of converting nutrients absorbed from the gastro-intestinal tract into body tissue or product.

When considering the trait feed efficiency, it should be realised that efficiency is not a directly measurable trait. Rather, direct measurements of growth (X_1) and feed consumption (X_2) are made and efficiency is then defined as an index (X_1/X_2 or X_2/X_1) of these two traits. Sutherland (1965) and Magee (1962) have considered the relationship between feed efficiency and weight gain and have indicated the situations in which this relationship will attain particular values. Whereas, Sutherland chose to use the index feed/gain as a measure of efficiency, Magee preferred the reciprocal form gain/feed which he termed 'desirable feed efficiency'. Titus *et al.* (1953) suggested feed efficiency (gain/feed) and feed conversion (feed/gain) which are now widely used.

Variations in the ability of the mice to consume, digest and utilise may all be involved in feed efficiency. Feed efficiency is difficult to interpret biologically since it is the end result of complex metabolic processes and it may vary with age, sex, season, stage of reproduction, behaviour and activity, temperature, humidity, and other factors.

1.6.1 THE HERITABILITY OF FEED EFFICIENCY AND SELECTION RESPONSE

The few available estimates of heritability of feed efficiency in mice indicate low to moderate values ranging from 0.16 ± 0.18 to 0.40 ± 0.20 (Sutherland *et al.*, 1970; Jara-Almonte and White, 1973; Yuksel *et al.*, 1981). The effectiveness of selection for feed efficiency was tested in four lines of mice, one of which was selected directly for feed efficiency by Sutherland *et al.* (1970). Estimates of heritability obtained from paternal half-sib analysis of data pooled over twelve generations of selection were 0.16 ± 0.18; 0.22 ± 0.18; 0.40 ± 0.20 and 0.35 ± 0.17 in the four lines. When the data from both sexes in all the lines and generations were pooled, the single estimate obtained was 0.27 ± 0.09. As the line under direct selection for feed efficiency had previously been selected for weight gain, this may have altered the relationship between efficiency and weight gain by fixing some of the genes for these traits, thus resulting in decreased responses to selection for feed efficiency. The estimate of realized heritability for feed efficiency reported by Yuksel *et al.* (1981) was only 0.13 ± 0.04 when averaged over two sets of lines selected for feed efficiency using different criteria of selection but the response in feed efficiency after 8 generations of selection was substantial (18-60% increase in efficiency). Gunsett *et al.* (1981) have reported realized heritabilities of 0.56 and 0.73 for feed conversion based on the amount of feed required for a fixed gain, and grammes of gains made on a fixed quantity of feed

respectively. Selection was practised for four generations and was effective in improving feed conversion ratio of the selected lines. The genetic and phenotypic standard deviations or the coefficients of variation in the base populations and in subsequent generations of selection together with the selection responses in feed efficiency in terms of genetic and phenotypic standard deviations are not available to analyse the genetic nature of this trait.

1.6.2 THE RELATIONSHIP OF FEED EFFICIENCY WITH OTHER TRAITS

Considerable evidence has accumulated to indicate the positive genetic and phenotypic relationships between feed efficiency, feed consumption and postweaning growth in mice (Fowler, 1962; Rahnefeld *et al.*, 1965; Lang and Legates, 1969; Sutherland *et al.*, 1970; Timon and Eisen, 1970; Stanier and Mount, 1972; Jara-Almonte and White, 1973; Robison and Berruecos, 1973; Brown and Frahm, 1975; Kownacki *et al.*, 1977; McPhee *et al.*, 1980). This has led to the increased interest in indirect improvement of feed efficiency through selection for growth rate. From a recent review of the effect of selection for growth rate in mice, McCarthy (1980) stated categorically that '... there is no case for straight forward selection for efficiency, since selection for weight achieves similar results without the expense of food recording'. But it has been observed that where selection was for increased efficiency, the changes in efficiency were greater than where selection was for growth rate alone (Sutherland *et al.*, 1970, 1974; Gunsett *et al.*, 1981; Yuksel *et al.*, 1981). Also, selection for growth rate does involve an assumption that the genetic correlation between body size and feed efficiency itself will not be altered with selection. Since feed efficiency in mice has largely been studied as a correlated response to selection for growth rate or body weight, it will be appropriate to review the available information in the following sections, in the context of selection lines.

1.6.3 BODY WEIGHT, FEED INTAKE AND FEED EFFICIENCY

Sutherland *et al.* (1974), McCarthy (1980) and Roberts (1979) have reviewed many aspects of feed efficiency and feed intake. The differences in efficiency between lines selected for body weight or growth rate and control lines are generally greatest in the one or two weeks after weaning and then decline abruptly, levelling off at about six to eight weeks of age (Fowler, 1962; Timon and Eisen, 1970; Hetzel, 1978). In an important study by Roberts (1981), selection for body size has been shown to change both feed intake and efficiency correspondingly. At the same age or weight, large mice consumed more than the controls, and small mice less. Feed intake/(week x unit body weight) was similar for large and small mice up to 4 weeks of age, but thereafter, the lines began to differentiate. Adult large mice ate about three-quarter of the amount of food consumed by the adult small mice on a per unit body weight basis. The control mice were similar to large mice until 6 weeks of age, and thereafter their feed intake was intermediate between the large and small lines. A higher feed efficiency of large mice as compared with the controls during the active growth of up to 8 weeks may be due to their relatively more efficient utilisation of energy for growth and reduced maintenance energy requirements which can be explained in terms of less surface area per unit of body weight with its implications for thermoregulatory thermogenesis. The differences in feed efficiency between small and control lines were not significant. Timon and Eisen (1970) observed that the gross efficiency of a line selected for postweaning gain compared to the control line was higher during a fixed postweaning weight gain (15-25g) period. They also reported higher feed efficiency in the selected line on restricted feeding than on *ad libitum* feeding which is difficult to explain. However, this is a common result in swine in which the reduction in fatness outweighs the decrease in intake with an overall effect of increase in efficiency.

Fowler (1962) and Stanier and Mount (1972) reported no differences in digestibility in selected and control lines of mice. As well genetic differences in net energetic efficiency of tissue growth have not been clearly demonstrated among selected and unselected lines of mice (Fowler, 1962; Timon and Eisen, 1970; Stanier and Mount, 1972). Therefore, it appears that the increased gross efficiency of the lines selected for increased growth rate may be due mainly to their increased capacity of feed consumption. Positive correlated responses in feed intake invariably accompany selection for body weight or growth rate. Roberts (1973) demonstrated that mice selected for large body weight at six weeks consumed about 20 percent more food than the controls. In two lines of mice selected for 21-day body weight and weight gain between 21 and 42 days of age, average daily feed consumption between 3 and 6 weeks increased by 17.4 and 26.9 percent respectively over the control line (Brown and Frahm, 1975).

More recent studies by Eisen *et al.* (1977), Eisen and Bandy (1977) and McPhee *et al.* (1980) also support this pattern of increased feed consumption and increased feed efficiency of mice selected for body weight or weight gain. Radcliffe and Webster (1976) from their observations on normal and obese rats suggested that the appetite control was mediated through the genetic capacity for protein deposition. If this hypothesis is valid, the higher efficiency of mice with larger appetites can readily be explained. However, other factors such as metabolic activity (James and Trayhurn, 1981; McCarthy, 1980; Trayhurn, 1980), carcass composition and energy cost of fat and protein deposition (Pullar and Webster, 1977), and the rates of protein and fat turn over (Paigen, 1971; Bates and Millward, 1981) are also involved in appetite regulation.

1.6.4 BODY COMPOSITION AND FEED EFFICIENCY

Many reports indicate that selection for increased growth rate *per se* may have effects on characters other than the efficiency of feed utilisation. Any increase in feed

consumption above that which is needed for maintenance requirements and protein synthesis may result in a greater fat deposition. It is logical to assume that low efficiency lines would store less protein and more fat than the lines with higher efficiency since fat has a higher concentration of gross energy than protein. The energy costs of depositing 1g of protein or fat are almost identical at 53 kJ ME (Puller and Webster, 1977). But due to a much higher content of water in the muscle than in fat, the cost of gaining 1g of body weight as fat and 1g of lean is 53 and 11 kJ respectively (Webster, 1977). The higher energy content of a fat carcass in comparison to a lean carcass must entail a greater food intake relative to weight gain.

Because fat has a higher gross energy content than protein, a group of mice depositing excess fat should be considerably less efficient than the corresponding group depositing relatively greater proportions of protein and water. On the basis of these relationships Brody (1935) predicted that a less efficient strain of animal would store less protein and more fat than a more efficient strain. Contrary to this prediction however, selection for feed efficiency has been associated with an increased fat percentage in mice (Dickerson and Gowen, 1947; McPhee *et al.*, 1980; Yuksel *et al.*, 1981) and in rats (Palmer *et al.*, 1946). For mice there are a number of reports in the literature which indicate that an improvement in feed efficiency is frequently associated with an increase in carcass fat percentage. These reports refer to comparisons of the lines selected for growth rate or body weight in which case feed efficiency was studied as a correlated response (Fowler, 1962; Timon and Eisen, 1970; Sutherland *et al.*, 1970; Brown and Frahm, 1975; Eisen *et al.*, 1977; Eisen and Bandy, 1977; McPhee *et al.*, 1980). In contrast a few researchers (Fowler, 1958 in 'C' strain of Falconer's mice; Lang and Legates 1969; Brown *et al.*, 1977) have indicated little change in body composition. This result can occur

due to insufficient direct response to selection at the time of carcass analyses; or due to sampling of the genes from the base population which could be revealed if line replicates were maintained. McPhee and Neill (1976) and Hayes and McCarthy (1976) demonstrated that at younger ages, the mice selected for increased body weight were less fat than the control mice, at equal weight. In chickens, Pym and Solvyns (1979) have reported no change in carcass composition of a line selected over 5 generations for increased weight gain between 5 and 9 weeks. Another line selected for decreased feed conversion ratio over this period showed lower proportion of fat and significantly higher proportion of water in their carcasses than the control line. It would thus seem that because of the complex nature of relationships between body weight, feed intake, and body composition, the simple energetic relationship between feed efficiency and carcass fat as proposed by Brody (1935) needs to be examined more carefully.

Recent research work on the aspect of thermoregulatory thermogenesis in the mouse may be useful in explaining the interrelationships of feed economy and fat deposition. Mice display changes in temperature regulation which have been shown quantitatively to link with their enhanced metabolic activity to store fat. At 20^{o}C, the metabolic rate of the normal resting mouse is twice that found at thermoneutral temperatures of 32 or 33^{o}C (James and Trayhurn, 1981). McCarthy (1980) reported that at 15^{o}C there was a clear evidence of differences between his large and small mice of the same age in oxygen consumption per unit body weight. Smaller mice due to their larger surface area for weight as compared to the larger mice should dissipate more heat through their body surfaces thus spending more energy in maintaining normal body temperature so that less energy is available for fat storage. Larger mice on the other hand have reduced energy demands for thermoregulatory thermogenesis resulting in excess energy ingested, after meeting normal growth requirement being stored as fat (Fowler, 1962; McCarthy, 1980). Mice in most laboratories around the world are kept at temperatures much below the

thermoneutral zone. Therefore, increased feed efficiency accompanied by greater fat deposition in mice selected for rapid growth rate in comparison to mice selected for slow growth rate may be due to their lower energy cost of thermoregulation in hypothermal environments. It has been shown in genetically obese and lean mice that under thermoneutral conditions, as the ability to display the thermogenic difference is eliminated, the differences in fat deposition are minimized (Thurlby and Trayhurn, 1979).

1.6.5 FEED INTAKE AND ENERGETIC EFFICIENCY

When animals are fed *ad libitum*, large differences in feed intake and feed efficiency are observed. Such differences in feed efficiency may arise from differences in the amount of energy required for (1) maintenance including the processes of thermoregulatory thermogenesis, basal metabolism, muscular activity and energy costs of protein and fat deposition, (2) muscular growth and fatty and bone tissue deposition and (3) the ability to redirect surplus dietary energy to tissue deposition and growth (Stephenson and Malik, 1984).

