CHAPTER 1

GENERAL INTRODUCTION

The how, when and why in the evaluation of farm animals for 'productive merit' is a basic requirement in animal production improvement. Obviously, the objective is optimum output for any combination of inputs. The main direction of research to attain this objective, until recently, has been toward selection to increase weight gain over a particular time interval, and/or increase weights at specific ages (Eisen, 1974; McCarthy, 1977). However, correlated and often undesirable responses have occurred in weights at later ages and in voluntary feed intake (Hayes and McCarthy, 1976). Concern with these undesirable correlated responses, particularly the associated increases in body fat at later ages, has initiated considerable thought into, and a re-appraisal of, the dynamic nature of animal growth.

Recent reviews by Roberts (1979) and McCarthy (1980) have presented models of the input/output relationships important in growth. These two models treat growth as a feedback control system, and by combining both models we arrive at Fig. 1.1.

The conclusions reached by both authors are essentially the same when comparing results from selection studies on growth, particularly with mice. Rather than simply repeating their reviews, a

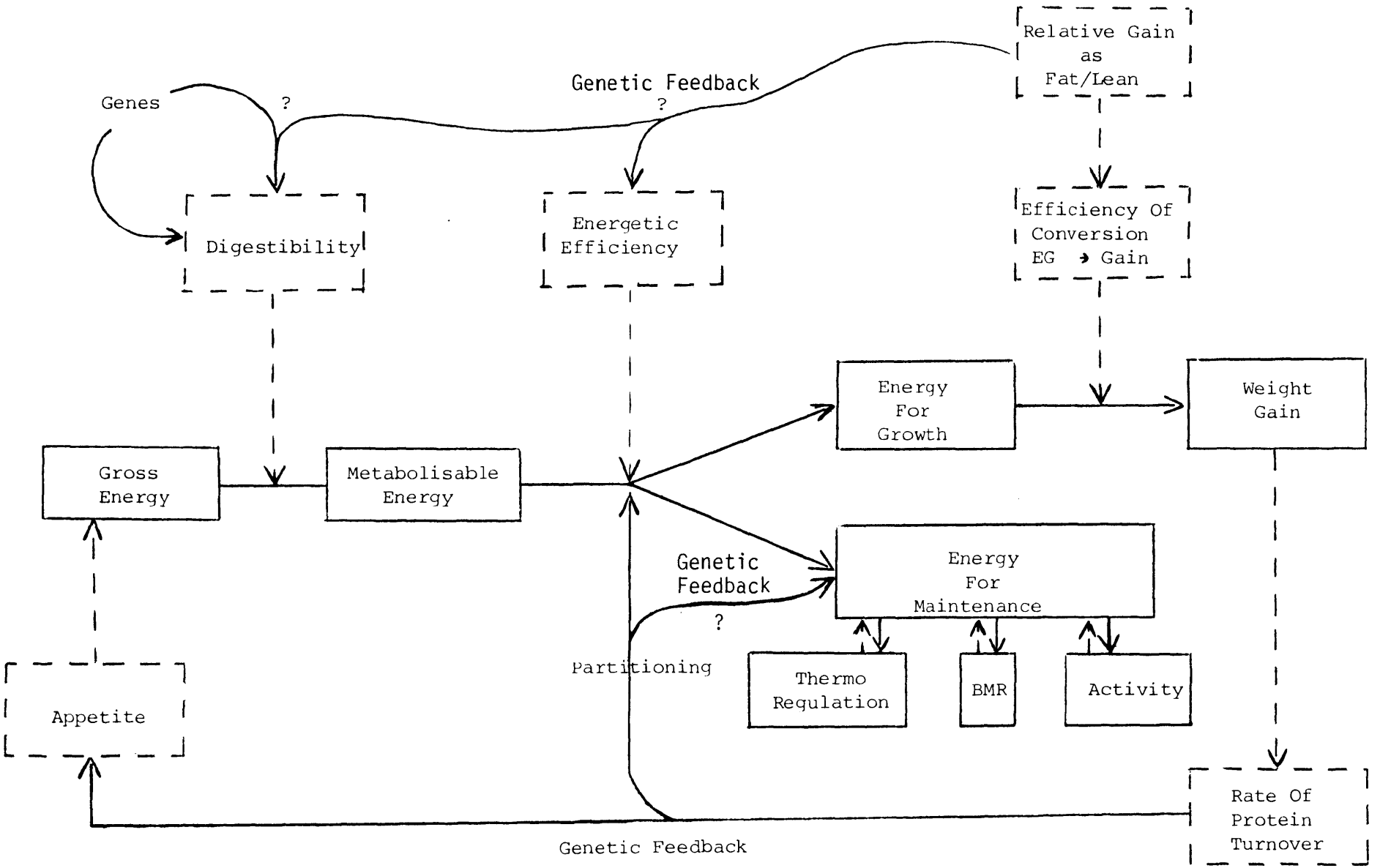

Figure 1.1: Simplified scheme of energy utilisation. Adapted from Roberts (1979) and McCarthy (1980).