The energy requirement for weight maintenance is the amount of energy needed to keep the animal in equilibrium and so to prevent any loss from or degradation of its tissues plus the normal turn over of fat and protein. Thus an intake of energy sufficient to offset the loss represented by the fasting catabolism and thermoregulation would be the requirement under the conditions specified for measuring the energy cost of these components of maintenance. The maintenance requirement during the active growth period increases regularly with the increase in body size. In addition, energy needs for growth itself vary with growth rate and with the composition of the tissue formed. Per unit of body weight, the amount of energy required for tissue growth decreases with age, reflecting the declining rate of tissue deposition. As the animal grows, the energy stored per unit of body weight increases due to a lower water and higher fat content of the tissue deposited (Sutherland *et al.*, 1974).

There is disagreement between the available reports over the effect of selection for body weight on the efficiency of utilisation of food energy. There is no evidence of increased digestibility due to selection for body weight but there may be changes in energy requirement for body maintenance (Fowler, 1962; McCarthy, 1980; Stephenson and Malik, 1984) and growth (Canolty and Koong, 1977, Stephenson and Malik, 1984).

A study on the energy expenditure of mice by Fowler (1962) showed as has been described earlier in this review, a lower maintenance cost in the large line than in the small line when calculated on the basis of per gram of body weight expressed against age. At similar body weights, irrespective of the age however, the maintenance requirement of the two lines was not different. Timon *et al.* (1970) suggested little effect of 9 generations of selection for postweaning weight gain on the net efficiency of tissue growth. The apparent advantage of the selected line over the control line in gross efficiency was attributed solely to the increased gain associated with increase in appetite. Deb *et al.* (1976) from a study on Zucker rats concluded that the maintenance cost was not an important factor in influencing efficiency of energy utilisation. Canolty and Koong (1977) reported that the selection for post-weaning gain did not alter the maintenance requirement but increased the efficiency of energy utilisation. Stanier and Mount (1972) and Hetzel (1978) observed that the mice of the lines selected for heavier body weights or increased growth rate when offered levels of feeding below their *ad libitum* feed intake grew faster than the control mice, an indication of their lower maintenance requirement. This result could occur if the large restricted fed mice were leaner. However, in both these studies neither body weight nor body composition differences of the lines were taken into account. McCarthy (1980) suggested that the differences in maintenance cost between his large and small mice at a fixed age arose mainly through scaling difference in the ratio of surface area to weight which affects heat loss and thus the energy cost of

thermoregulatory heat production. There were no differences in maintenance requirement of the large and the small line mice at similar weights.

In summary, there is little doubt about the corresponding increases in feed consumption as a result of selection for body weight or growth rate. Increases in feed efficiency are also observed but the interpretations with regard to the changes in energetic efficiency are somewhat conflicting and ambiguous.

1.6.6 RESTRICTED FEEDING AND FEED EFFICIENCY

The increased feed intake which accompanies an increase in body size could result in increases in metabolisable energy (Fowler, 1962; Timon and Eisen, 1970). Efficiency of protein deposition may also be altered. Increased efficiency of protein synthesis has been reported by Bates and Millward (1981) in a fast growing strain of rats in comparison to a slow growing strain on an age basis. On a body weight basis a more complex picture was presented; the fast growing rats exhibiting higher rates of protein synthesis and lower rates of degradation at lighter weights.

Besides efficiency of protein deposition there is the additional aspect of carcass fat deposition. After meeting energy requirement for body maintenance and the complex processes of protein synthesis and degradation, the surplus ingested energy is then stored as fat (Roberts, 1979). Selection under restricted feeding regimes has been attempted by a number of researchers with the idea of reducing excessive fat deposition and increasing feed efficiency.

One of the earlier reports of selection in mice on restricted diet was that of Falconer and Latyszewski (1952). After 8 generations of selection, the mice selected for increased body weight on a restricted diet were superior in weight gain betewen 3 and 6 weeks to those selected on an *ad libitum* diet, when both groups were reared on a restricted diet.

Since their experiment was directed primarily at studying the genotype-environment interaction for 6 week body weight, the correlated responses in food intake and body composition were not measured. Timon and Eisen (1970) observed greater differences in feed efficiency on a restricted level of feeding between a line selected for increased postweaning gain on *ad libitum* feeding and the control line. The differences between the selected and control lines for fat were more fully expressed under full feeding. For non-fat components the differences between lines were expressed more fully under restricted feeding. The authors suggested that the increased carcass fat content of the mice selected on full feeding was a consequence of their increased food consumption capacity. This interpretation however, does not explain why the differences between the lines for protein, ash and water were more fully expressed under restricted feeding on an age basis. The energetic efficiency of the selected line was higher than the control both on restricted and on *ad libitum* feeding. At the same weight, the energetic efficiency of the two lines was simialr at both levels of feeding.

Kielanowski (1968) predicted that the elimination of appetite as a source of variation in selecting for body weight gain would lead to a change in the partitioning of metabolisable energy more toward protein and less toward fat synthesis. This prediction was put to experimental test by McPhee *et al.* (1980). They selected two lines of mice for weight gain between 5 and 9 weeks. The daily feed allowance over the test period was fixed at 83 percent of the average *ad libitum* intake of the control line. After 6 generations of selection, there was no evidence of an increase in protein at the expense of fat in one line, while in the other an actual increase in fat as compared to control was observed. Reduced maintenance requirement and higher retention of metabolisable energy, although not measured may be the likely explanation for increased growth efficiency observed in these selection lines. Reduction in maintenance requirement of the selected mice may have been due to lower heat loss relative to their larger size and heavier body weights than the control mice. Hetzel (1978) and Yuksel *et al.* (1981) also

selected for gain on restricted levels of feeding. No changes in food consumption were observed in either of these studies when their lines were compared with the control under *ad libitum* feeding. At the same time, gross feed efficiency increased in the lines in both experiments. A decline in percentage fat was observed by Hetzel, while Yuksel and his co-workers reported an increase in fatness. The food restriction was 15 percent and 10 percent below the control mice *ad libitum* intake in the two studies, respectively. This may account for a part of the differential response in fat deposition in the two lines. The overall increases in feed efficiency in spite of differences in body composition of the two lines may have arisen as a consequence of differential correlated responses in energy costs of maintenance and tissue metabolism.

1.7 PARTITIONING OF GENETIC EFFECTS OF OFFSPRING AND DAM

Traits of mammals are influenced by the quantitative gene effects of the dam and those of her offspring. It is thus important that the genetic effects of both the dam and the offspring should be considered when comparing traits of two or more populations. Where populations are utilised in crossing these may be studied as direct genetic and maternal genetic effects, direct and maternal heterosis, and recombination effects of the offspring and the dam. Dickerson (1969) gave a theoretical model for the choice of various crossbreeding alternatives. Estimates of genetic effects using Dickerson's model are frequently reported in the literature but they are often confounded owing to the inadequacy of mating schemes. An appropriate mating scheme and the procedures of obtaining unconfounded estimates of these effects are discussed in detail in Section 4.

The partitioning of the average differences between populations into effects of the offspring and dam may generally be used for all traits. However, the relative importance of any single component will be different for different traits.

Characters of mature animals are largely determined by the genotype of the individual and the environmental factors. Alternatively, traits of young animals are influenced not only by the genotype of the individual but also to a varying extent by maternal effects.

Eisen (1973) evaluated the response to selection for 12-day litter weight in terms of direct and maternal genetic effects, using one of the lines plateaued for 12-day litter weight and another unselected control. An unbalanced back-crossing design was used and comparisons were made among selected and control lines, reciprocal F_1 crosses, F_2's and backcrosses. Selection response in 12-day body weight was primarily due to direct genetic effects (92 percent). Maternal genetic effects contributed little to direct or correlated responses in body weight. Direct heterosis was significant for postweaning weights. In comparison, maternal heterosis was more important for preweaning weights and declined after weaning. Recombination effects were not significant for either pre- or postweaning body weights.

Direct genetic, maternal genetic and direct heterotic effects on body weight at 3 and 6 weeks and weight gain during this period were analysed by Bakker *et al.* (1976). Two selected populations and their reciprocal F_1 crosses, and two control populations and their F_1 crosses were studied. Of the two selected populations one had been selected over 73 generations for 6-week body weight and another selected over 37 generations for 3-6 week weight gain. Direct genetic effects accounted for almost all the differences between the two selected populations in body weight at 3 and 6 weeks and weight gain, but at 3 weeks of age 82 percent of the differences in body weight between the two control populations were determined by maternal genetic effects. However, direct genetic effects accounted for 73 percent of the differences in 6-week body weight and almost all the differences in weight gain. Heterosis was significant for 3 and 6 week body weights and was higher in F_1 crosses between control lines than between selected lines.

An extension of the above study was reported by Nagai *et al.* (1976). They partitioned direct and heterotic components of the individual and maternal genetic effects for birth, 12, 21, 31, 42 and 63 day body weights and weight gains between these ages. Maternal genetic effects were responsible for a greater part of the differences between populations in 12-day body weight. In comparison, direct genetic effects were more important for observed differences in postweaning body weigths and pre- and postweaning weight gains. Direct heterosis was significant for almost all the traits, whereas maternal heterosis was significant for weight gains at early ages and for body weights. Direct heterosis tended to be larger than maternal heterosis in both selected and control crosses. Direct heterosis in both the studies (Bakker *et al.*, 1976 and Nagai *et al.*, 1976) was calculated as a deviation of the F_2 progney mean from the parental mean multiplied by a factor of 2 since only one-half of the direct heterosis is expected in F_2. This would have resulted in doubling of the recombination effects which were confounded with the direct heterosis. Consequently, the reported estimates of direct heterosis were in fact combined estimates of direct heterosis and recombination effects ($h^O + r^O$). Similarly, estimates of maternal heterosis (Nagai *et al.*, 1976) were confounded with one-half component of recombination effects ($h^M + \frac{1}{2} r^O$)*. Therefore, if recombination effects were significant, estimated values of direct and maternal heterosis would be biased. The discrepancy between the results of these two studies (Bakker *et al.*, 1976 and Nagai *et al.*, 1976) and Eisen (1973) was probably due to different criteria of selection used.

Eisen *et al.* (1977) partitioned the differences between selected and control populations for body composition (water, fat, protein and ash) at 3, 6 and 9 weeks, and feed and energetic efficiencies during 3-6 and 6-9 week age intervals into genetic effects of the dam and the offspring. Neither

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* For definition of genetic parameters see Dickerson (1973).

direct genetic nor maternal genetic effects were significantly different between the two control populations for a majority of traits. Differences beteen maternal genetic effects of the selected populations were also generally not significant. Direct genetic effects were responsible for major differences between the selected populations. Direct heterosis in F_1 crosses involving selected or control populations were in general not significant.

Hayes and Eisen (1979b) studied differences in preweaning body weight and carcass composition between three lines of mice, two of which had been selected for high and low 6 week body weight, and a third unselected control. Positive correlated responses to selection in direct genetic and postnatal maternal genetic effects on body weight, weight of lean and weight of fat were observed in both the selected lines. The correlated responses in postnatal maternal genetic effects for these traits were of the same order of magnitude as direct genetic effects. Eisen and Roberts (1981) determined correlated responses in direct genetic, postnatal maternal genetic and litter size effect on fat deposition at 6 week age using gonadal fat as an index of adiposity. The direct genetic effects were three times as large as postnatal maternal genetic effects. Increases in litter size reduced both the weight and proportion of gonadal fat but this factor was of less importance than the direct genetic effects.

In summary, the foregoing studies indicate that the phenotypic differences between populations for body weight and weight gain are due primarily to direct genetic effects, the contribution of maternal genetic effects is small and variable depending upon the age and the specific population considered. Maternal genetic and maternal heterotic effects are more important for preweaning growth whereas, direct heterosis is more important for postweaning growth. The situation with regard to body composition, feed efficiency and energetic efficiency is less clear. In addition, due to inadequacy of mating designs, the reported estimates of various genetic effects are often biased.

SECTION 2

A COMPARISON OF THE LINES SELECTED FOR INCREASED AND DECREASED EIGHT WEEK BODY WEIGHT

I. GROWTH AND BODY COMPOSITION

2.1 INTRODUCTION

In simple chemical terms the body is the sum of four major chemical components - water, protein, fat and minerals. In a normally growing mouse the percentage of water decreases while that of protein and minerals increases up to the age of sexual maturity, after which there is a fair degree of constancy in the chemical composition of the fat-free body. The percentage of fat increases consistently and well beyond the age of sexual maturity (Sutherland *et al.*, 1974).

Selection for growth rate or body weight is known to affect the carcass composition of mice. In a number of reports an increase in the proportion of fat content was observed in the lines selected for increased body weight or weight gain (Fowler, 1958; Biondini *et al.*, 1968; Clarke, 1969; Timon *et al.*, 1970; Hayes and McCarthy, 1976; Eisen *et al.*, 1977; Hetzel, 1978; Allen and McCarthy, 1980; McPhee *et al.*, 1980). In two studies there was no evidence of differences between the selected and control lines for the relative proportion of carcass fat (Lang and Legates, 1969; Brown *et al.*, 1977). In a majority of these studies comparisons between lines were made on an age basis and chemical components were expressed either as absolute values or more commonly as percentages of fresh carcass weight. On a weight basis (regression of log fat on log body weight); Clarke (1969), Hayes and McCarthy (1976), Allen and McCarthy (1980) and Eisen *et al.* (1977) reported increased relative rate of fat deposition in large lines. Hayes and McCarthy (1976) also observed a reduced relative rate of fat deposition in small lines. McPhee and Neill (1976) using the allometric relationship ($y = ax^b$; Huxley, 1932) between the body and its chemical components showed that the mice selected for a high 8 week body weight were leaner than the control and low body weight lines at earlier, lighter body weights, but rapidly became fatter at later, heavier body weights.

The carcass composition of mice from different selection lines therefore is dependent upon the age at which selection is performed and the age at which carcass composition is determined. Estimates from a number of experiments (Fowler, 1958; Hull, 1960; Clarke, 1969; Hayes and McCarthy, 1976; McPhee and Neill, 1976; Allen and McCarthy, 1980), with diverse experimental material and with fat estimated over a wide age range provide the basis for the following conclusions. Firstly, prior to the age of selection, the lines selected for high body weight show a reduction in the proportion of fat at low body weights relative to low body weight and control lines but they have a tendency to grow fatter at later ages. Secondly, selection for increased weight at an early age appears to result in an ability to deposit more fat at an earlier age compared with selection at an older age.

In a majority of selection experiments reported in the literature, composition analyses were carried out on the whole body. In one experiment (Allen and McCarthy, 1980), fat distribution was studied at different anatomical locations within the body. Separate chemical analyses (water, fat, protein and ash) of carcass and non-carcass parts of the mouse have not been reported. Non-carcass parts of the body in meat animals are non-edible and less valuable from consumers point of view but may account for 30 to 60% of the total body weight, In the mouse, non-carcass part includes the head, feet, skin, fur, tail and viscera, which make up 60 to 70% of the whole body weight. The nitrogen content, the fat content and also the total energy content of the non-carcass parts of the mouse are more than the carcass part. However, the effects of selection on carcass and non-carcass parts of the mouse have not been studied separately.

This Chapter deals with the comparison of selected and unselected lines of mice for differences in the composition of the whole body, and the carcass and non-carcass parts. Comparisons are made on a constant age and body weight basis in the postweaning period in an attempt to understand the

patterns of tissue growth leading to differences in body composition during this period.

2.2 MATERIALS AND METHODS

Mice used in this study were from lines selected for high and low body weight at eight weeks of age (H and L respectively) and a randombred control line (R). The lines were produced and maintained by Associate Professor S.K. Stephenson and Mr D.K. Fredline of the Department of Animal Science, University of New England. The base population was constructed by crossing the following inbred lines: 101, CBA, C_3H and an unspecified albino stock. This base was the foundation of the control population and a high and low index line where selection was for leg length and body weight (Dawson *et al.*, 1972). The index lines were selected for 18 generations, at which point they were crossed with the control to give a gene pool containing 50 percent of the control, 25 percent of the high and 25 percent of the low index genotypes. From this gene pool the H and L lines had been selected for ten generations. There were two generations of relaxed selection. The R line was in 30th generation at the time of the present study. A diagrammatic presentation of the history of these lines is given in Figure 2.1. Females were mated at 8 weeks of age with males of the same age by allotting one female to each male. Matings were random with the exception that full-sib matings were avoided to reduce inbreeding. The H and L lines were maintained by selecting 25 pairs each generation and R line was maintained by randomly selecting 100 pairs for breeding in every generation. Throughout the selection the mice were housed at 24^{o}C, uncontrolled humidity and a light to darkness ratio of 14:10 hours. The mice had *ad libitum* access to water and pelleted commercial food formulated by Fielders mill, Tamworth, New South Wales.

In the present experiment, litters from each population were standardized to 8 young at 3 days of age, except in cases where litter size was less than eight. Progeny were weaned at 21 days of age and fed *ad libitum* in individual cages. One male and one female from each litter was randomly assigned for

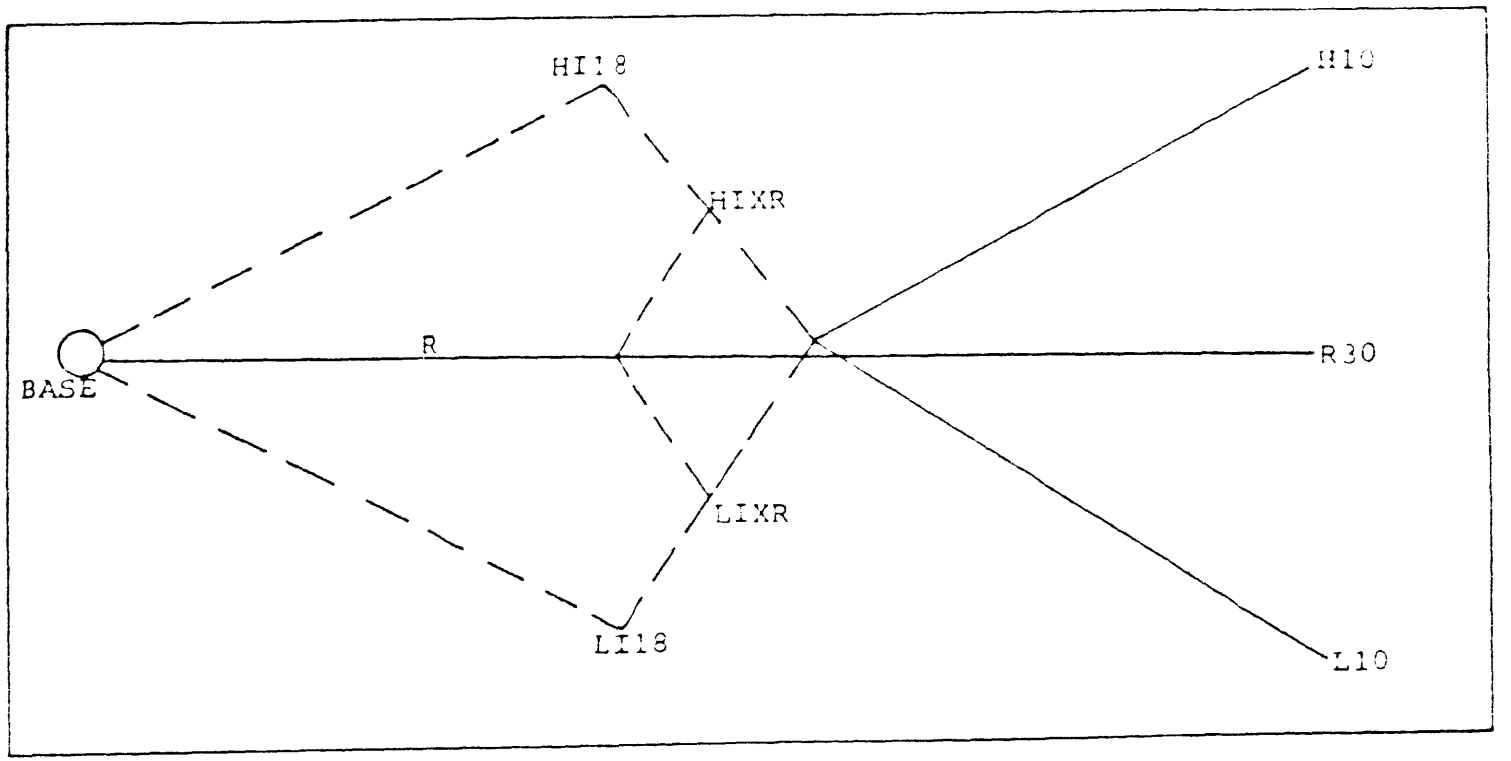


Figure 2.1 A diagrammatic presentation of the history of the lines used. HI and LI refer to the high and low index selection lines, H and L to high and low body weight lines and R is the unselected line. The numerics with each line represent the number of generations. The HI and LI were crossed with the R line at generation 18 and the resultant HIXR and LIXR genotypes were subsequently crossed to give a gene pool from which H and L lines were selected.

carcass analyses between three to eight weeks of age. The data were recorded on the exact day assigned for the measurement. The carcass analyses were performed at weekly intervals after killing the sampled mice by a lethal dose of ether. The number of mice allotted to each population-age subclass is given in Table 2.1.

Killed mice were immediately dissected, skinned and partitioned into carcass and non-carcass parts which were weighed separately. Non-carcass parts included skin, fur, viscera, head, tail and feet. The ingesta from the gastro-intestinal tract were removed before weighing the non-carcass parts.

Table 2.1 Numbers of mice sampled from three to eight weeks of age for composition analysis

Line		Age in weeks						Total
		3	4	5	6	7	8	
L	M	15	10	9	14	9	20	77
	F	10	11	11	10	8	16	66
H	M	10	10	10	10	11	16	67
	F	11	10	10	11	11	14	67
R	M	10	10	10	11	11	19	71
	F	10	9	10	9	9	26	73

2.2.1 Chemical Analyses

The chemical analyses of carcass and non-carcass parts for individual mice were carried out separately as follows:

Water:

The carcass and non-carcass parts were weighed separately in pyrex containers and dried in an oven at 90^{o}C for 72 hours. The difference in weight before and after drying was taken as the water content.

Fat:

The dried material was crushed in a glass mortar with a pestle and was transferred into an extraction thimble. The thimble was then transferred into the oven for 24 hours in order to evaporate any moisture. After weighing, the thimble was placed in Soxhlet extraction apparatus containing a 2:1 (V/V) mixture of methyl alcohol and diethyl ether and the fat was extracted for 24 hours. After extraction the thimble + contents were air dried for 24 hours and then oven dried for another 24 hours. The change in weight before and after extraction was recorded as the fat content.

Ash:

The fat-free dry matter from the thimble was emptied into a porcelain crucible, dried in an oven for 2 hours and weighed. Subsequently, it was placed in a muffle furnace for ashing, gradually increasing the temperature to 600^{O}C and maintaining this temperature for 24 hours. The crucible was then allowed to cool before weighing. Difference in weight of the empty crucible and that of the crucible + ash was taken as the weight of the ash.

Protein:

The weight of the crucible + fat-free matter minus weight of the crucible + ash was taken as fat-free combustible matter (FFCM). The FFCM thus recorded was taken as protein content, although it would also contain small amount of carbohydrates but this would not be likely to have biased the line comparisons.

All weights were recorded to the nearest 0.1 mg. Throughout the chemical analyses, the material was handled in a dessicator containing calcium chloride, due to the hygroscopic nature of the dry matter.

2.2.2 Statistical Analyses

The analyses of variance were conducted for carcass (C) and non-carcass (NC) parts separately as well as for the whole body (WB). The traits analysed were water, fat, protein and ash.

Line comparisons were made separately on an age and weight basis. Each trait was analysed by least squares procedures (Harvey, 1960).

For comparisons of carcass composition traits on an age basis, the statistical model contained fixed effects of line, sex, age and, line x sex, line x age, sex x age interactions as follows:

$$Y_{ijkl} = \mu + L_i + S_j + A_k + (LS)_{ij} + (SA)_{jk} + (LA)_{ik} + e_{ijkl}$$

where Y_{ijkl} = l^{th} observation of the ijk^{th} subclass

μ = Overall mean

L_i = Fixed effect of the i^{th} line (i = 1,.,3)

S_j = Fixed effect of the j^{th} sex (j = 1,2)

A_k = Fixed effect of the k^{th} age group (k = 1,2,---,6)

$(LS)_{ij}$, $(SA)_{jk}$ and $(LA)_{ik}$ are two way interactions involving line, sex and age

e_{ijkl} = Random error (NID,0,σ^2)

Actual weights as well as the percentages of water, fat, protein and ash of C, NC and WB were analysed by this method.