summary of their conclusions in relation to the flow of Fig. 1.1 are:

1. Food consumption is increased when selection has been for either body weight or growth rate. It may be possible that selection under *ad libitum* feeding will in fact be for animals whose 'capacity for protein deposition' is higher, as the efficiency of lean tissue deposition is greater than that of fat. However, Roberts warns against misinterpretation of this relationship, as the relevant energies, energy required to synthesise fat or protein, are essentially equal when considered on a water-free basis. The animal appears to be unable to regulate its former desire for increased consumption once protein mass has reached an asymptote, and the excess energy then entering the system is laid down as fat.

2. McCarthy dismisses the possibility of genetic variation in the efficiency with which gross energy (GE) goes to metabolisable energy (ME).

3. Increased food consumption in lines selected for increased weight or weight gain is associated with increases in gross efficiency. Partitioning of the increased food consumption may not be strictly linear, particularly at older ages. That is, increases in food consumption are not necessarily split equally at all ages between the energetic demands of the animal.

4. Selection for weight or weight gain to a fixed age will have little effect on fatness up to the age of selection, but at later ages animals lay down more fat.

5. There appears, at least when animals are fed *ad libitum*, to be no difference between large and small mice in basal metabolic rate (BMR) per unit of body weight. Selection on restricted intakes (Stainer and Mount, 1972; Hetzel, 1978) suggests that there may have been reductions in relative maintenance requirements for the large lines. McCarthy (1980) does stress the point though, that 'the mice of the different strains were placed on test at different weights when they might exhibit differences in relative maintenance cost due to their differences in size and in body composition.' This begs the question; when then should animals be compared; at the same weights, at the same degree of maturity, at the same level of fatness, or as Parks (1982) suggests, at the same distance along the animal's biotrace?

Comparisons and concomitant selection of animals are complicated by the dynamic nature of the variables involved in production and efficiency. Feed intake, body mass and body composition change simultaneously both in magnitude and direction as the animal grows and ages. The interpretation of the 'merit' of individuals either within a breed or across breeds may change when comparisons are made at different points along the growth plane (Parks, 1982).

Comparisons between animals for efficiency of feed utili-

sation or body composition, made at specific ages or body masses, may have economic justification but no biological meaning or significance (Taylor, 1968). Even so, this economic justification is itself dynamic and changes over time. A number of comparisons enabling greater biological interpretation have been suggested:

a) similar degrees of fatness (Guillbert and Gregory, 1944; Berg and Butterfield, 1966);
b) Brody's 'physiological age' (1945);
c) over equivalent segments of the growth curve (Guillbert and Gregory, 1952; Koch, Dikeman, Allan, May, Grouse and Campion, 1976);
d) at similar degrees of maturity (McClelland and Russel, 1972; McClelland, Bonaiti and Taylor, 1976; Fitzhugh, 1976);
e) at equal degrees of 'chemical maturity' (Moulton, 1923 cited by Lohman, 1971);
f) metabolic age (Taylor, 1965, 1968, 1980, 1982).

Comparisons between these criteria would be likely to differ and thus still be inadequate. Some are inaccurate (chemical maturity, as shown by Spray and Widdowson, 1950), limited (segments of the growth curve or body fat percentage), or are difficult to obtain and/or vaguely defined ('physiological' or 'metabolic age'). The only truly feasible way to overcome these problems is an understanding of the complete growth curve, its phenomenology and aetiology.

There appears to be two major points at issue in developing

an understanding of an animal's lifetime growth in the above context. Firstly, by developing a knowledge of the bioenergetics of growth, a greater understanding of the physiological changes that have resulted from selection for weight at a particular age or weight gain over a specific time interval may be achieved. Secondly, by developing the knowledge of an individual's long term growth, an understanding may be achieved of how to manipulate the growth patterns of an individual, breed or species. Certainly, it has been shown that it is possible to achieve changes in the weight/age growth curve either nutritionally or genetically (Ricard, 1975; Parks, 1982) but, the question remains as to whether the 'economic' objective is reconcilable with 'biological' efficiency of an animal or an animal production system (Carter, 1982).

Brody (1945) recognised the potential for utilising the parameters of a growth model as selection criteria to change the structure of the weight/age growth curve. Though there has been considerable effort to describe the sigmoid shape of growth curves empirically and stochastically, there has been little attention focused on the utilisation of the parameters of nonlinear growth models in selection experiments. Until alternative growth models are compared and accurate estimates of the genetic variability in growth curve parameters are obtained, there will continue to be questions on their potential as selection criteria.