The allometric equation $y = a\ x^b$ (Huxley, 1932) was used for describing the part, y (water, fat, protein or ash) to whole, x (C, NC or WB) relationship and for making comparisons between lines on a body weight basis. The data were transformed to logarithms and linear regressions of $\log_{10}$ component weight (y) on $\log_{10}$ WB, C and NC (x) were computed as, $\log y = \log a + b \log x$, where a is a constant and denotes the elevation of the regression line and b is a measure of the rate of growth of the part relative to the rate of growth of the whole. If $b > 1$, the part is growing relatively faster than the whole, and the parts contribution to the whole is increasing. The part in question is described as late maturing. If $b < 1$, the part is growing relatively slower than the whole and is early maturing.

Separate analyses were carried out using fresh, dry or fat-free C, NC or WB as independent variables in any particular analysis.

2.3 RESULTS

2.3.1 Composition of the Fresh Body

The least-squares averages for the body weights and weights of the chemical components - water, fat, protein and ash of the WB, C and NC parts of the mice slaughtered at weekly intervals from 3 to 8 weeks of age are presented in Tables 2.2 to 2.4. The averages of water, fat, protein and ash expressed as percentages of the WB, C and NC parts are shown in Figures 2.2 and 2.3 and in Tables (Appendices F to H).

The main changes in body composition of the H line from the R line were an increase in the fat percentage and a reduction in the percentage of water, protein and ash. In the comparison between L and R lines, fat percentages decreased while that of other components increased in the L line. Water percentage of the three lines showed an initial gain from 3 to 4 weeks and a corresponding decline in the fat percentage in this period. From 4 to 8 weeks, water percentage showed a decrease and fat an increase in the L, H and R lines. Comparisons between the L and H lines for water and fat percentages were significant at each age except for water at 4 weeks; H and R line comparisons were significant at 3, 4, 7 and 8 weeks for water and during 6 to 8 weeks for fat; and R-L contrasts were significant at 3, 4 and 8 weeks for water and from 3 to 5 weeks for fat. Apart from this, the other significant differences among lines were a reduction in protein percentage from 6 to 8 weeks and in ash percentage at 8 weeks in the H line compared with the R and L lines.

Sex effects were significant mainly for percentage body fat and these are presented in Appendix D. Females had a higher proportion of fat than males at every age from 3 to 8 weeks in the H line. The difference between sexes in the L line was significant only at 5 weeks of age ($P<0.05$, $M<F$). In the R line

Table 2.2 Least-squares averages ± s.e. for weight and chemical constituents of the fresh whole body

Trait/Line	Age					
	3 weeks	4 weeks	5 weeks	6 weeks	7 weeks	8 weeks
Whole body weight (g)						
L	8.405±0.388	11.664±0.420	14.384±0.431	16.148±0.395	17.221±0.466	18.447±0.321
H	13.063±0.420	19.321±0.430	23.778±0.430	26.797±0.420	28.562±0.410	29.879±0.351
R	10.993±0.430	15.475±0.441	19.088±0.430	20.815±0.431	21.956±0.431	23.436±0.289
Water (g)						
L	6.029±0.261	8.393±0.282	10.129±0.290	11.187±0.266	12.017±0.314	12.565±0.211
H	9.201±0.282	13.762±0.289	16.450±0.289	18.241±0.282	19.122±0.276	19.780±0.236
R	7.493±0.289	10.911±0.297	13.126±0.289	14.316±0.290	15.204±0.290	15.705±0.194
Fat (g)						
L	0.695±0.099	0.880±0.107	1.191±0.109	1.384±0.100	1.422±0.119	1.827±0.082
H	1.283±0.106	1.706±0.109	2.324±0.109	2.978±0.106	3.450±0.103	3.625±0.089
R	1.062±0.109	1.375±0.112	1.849±0.109	1.909±0.109	1.982±0.109	2.486±0.073
Protein (g)						
L	1.451±0.072	2.054±0.078	2.644±0.080	3.050±0.073	3.324±0.087	3.479±0.060
H	2.200±0.078	3.323±0.080	4.277±0.080	4.837±0.078	5.130±0.076	5.541±0.065
R	1.834±0.080	2.718±0.082	3.501±0.080	3.875±0.080	4.222±0.080	4.479±0.054
Ash (g)						
L	0.199±0.013	0.303±0.014	0.390±0.014	0.468±0.013	0.514±0.015	0.560±0.011
H	0.309±0.014	0.474±0.014	0.624±0.014	0.708±0.014	0.804±0.014	0.846±0.012
R	0.248±0.014	0.386±0.015	0.534±0.014	0.597±0.014	0.640±0.014	0.706±0.010

Table 2.3 Least squares averages ± s.e. for weight and chemical constituents of the carcass part of the fresh body

Trait	Age					
	3 weeks	4 weeks	5 weeks	6 weeks	7 weeks	8 weeks
Carcass weight (g)						
L	3.008±0.160	3.912±0.137	4.928±0.177	6.168±0.163	6.781±0.192	7.320±0.132
H	4.491±0.173	6.421±0.177	8.523±0.177	10.109±0.173	11.062±0.169	11.473±0.145
R	3.998±0.177	5.316±0.182	6.911±0.177	8.184±0.177	8.700±0.177	9.338±0.119
Water (g)						
L	2.189±0.113	2.840±0.122	3.552±0.125	4.420±0.115	4.892±0.135	5.147±0.093
H	3.218±0.122	4.642±0.125	6.066±0.125	7.105±0.122	7.730±0.119	7.959±0.102
R	2.827±0.125	3.815±0.128	4.916±0.125	5.811±0.125	6.223±0.125	6.495±0.084
Fat (g)						
L	0.212±0.028	0.221±0.030	0.286±0.031	0.380±0.028	0.411±0.033	0.524±0.023
H	0.342±0.300	0.426±0.031	0.595±0.031	0.855±0.030	0.922±0.029	0.936±0.025
R	0.327±0.031	0.333±0.032	0.473±0.031	0.556±0.031	0.578±0.031	0.728±0.021
Protein (g)						
L	0.506±0.029	0.709±0.032	0.902±0.033	1.152±0.030	1.152±0.030	1.378±0.024
H	0.767±0.032	1.126±0.033	1.536±0.033	1.815±0.032	2.000±0.031	2.120±0.027
R	0.650±0.033	0.960±0.034	1.254±0.033	1.511±0.033	1.625±0.033	1.743±0.022
Ash (g)						
L	0.075±0.008	0.124±0.009	0.162±0.009	0.219±0.008	0.254±0.016	0.274±0.007
H	0.126±0.009	0.210±0.009	0.291±0.009	0.365±0.009	0.404±0.009	0.437±0.007
R	0.101±0.009	0.168±0.009	0.251±0.009	0.303±0.007	0.336±0.007	0.367±0.005

Table 2.4 Least squares averages ± s.e. for weight and chemical constituents of the non-carcass part of the fresh body

Trait	Age					
	3 weeks	4 weeks	5 weeks	6 weeks	7 weeks	8 weeks
Non-carcass weight (g)						
L	5.397±0.249	7.752±0.277	9.457±0.277	9.980±0.253	10.440±0.300	11.130±0.210
H	8.570±0.270	12.900±0.280	15.260±0.280	16.690±0.270	17.500±0.260	18.410±0.230
R	6.935±0.280	10.160±0.280	12.180±0.280	12.630±0.280	13.260±0.280	14.100±0.190
Water (g)						
L	3.839±0.168	5.552±0.181	6.577±0.186	6.766±0.171	7.125±0.202	7.418±0.139
H	5.983±0.181	9.120±0.186	10.384±0.186	11.137±0.181	11.391±0.178	11.821±0.152
R	4.666±0.186	7.096±0.191	8.210±0.186	8.505±0.186	8.981±0.186	9.210±0.125
Fat (g)						
L	0.483±0.076	0.659±0.083	0.906±0.085	1.004±0.078	1.011±0.092	1.304±0.063
H	0.942±0.083	1.281±0.085	1.730±0.085	2.120±0.083	2.527±0.081	2.689±0.069
R	0.735±0.085	1.042±0.087	1.376±0.085	1.353±0.085	1.404±0.085	1.758±0.057
Protein (g)						
L	0.945±0.050	1.344±0.054	1.743±0.055	1.897±0.050	2.053±0.060	2.101±0.041
H	1.433±0.054	2.197±0.055	2.740±0.055	3.022±0.054	3.130±0.054	3.421±0.045
R	1.184±0.055	1.758±0.056	2.247±0.055	2.364±0.055	2.596±0.055	2.736±0.037
Ash (g)						
L	0.123±0.007	0.179±0.008	0.227±0.008	0.248±0.007	0.259±0.009	0.287±0.006
H	0.183±0.008	0.265±0.008	0.333±0.008	0.343±0.008	0.400±0.008	0.409±0.007
R	0.147±0.008	0.218±0.008	0.283±0.008	0.319±0.008	0.322±0.008	0.354±0.005

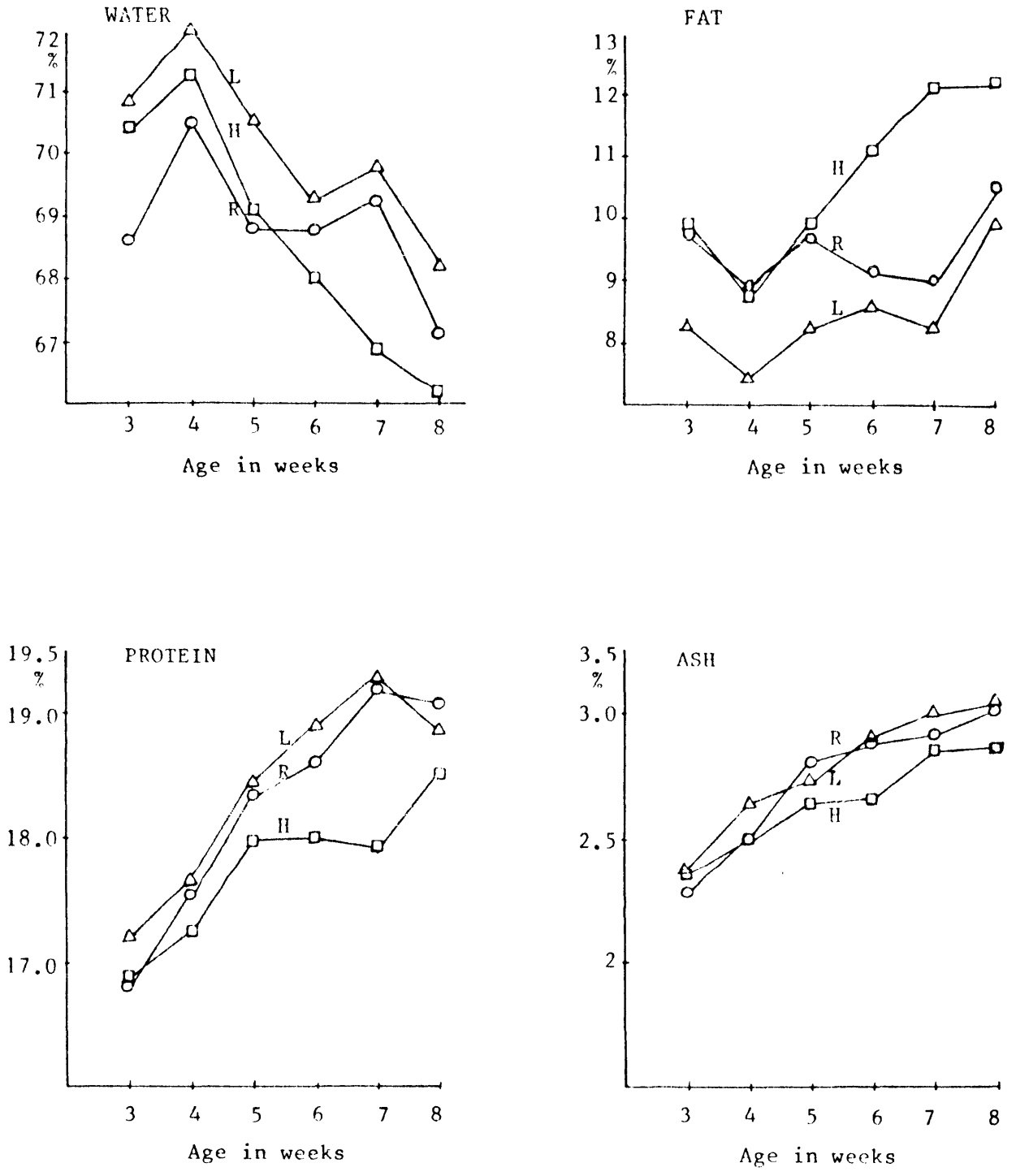


Figure 2.2 Water, fat, protein and ash as percentages of fresh whole body weight.

Lines: L and H = Low and high body weight selection lines

R = Randombred (unselected) line

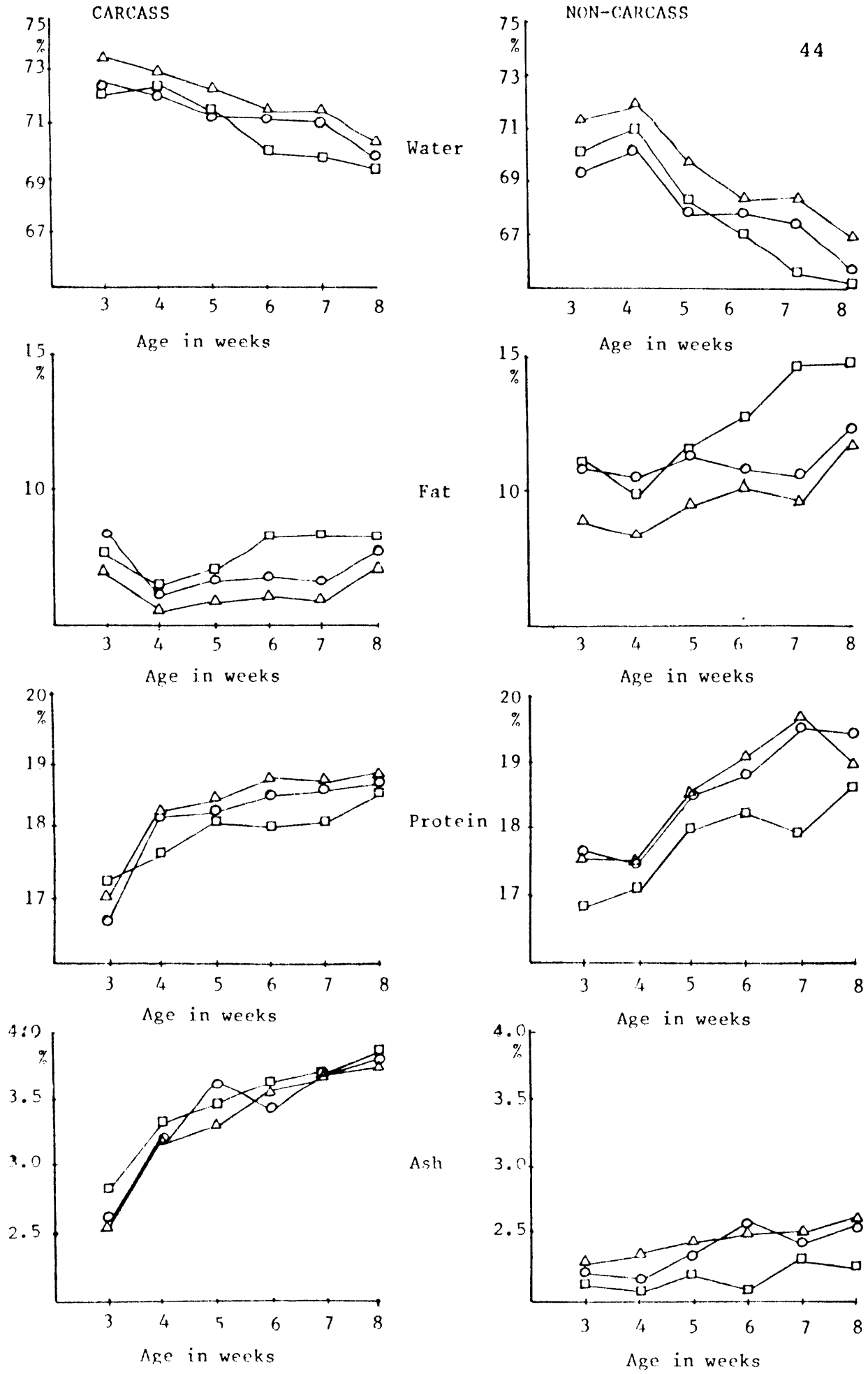


Figure 2.3 Water, fat, protein and ash as percentages of weights of carcass and non-carcass parts of the fresh body.
Lines: H □; RO; LΔ. H and L refer to the high and low body weight selection lines and R refers to the randombred (unselected) line.

sex effects were not important at any age of determination of fat in this study. Analysis of data combined over the three lines showed higher percentage of fat between 3 and 5 weeks ($P < 0.01$) and at 7 weeks ($P < 0.05$) in females compared to males. Line x sex interactions were generally not significant. Of the 24 (4 traits x 6 ages) separate analyses conducted, line x sex interaction effects were significant ($P < 0.05$) only for one line-age subgroup with regard to fat and water. Hence the interaction effects were ignored.

As for the whole body, C and NC parts were analysed separately for their compositional components. Averages of chemical constituents in terms of percentages of C and NC parts showed large differences (Appendices G and H). Water percentages were significantly ($P < 0.01$) lower and fat percentages were higher in the NC than in the C parts at all ages. Within each age the differences in the protein percentages of the C and NC parts were not significant. Ash percentages were significantly higher ($P < 0.01$) in the C part than the NC part at every age. The H line had a higher ash percentage at 3 weeks (H<R and L) and again at 6 weeks (H<R) in the C part and a lower ash percentage than the L line at every age from 3 to 8 weeks in the NC part. When compared with the R line, the H line had a lower ash percentage in the NC part at 6 and 8 weeks only. Despite these differences between the C and NC parts for the proportion of various tissues, the growth curves of the constituents of the two parts followed an overall pattern similar to the growth curve of the whole body.

Growth coefficients b for each of the composition traits obtained from the regressions of the $\log_{10}$ constituent weights on the $\log_{10}$ weights of the WB, C or NC parts are given in Tables 2.5-2.7. Figure 2.4 shows allometric relationship between $\log_{10}$ fat weight and $\log_{10}$ fresh and dry body weights. All the growth coefficients were significantly different ($P < 0.01$) from zero. Since only linear terms were significant, the linear regressions were included in the models for the analyses

Table 2.5 Coefficients a and b of allometric equation $Y = ax^b$ for the whole body

	Water			Fat			Protein			Ash		
Line	a	b	r^2	a	b	r^2	a	b	r^2	a	b	r^2
Fresh body												
L	0.80^{x}	0.95 ± 0.01^{x}	0.996	0.02	1.60 ± 0.12^{x}	0.871	0.25^{x}	0.89 ± 0.03^{x}	0.984	0.05	0.80 ± 0.07^{x}	0.945
R	0.86^{xy}	0.92 ± 0.02^{x}	0.992	0.02	1.48 ± 0.10^{xy}	0.775	0.20^{x}	0.97 ± 0.04^{x}	0.985	0.03	0.99 ± 0.08^{y}	0.949
H	0.79^{xz}	0.96 ± 0.02^{x}	0.993	0.01	1.73 ± 0.10^{xz}	0.849	0.30^{x}	0.83 ± 0.05^{x}	0.980	0.08	0.64 ± 0.08^{z}	0.947
Dry body												
L				0.12^{x}	1.61 ± 0.08^{x}	0.929	0.85^{x}	0.78 ± 0.03^{x}	0.982	0.14^{x}	0.71 ± 0.06^{x}	0.946
R				0.11^{x}	1.61 ± 0.09^{x}	0.897	0.94	0.73 ± 0.04^{xy}	0.977	0.13^{x}	0.76 ± 0.07^{x}	0.944
H				0.06	1.87 ± 0.09^{y}	0.936	1.22^{y}	0.61 ± 0.05^{yz}	0.969	0.22	0.51 ± 0.07^{y}	0.945
Fat-free body												
L	0.76^{x}	1.00 ± 0.01^{x}	0.999				0.24^{x}	0.93 ± 0.03^{x}	0.986	0.05^{x}	0.84 ± 0.07^{x}	0.946
R	0.74^{x}	0.97 ± 0.02^{x}	0.996				0.20^{x}	1.00 ± 0.04^{x}	0.986	0.03	1.02 ± 0.08^{y}	0.950
H	0.73^{x}	1.02 ± 0.01^{x}	0.998				0.26^{x}	0.91 ± 0.04^{x}	0.986	0.08^{y}	0.68 ± 0.09^{x}	0.948

Dissimilar lower case letters indicate significant differences between lines ($P<0.05$). Where slopes (b) were significantly different among lines, the test of elevation (a) was not carried out.

Table 2.6 Coefficients a and b of allometric equation $Y = ax^b$ for carcass part

	Water			Fat			Protein			Ash		
Line	a	b	r^2	a	b	r^2	a	b	r^2	a	b	r^2
Fresh body												
L	0.74^x	0.99 ± 0.01^x	0.998	0.03^x	1.48 ± 0.12^x	0.841	0.21^x	0.92 ± 0.03^x	0.988	0.03^x	1.00 ± 0.08^x	0.941
R	0.76^x	0.97 ± 0.01^x	0.997	0.04^x	1.32 ± 0.11^x	0.796	0.17^x	1.02 ± 0.04^x	0.979	0.03^x	1.08 ± 0.09^x	0.937
H	0.71^x	1.00 ± 0.02^x	0.997	0.03^x	1.46 ± 0.10^x	0.819	0.21^x	0.93 ± 0.03^x	0.991	0.07	0.67 ± 0.08^y	0.959
Dry body												
L				0.18^x	1.58 ± 0.09^x	0.901	0.69^x	0.84 ± 0.03^x	0.986	0.12^x	0.92 ± 0.07^x	0.941
R				0.19^x	1.41 ± 0.10^{xy}	0.933	0.69^x	0.88 ± 0.04^x	0.990	0.12^x	0.90 ± 0.08^x	0.966
H				0.13^x	1.79 ± 0.13^{xz}	0.894	0.74^x	0.78 ± 0.04^x	0.990	0.16	0.62 ± 0.08^y	0.979
Fat-free body												
L	0.76^x	1.01 ± 0.01^x	0.999				0.21^x	0.95 ± 0.03^x	0.994	0.03^x	1.03 ± 0.08^x	0.971
R	0.79^x	0.99 ± 0.01^x	0.999				0.18^x	1.04 ± 0.04^x	0.990	0.03^x	1.11 ± 0.09^x	0.968
H	0.73^x	1.02 ± 0.01^x	0.999				0.21^x	0.96 ± 0.03^x	0.993	0.07	0.69 ± 0.08^y	0.980

Dissimilar lower case letters indicate significant differences between lines ($P<0.05$). Where slopes (b) were significantly different among lines, the test of elevation (a) was not carried out.

Table 2.7 Coefficients of a and b of allometric equation $Y = ax^b$ for non-carcass part

	Water			Fat			Protein			Ash		
Line	a	b	r^2	a	b	r^2	a	b	r^2	a	b	r^2
Fresh body												
L	0.76^x	0.96 ± 0.02^x	0.992	0.02^x	1.69 ± 0.13^x	0.845	0.23^x	0.89 ± 0.04^x	0.974	0.05^x	0.65 ± 0.09^x	0.943
R	0.81^x	0.93 ± 0.03^x	0.985	0.02^x	1.63 ± 0.12^x	0.878	0.22^x	0.92 ± 0.05^x	0.986	0.04^x	0.81 ± 0.09^x	0.959
H	0.74^x	0.97 ± 0.03^x	0.986	0.02^x	1.70 ± 0.12^x	0.906	0.31^y	0.80 ± 0.06^x	0.980	0.06^x	0.61 ± 0.12^x	0.925
Dry body												
L				0.16^x	1.65 ± 0.08^x	0.957	0.79^x	0.72 ± 0.04^x	0.985	0.13^x	0.53 ± 0.07^x	0.942
R				0.15^x	1.66 ± 0.08^x	0.950	0.87^x	0.68 ± 0.04^x	0.983	0.13^x	0.57 ± 0.07^x	0.955
H				0.10^y	1.84 ± 0.09^x	0.962	1.10^x	0.54 ± 0.06^y	0.972	0.21^y	0.42 ± 0.10^x	0.921
Fat-free body												
L	0.73^x	1.02 ± 0.01^x	0.997				0.22^x	0.96 ± 0.40^x	0.989	0.05^x	0.70 ± 0.09^x	0.945
R	0.74^x	1.01 ± 0.02^x	0.996				0.22^x	0.97 ± 0.05^x	0.987	0.07^x	0.87 ± 0.09^x	0.961
H	0.71^x	1.03 ± 0.02^x	0.996				0.26^x	0.90 ± 0.05^x	0.971	0.05^x	0.69 ± 0.11^x	0.863

Dissimilar lower case letters indicate significant differences between lines ($P<0.05$). Where slopes (b) were significantly different among lines, the test of elevation (a) was not carried out.