Several authors have suggested that there is a need to alter the basic structure of the growth curve, particularly the weight/age growth curve, of livestock species. Fitzhugh (1976) succinctly summarised the reasons for attemtping to change the form of an

animal's weight/age growth as:

1. Attempting to resolve the genetic antagonism between
   a) desired efficient, fast, early growth of slaughter progeny; and
   b) the desired small size and reduced maintenance costs of breeding stock. In terms of the dynamics of the weight/age growth curve, this would involve shifting the curve to the left on the time axis whilst decreasing mature weight.

2. Improving the intrinsic efficiency of individuals through increased maturation rate. This would involve the objectives of 1. above and an increased efficiency of conversion of metabolisable energy (ME) to lean tissue at ages prior to slaughter.

3. Reducing birth weight relative to dam size, thus alleviating the problems of dystocia.

4. Decreasing age at first breeding by decreasing time to sexual maturity.

5. Decreasing carcase fatness by increasing time to chemical maturity.

Fitzhugh had grouped the last two objectives together although the two may not be reconcilable, that is, decreasing time to first breeding may involve decreasing time to chemical maturity.

Any attempt to change the shape of the weight/age growth curve by selection will ultimately depend upon the degree of genetic flexibility of the total curve, whether measured by parameters of nonlinear models or weights at various ages. Thus, this flexibility will ultimately depend upon the degree of genetic independence between either weights, weight gain or parameters of any model fitted to the data set.

Results reported for experiments with mice and poultry suggest that it may be possible to change the structure of the weight/age curve. Ricard (1975) reported significant changes in early and late weights in poultry. Using independent culling for weight at 8 and 36 weeks of age, he selected lines with all four possible combinations of directions. It is apparent from Ricard's results, presented in Table 1.1, that in poultry Fitzhugh's objectives could, in part, be achieved. Parks (1982) re-analysed Ricard's data using a two parameter model and suggested that correlated changes had occurred in the parameters (Table, 1.1). He intimated that there could be sufficient genetic variation for the parameters, A and t*, so as to produce similar results to those of Ricards'.

TABLE 1.1

DIRECT AND POSSIBLE CORRELATED RESPONSES TO SELECTION FOR COMBINATIONS OF LOW AND HIGH BODY WEIGHT IN CHICKENS

Selection Criteria		Responses After 13 Generations of Selection			
8 Weeks	36 Weeks	8 Week Weight (gms)	36 Week Weight (gms)	A[1] (gms)	t* (weeks)
Low	Low	500	1690	1927	10.24
Low	High	580	2890	3766	13.65
Control		760	2300	2162	8.11
High	High	970	3090	3339	8.73
High	Low	860	1940	2039	6.88

[1] Parks' parameters A (estimated mature weight) and t* (internal resistance to growth of appetite).

Although similar results have been reported for mouse populations none have shown the same magnitude of responses to selection. Bakker (1974) and McCarthy and Bakker (1979) reported changing the weight/age growth curve in mice. McCarthy and Bakker (1979) presented correlated changes in the asymptote and rate parameters of the Gompertz nonlinear model. Selection had been for 5 and 10 week weights using single trait, independent culling levels and restricted selection index procedures for between 14 and 22 generations. Their analyses suggested that 75% of the variation in the rate parameter, k, was independent of the asymptote, A. This would infer that direct selection for either parameter would result in only small changes in the other, providing there was genetic variation in both. However, McCarthy and Bakker diminished the role of the third parameter of the model they fitted, the 'integration constant', b. As age at the point of inflection, for the Gompertz model they fitted, is given by log b/k and measures the age of maximum absolute growth rate, it is difficult to concur with their dismissal of the b parameter as being unimportant.

Similar correlated changes in parameters of nonlinear models fitted to data from selection experiments, for weight or weight gain have been reported (Eisen *et al.*, 1969; Parks, 1982; Timon and Eisen, 1969). Eisen *et al.* (1969), after fitting a logistic nonlinear equation to weight/age data, suggested that up to 78% of the variation in the parameter k was independent of the asymptote parameter A. Timon and Eisen (1969) suggested that up to 88% of the variation in k was independent of A. Parks (1982) fitted both weight and feed intake nonlinear models to Timon and Eisen's data. Expressing changes in the parameters of his models as percentage

deviations from the base population, he found differences between males and females and that some parameters were changed by over 25% from the base population. Parks' results from his analyses of Timon and Eisen's lines could have large errors as the data was obtained by extracting from the published graphs.