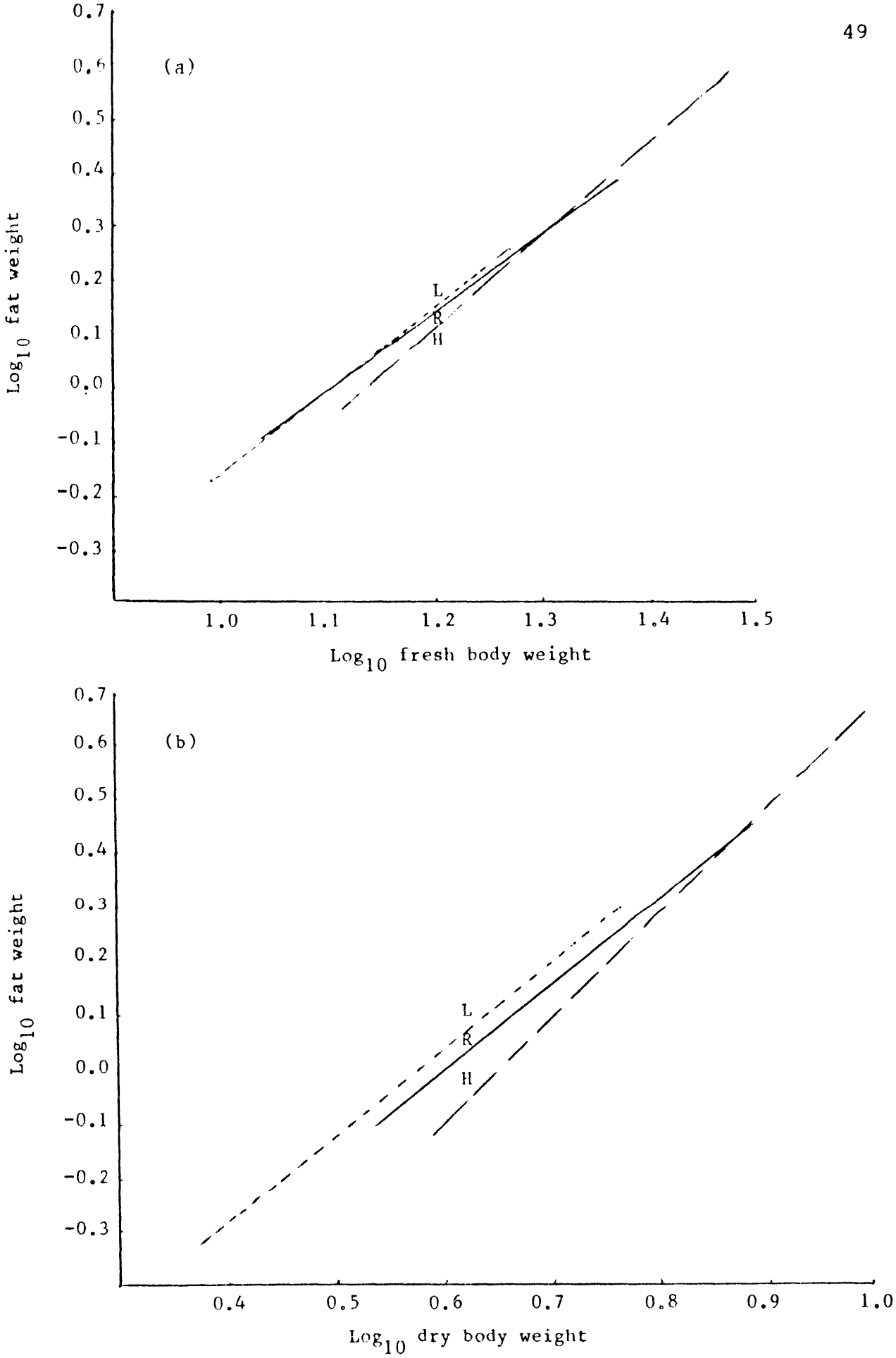


Figure 2.4 Allometric relationship between $\log_{10}$ fat weight and (a) $\log_{10}$ fresh whole body weight (b) $\log_{10}$ dry body weight in the low body weight (L), high body weight (H) and randombred (R) lines.

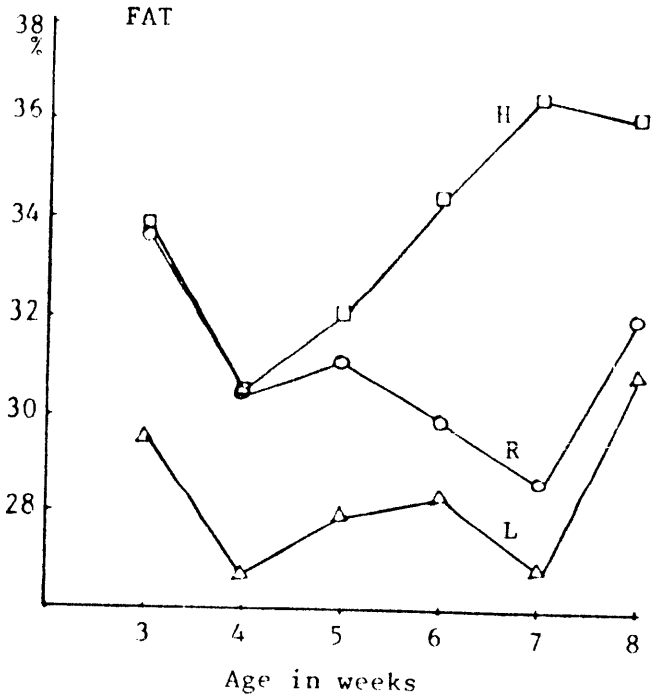
of regression for each component across ages. The *b* values for water and protein were not significantly different between the three lines, whereas significant between-line differences were observed with regard to fat and ash. Growth coefficients *b* obtained from log-log relationships between fat weight and whole body weight, and ash weight and whole body weight were significantly different between the H and R lines for fat (H>R) and among H, R and L lines for ash (R>H, L>H). The growth coefficients of water, protein and ash were higher for C as compared to NC part. The situation was reversed with respect to fat.

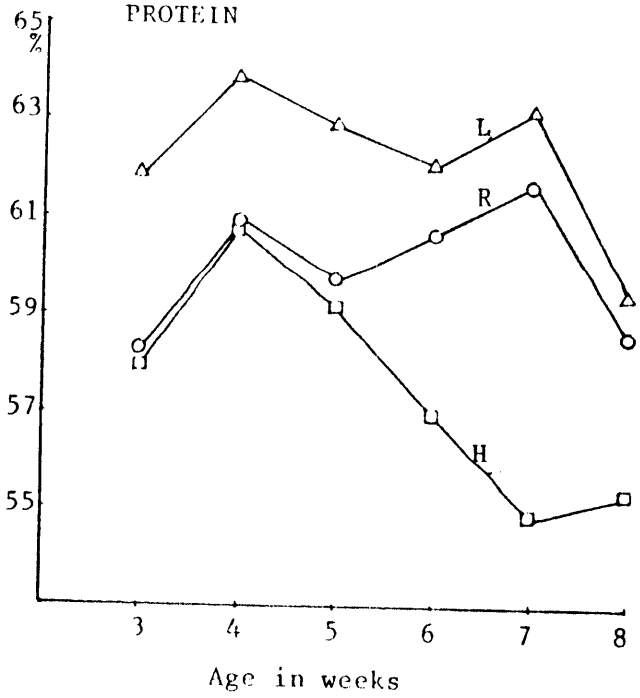
2.3.2 Composition of the Dry Body

The analysis of fresh carcass presented in the preceding section provided evidence for significant between-line differences in the percent water content of the body. As the water constitutes a major proportion of the body, it was considered important to compare the other constituents after eliminating its effect. The data were thus rearranged and a comparison of the H, R and L lines with respect of fat, protein and ash expressed as percentages of dry matter in the whole body and its C and NC parts is shown in Figure 2.5 and 2.6.

When the body constituents were expressed as percentages of dry matter (Appendices I-K), the rank order of the differences between lines was not altered. Rather, the differences between lines for fat, protein and ash percentages were increased as compared with the situation when the components were expressed as percentages of the weight of the fresh body. This effect of accentuated line differences was most evident in relation to protein and ash percentages which showed an increased range of significant differences between lines to cover all ages.

The allometric relationship between $\log_{10}$ fat weight and $\log_{10}$ dry body weight is shown in Figure 2.4. Regression of $\log_{10}$ fat weight on $\log_{10}$ weight of the dry matter of the WB, C and NC parts separately resulted in larger coefficients of *b* for the H line than obtained from the regression on $\log_{10}$ fresh carcass weight in this line. The *b* value of H line was





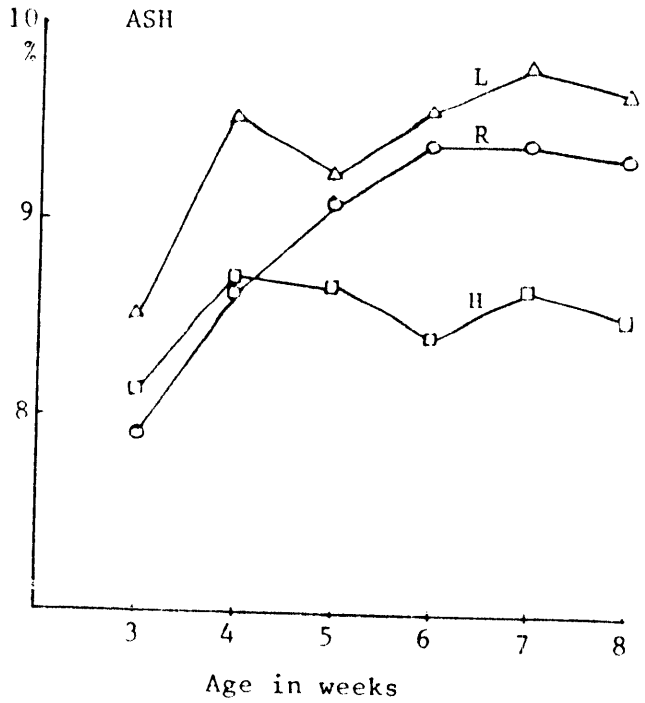


Figure 2.5 Fat, protein and ash as percentages of dry body weight

Lines: L and H = Low and high body weight selection lines
R = Randombred (unselected) line

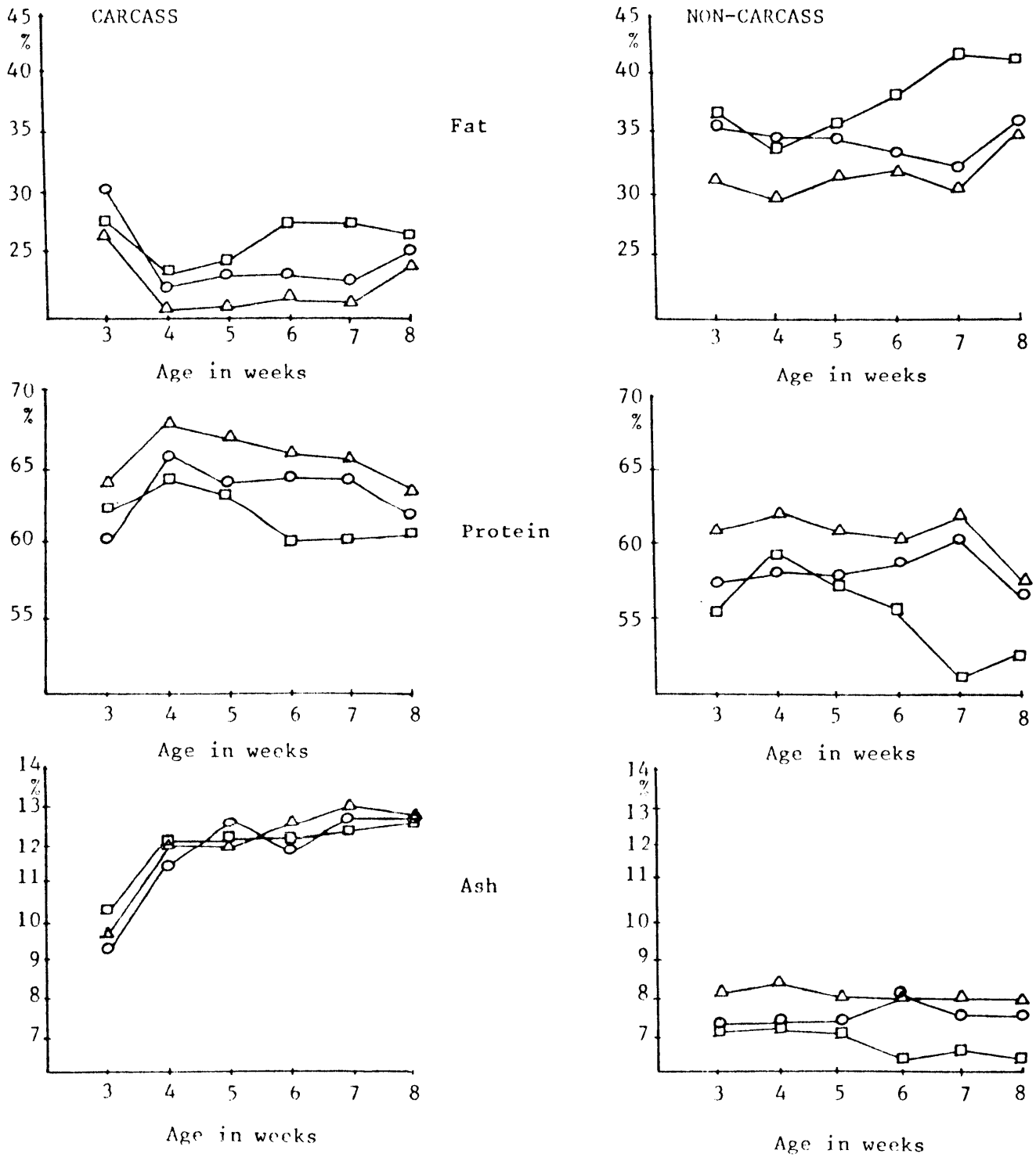


Figure 2.6 Fat, protein and ash as percentages of weights of carcass and non-carcass parts of the dry body.

Lines: H □ ; RO; LΔ . H and L refer to the high and low body weight selection lines and R refers to the randombred (unselected) line.

significantly higher than the R and L lines. However, the increase in b value for fat in the H line appeared to be at the cost of the b values for protein and ash which were reduced by 26.5 and 20.3 percent respectively.

2.3.3 Composition of the Fat-free Body

Fat is the tissue making the major contribution to variation in body composition. In order to remove variation in the other components as a result of variation in fat, the percent chemical composition was calculated on a fat-free basis. The graphical presentation of the chemical constituents expressed as percentages of the fat-free whole body, C and NC parts is given in Figures 2.7 and 2.8.

Least-squares averages for the chemical constituents expressed as percentages of the fat-free WB, C and NC parts are given in Appendices L, M and N, respectively. The comparisons for water percentage were significant at 6 and 8 weeks only. Among line differences for protein percentage were significant only at 8 weeks and for ash percentage at 5, 6 and 8 weeks.

Growth coefficients b obtained from the within-line regressions of $\log_{10}$ weight of each chemical component on $\log_{10}$ weights of fat-free WB, C and NC parts (Tables 2.5-2.7) were higher and closer to unity compared with those obtained from the regression on $\log_{10}$ weights of fresh WB, C or NC parts. This result is expected because the proportion of the other chemical components will rise at a faster rate in the fat-free body compared with the whole body. The growth coefficients for $\log_{10}$ ash weight were significantly lower for the H line than the R line with respect to WB and C but not the NC parts.

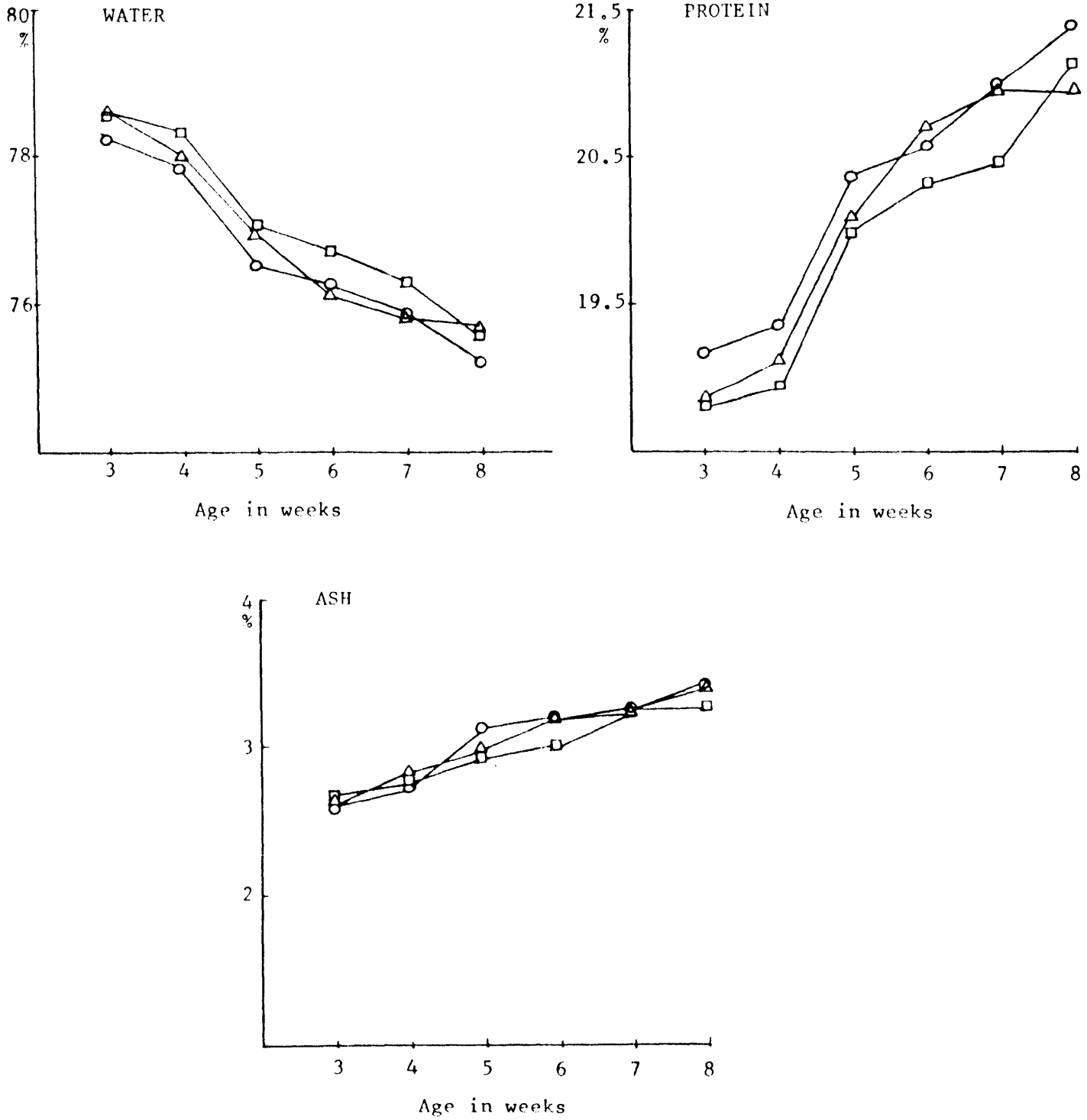


Figure 2.7 Water, protein and ash as percentages of fat-free body weight Lines: H □ ; RO: LΔ. H and L refer to the high and low body weight selection lines and R refers to the randombred (unselected) line.

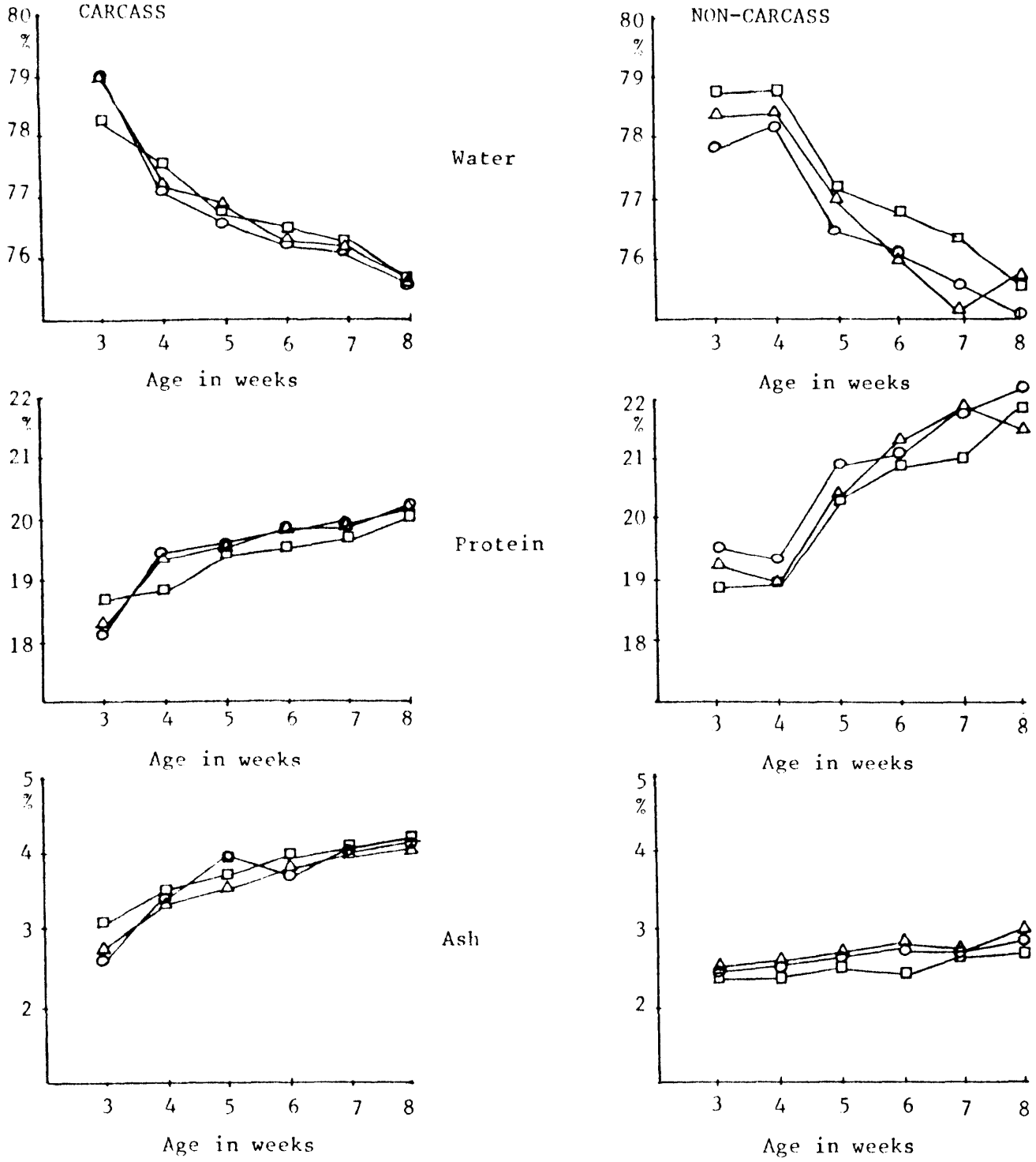


Figure 2.8 Water, protein and ash as percentages of weights of carcass and non-carcass parts of fat-free body.
Lines: H □ ; RO: LΔ. H and L refer to the high and low body weight selection lines and R refers to the randombred (unselected) line.

2.4 DISCUSSION

The main aim of selection for high or low body weight at a given age is to increase or decrease the body weight of progeny at that age relative to the population mean. Ten generations of selection for high and low eight week body weight produced significant differences in the body weights of the selected and unselected lines during the three to eight week growth period. The changes in body weight, mediated through the changes in the level of food intake and growth rate, may be associated with alterations in the proportion of various tissues. Even though there are a number of published analyses of composition for the body as a whole, no separate analyses of the composition of the carcass and non-carcass parts have been reported. Separate analyses of C and NC parts in this study have demonstrated different rates of tissue deposition in these parts. In the following sections the composition of the whole body and its carcass and non-carcass parts will be discussed.

2.4.1 Composition of the Fresh Body

2.4.1.1 Whole body

Selection for high and low 8 week body weight has led to positive correlated changes in the absolute weights of all measured body components. As expected, the H line mice had higher whole body weights of water, fat, protein and ash than the R and L line mice because they were heavier at slaughter at each age from 3 to 8 weeks; and the L line mice had lower body weights of these chemical components than the R and H mice because they were lighter at each slaughter age. When all four components were expressed as percentages of body weight, the H line showed higher percentage of fat than the R and L lines. Water and protein percentages together were decreased in the H line to approximately the same extent as fat percentage was increased. In the L line water percentage

increased to approximately the same extent as fat percentage was decreased. The differences in protein percentage between R and L lines and in ash percentage between H, R and L lines were small. As seen in this study and in the studies reported elsewhere (Fowler, 1958; Biondini *et al.*, 1968; Timon *et al.*, 1970; Eisen *et al.*, 1977; Hetzel, 1978) when percentage of fat increases, the percentage of other components is slightly decreased.

The results of Fowler (1958) agree partially with the present data. Both her large and small mice were fatter than the control at 6 and 9 weeks. A number of reports reviewed by McCarthy (1980) agree with the present results that at equal ages, mouse lines selected for large body size tend to have a higher percentage of fat, and those selected for small body size, a lower percentage of body fat compared with the control populations. Lang and Legates (1969) found no increase in carcass fat, however, in mice selected for high body weight at 6 weeks and suggested that the associated physiology of weight changes in response to selection is not fully understood and that there are various metabolic alternatives such as fat versus protein deposition. The discrepancy between the results of this study and those of Lang and Legates (1969) in fat percentage can be explained on the basis of different base populations from which the mouse lines were derived. The genes present in the foundation population would undoubtedly affect the physiological nature of the response to selection.

Females were fatter than the males at each age in the H line which agrees with the findings of Lang and Legates (1969) for 4 to 7 week old mice and Kownacki *et al.* (1977) for 6 week old mice. Timon *et al.* (1970) have reported males to be fatter than females at 8 weeks. Differences in fat percentage of male and female mice in the present study, were complicated by a Line x Sex interaction because only the H line showed a marked sex effect whereas, R and L lines did not. Because the H line has more potential for laying down fat, may have as a result, showed a greater sex difference.

On a body weight basis, the allometric equation has been commonly used for comparing the body composition of growing animals and in developmental studies of body composition (Seebeck, 1968). Linear regression is suitable only in linear models where the growth is isometric ($b = 1$) and will be inferior when the growth is allometric ($b \neq 1$) in which case an allometric equation should be the automatic choice (Berg *et al.*, 1978). In the present study, as judged by the r^2 values, the allometric equation adequately described the relationship between water, fat, protein and ash and body weight. The r^2 values were smaller for fat and ash compared with water and protein.

There was a large difference between lines in the development of fat when examined as a component of the body weight. A comparison of the fat curves of the H, R and L lines (Figure 2.4) showed that the H line mice were leaner than the mice of R and L lines at equivalent body weights at younger ages, but fatter at heavier body weights. By back transformation of the regression equation $\log y = \log a + b \log x$ to the original allometric equation $y = ax^b$, the actual body weights of the lines at the point of intercept of the fat curves were calculated. The H and R line fat curves crossed at 1.95 g of fat at a body weight of 20 g ($\log_{10}^{0.29}$ and $\log_{10}^{1.30}$ respectively). The fat curves of the L and R lines crossed at 0.91 g of fat at a body weight of 12 g ($\log_{10}^{-0.04}$ and $\log_{10}^{1.08}$ respectively). The H line mice were both younger and leaner than the control mice at body weights prior to the point of crossing of fat curves. The R line mice were younger but not leaner than the L line mice before the point of crossing of fat curves of these two lines. Fowler (1958) did not interpret in this way but her results show the small line to be clearly fatter between 10 and 18 g, a degree of fatness not reached by the large line until a carcass weight of 22 to 25 g. McPhee and Neill (1976) reported a crossing of fat curves for their large line selected for 8 week body weight and the control line at 2.9 g of fat and 29 g of body weight at generation 14 and 1.6 g

of fat at a body weight of 21.6 g in generation 25. Clarke (1969) and Hayes and McCarthy (1976) have also reported an initial delay in fat deposition followed by a period of rapid growth in the large line. Hayes and McCarthy (1976) interpreted these changes in the relative rate of fat as a correlated response to selection for body weight arising from the discrepancy between the energy costs of producing muscle and fat. The data obtained in the present study which demonstrate differences between lines in the proportion of fat on a body weight basis support the conclusions of Hayes and McCarthy (1976) and McPhee and Neill (1976) that the lines selected for high body weight were leaner at lighter body weights and fatter at heavier body weights relative to the control lines and low body weight lines.

2.4.1.2 Carcass and non-carcass parts

The information discussed above was obtained from the chemical analyses of whole body. Whole body analysis has the advantage that it can be used to calculate an inventory of food nutrients in relation to maintenance and tissue deposition. This approach is useful from the point of view of understanding overall metabolism and growth. If the mouse is to be used as a model for growth of meat producing livestock, whole body analysis has disadvantage in that it does not differentiate between carcass tissues comparable to the edible portion and non-carcass tissues comparable to the non-edible portion in the meat animal.

The patterns of deposition of different tissues in the C and NC parts varied considerably. Not only was the water percentage of the NC considerably lower than the C part at all ages, it also decreased more rapidly with age. Fat percentages were much lower in the C compared to NC at all ages. While fat percentages showed appreciable changes in both the C and NC parts over ages, the increases were larger and consistent in the NC part. Protein percentages were similar in the two parts. Percent ash was higher in the C part and increased with age at

a faster rate in this part than in the NC part. Allometric coefficients derived for the relationship of water, fat, protein and ash with body weight on a double logarithmic grid (Tables 2.6-2.7) showed more clearly the differential rates of growth of these constituents in the two parts of the body. The allometric coefficients for water, protein and ash were higher in the C part and for fat were higher in the NC part. On a fat-free basis, ash was the only constituent which showed differential rates of development in the C and NC parts, whereas on a dry weight basis the differences in the two parts were large, both for protein and ash. As observed for the whole body, the comparisons between the C and the NC parts for protein and ash were greatly influenced by the larger growth coefficients for fat.

The reasons for differential patterns of development of various tissues in the C and NC parts can be assessed readily if one considers what constitutes these parts. Carcass part includes the fore and hind limbs, the trunk and a small portion of the neck, and is comprised mainly of long bones, ribs, vertebral column and skeletal muscle. The rest of the body, minus ingesta, is designated as NC part. Water content of the C part is higher because it is associated largely with the skeletal muscle which forms a predominantly large proportion of the overall weight of the C part. Alternatively, the NC part has a lower proportion of skeletal muscle and a substantial proportion of relatively drier components such as skin, head and appendages. The higher ash percentage of the C part compared to the NC part is due to the greater bone weight particularly since it includes long bones and a long vertebral column. Since the long bones and vertebrae continue to grow until the animal reaches its mature size, a consistent increase in ash percentage is likely to result in the C part. The NC part, except for the tail, contains a large proportion of relatively mature bones such as skull and appendages. The skeletal growth gradients have been shown to increase from head to tail longitudinally and from foot (claws in the case of mice) to shoulder on a vertical scale (Hammond *et al.*, 1971).

The location of fat depots in the mouse favours the NC part but this is not always the situation in livestock. Allen and McCarthy (1980) have reported five main depots in the body of the mouse, located under the fore and hind limbs, around kidneys and gonads and in the mesentary. The fore and hind limb depots are difficult to delineate from the subcutaneous fat and are often peeled off with the skin. In this situation, C fat would mainly be characterized by the intramuscular fat plus any remnants of subcutaneous fat. These together form only a small percentage of the whole body fat and show relatively small increases with age and weight of the animal. Non-carcass fat depots are bigger and contribute unequally to changes in the relative rate of fat deposition. The mesenteric fat depot is the largest of all the fat depots, the kidney and gonadal fat depots are late maturing but faster developing and make a greater contribution to the increase in fat percentage of the non-carcass part as the body weight increases (Allen and McCarthy, 1980).

From the above discussion, the differences in the overall pattern of tissue deposition within and between lines were greatly influenced by the pattern of tissue deposition in the NC part. Fat was the major tissue component contributing to these differences. Energetically, NC parts were richer, with about two-third of the total body energy accumulating in them. The fact that such a large proportion of metabolisable energy is directed to the NC part, demonstrates the significance of genetic manipulation in this region of the body.

2.4.2 Composition of the Dry Whole Body

Differences in moisture percentage affect the estimation of the proportion of fat, protein and ash in the whole body particularly since water is a large proportion of the total. On an age basis, the line differences for the ash percentages (WB) were increased and line differences were significant over the whole range of the growth period studied with a greater proportion of ash in the L and R than in the H line. The growth coefficient b of $\log_{10}$ fat weight on $\log_{10}$ dry WB weight was

significantly larger for the H line than the L line, whereas on a fresh body weight basis the differences in the *b* values of lines H and L were not significant. Proudman *et al.* (1970) and Pym (1977) also observed certain group comparisons in the selected lines of chickens to assume statistical significance only when expressed in terms of dry carcass weight. The former workers suggested that unless the variation in the moisture content of the lines was removed, the proportion of other carcass constituents could be altered to the extent of obscuring the real differences between lines.

2.4.3 Composition of the Fat-free Whole Body

The demonstration of significant between-line differences for percent fat necessitates studying the chemical composition on a fat-free basis. This is so because when fat is considered the picture becomes less consistent, for fat is much more variable than the other body components.

On a fat-free basis, a majority of comparisons between lines for water, protein and ash percentage in the 3 to 8 week growth period were not significant. Allometric coefficients for water, protein and ash were near unity in all the three lines, indicating proportionate growth of these tissues in relation to the fat-free body weight. Timon *et al.* (1970) have also reported non-significant differences in their selected and unselected lines for any of the three components (water, protein and ash) of the whole carcass when expressed as a percent of the fat-free carcass at 8 weeks of age. Sutherland *et al.* (1974) showed constant proportions of water, protein and ash in the fat-free body of their selected and unselected mice after seven weeks of age until 13 weeks, the end point of the serial slaughter. In the present study and from a number of reports in the literature, a common feature of selection for body weight on *ad libitum* feeding in mice is that as the proportion of fat increases the relative proportion of other components decreases. Therefore, the greatest potential for increasing the proportion

of lean lies in the reduction of fat by genetic or nutritional means, or by an appropriate combination of these two factors. The constancy of the tissue proportions in the fat-free body of the different selection lines suggests an important homeostatic control of the metabolic body system.

Moulton (1923) suggested that if the fat-free composition is considered, there comes a point, which he termed the point of 'chemical maturity', when the percentages of water, protein and ash become stationary and thereafter no appreciable changes take place. On the basis of the constancy of water, protein or ash percentages in the fat-free body, it would appear logical to assume that water, lean mass or bone may serve as useful indicators of mature age. Expression of percent changes in protein and water (protein/water) has been described as an index of physiological age in mice (Bailey *et al.* 1960). Timon *et al.* (1970) have used the difference in the weights of protein and ether extract as a percentage of fat-free carcass weight 100 (P - E)/FFCW in the form of an index of stage of physiological maturity.

In summary, the results of this study showed that the H line mice were heavier and fatter than mice of both the R and L lines on an age basis. On a body weight basis the H mice were leaner than the R and L mice at lighter body weights but were fatter at heavier body weights. When chemical composition was expressed as percentages of dry whole body, the line differences for protein and ash were accentuated. The differences between lines for growth coefficient 'b' for fat were also increased. On a fat-free basis the comparisons between lines for water, protein and ash percentages were not significant at most ages. The growth coefficients for water, protein and ash for fat-free body were higher in comparison with those obtained from the allometric relationship with fresh or dry body. The C and NC parts showed significant differences in percentage chemical composition. The C part had higher percentages of water and ash. In comparison the NC part had a higher percentage of fat. The protein percentages were not significantly different between the C and NC parts. The growth coefficients for water, protein and ash were higher in the C part and for fat were higher in the NC part. On a fat-free basis, ash was the only component which showed different rates of development in the C and NC parts. On a dry weight basis, the differences in the two parts were large for both protein and ash.