It would appear from the re-analyses of data gained from selection experiments, whether on mice or poultry, that there is genetic and phenotypic variation in the parameters of nonlinear models. However, because of the limited nature of the genetic analyses that could be undertaken on these data sets, there are still unanswered questions on the extent of the genetic variation for parameters of different models. Grossman's (1969) study of two chicken populations was the only work cited for which genetic analyses were undertaken on parameters of a nonlinear model fitted to data from large unselected populations. He concentrated on a form of the logistic equation and gave heritability estimates, based on the sire component of variance, ranging from 0.05 $\pm$ 0.31 to 0.67 $\pm$ 0.43 for the k parameter, and genetic correlations between k and the asymptote or mature weight, A, of -0.16 $\pm$ 0.66 to 1.93. No estimates for the heritability of the A parameter were reported.

Clearly, there is a paucity of adequate and accurate information of the heritabilities, and genetic and phenotypic correlations for the parameters of non linear models fitted to animals growth data. However, as part of any consideration of growth as described by a nonlinear model, it is important that the relationships between the parameters and the biology of growth are understood. An examination must

be undertaken of the repercussions of using parameters as selection criteria on the input/output relations involved in growth (Fig. 1.1). In concert with the biological ramifications of describing growth by a set of parameters, and any proposed selection based on such a set to alter the structure of an individual's growth curve, consideration should be given to the accuracy, predictive ability and statistical properties of the parameter set. It was within these constraints that the studies reported in this thesis were undertaken.

EXPERIMENTAL OBJECTIVES

1. To examine the phenotypic and genetic variation for growth in a mouse population from birth up to estimated mature weight.

2. To investigate various nonlinear models as descriptors of growth from birth to maturity.

3. To estimate the genetic and phenotypic variances and covariances for parameters of the alternative nonlinear models and to examine the potential of using the parameters as selection criteria.

Basic to any model fitting process and consequent use of a model is an understanding of the statistical problems associated with the model, whether it is a linear or nonlinear model. Therefore

4. To examine the distributional and statistical properties of the nonlinear models considered in this thesis.

5. Although not originally considered as part of this project, additional assistance allowed the role of maternal effects on growth to be investigated.

CHAPTER 2

PHENOTYPIC AND GENETIC ANALYSIS OF WEIGHT, WEIGHT GAIN, FRACTION OF MATURITY, FEED INTAKE AND FEED EFFICIENCY

2.1 INTRODUCTION

Growth, from birth to maturity, represented by increases in weight and body size and in association with changes in body composition can be of great economic importance in animal production. The literature on growth and development of farm and laboratory animals has been thoroughly reviewed by Brody (1945), Kleiber (1961), and more recently in a number of edited proceedings (Lister *et al.*, 1976; de Boer and Martin, 1978; and Lawrence, 1980).

Although there have been numerous studies of growth over specific segments of the growth curve, there is little information on long-term growth. Grossman (1969) described the genetic and phenotypic relationships for weight in chickens from birth to 45 weeks, but the lack of adequate information on the genetic interrelationships between various measures of growth and the absence of feed intake data detracted from the study. Roberts (1981) reported on long-term growth and feed intake data of mice previously selected for high and low six-week body weight. The purely descriptive approach taken by Roberts suggested that mice selected for large size showed increases in both feed intake and efficiency. Because of the small sample size (a total of 98 male mice), measures of

genetic and phenotypic variation were not calculated.

There is a distinct paucity of results on the phenotypic and genetic relationships between weight and feed intake measures at ages approaching maturity, and those recorded at young ages. The aim of the work reported in this chapter was to characterise growth for a particular mouse population from birth to 12 weeks of age and to provide a framework for later analyses and studies. Within this framework, an investigation of the genetic and phenotypic variation and covariation was done for weight, maturity and feed intake patterns.

2.2 MATERIALS AND METHODS

2.2.1 Mice

The mice in this study were established at the University of New England, Armidale, by two separate samples of a random mating laboratory population (Quackenbush strain; Univ. of Sydney, N.S.W.) with an effective population size greater than 500. A total of 300 mice (150 males and 150 females) were single pair mated to establish the strain at Armidale. Inbreeding in the foundation stock was minimised by avoiding matings of close relatives. The mice were maintained in a controlled environment at an average temperature of 22° $\pm$ 1°C with 16 hours light and 8 hours darkness each day.

2.2.2 Management

The mice used in this and subsequent studies were sampled from

the foundation stock at Armidale. Three different generations were measured over an eighteen month period. For clarity, these are designated groups 1, 2 and 3 (Table 2.1).

TABLE 2.1

MATING STRUCTURE

	No. of Males	No. of Dams	No. of Progeny
Group 1	16	48	379
Group 2	18	48	168
Group 3	50	100	533
Total	84	196	1080

The variation in numbers of parents in each group was related to the ability to maximise the efficiency of utilisation of resources and time. Mice in group 2 were part of a study on maternal effects (Chapter 4), only mice raised as full sibs within a litter are described in this chapter.

In all groups, each male was mated to randomly assigned females. Males and females were 10 - 12 weeks old when mated. After 15 days, the males were removed.

Dams were checked daily and individual birth weights of progeny were recorded within 24 hours of birth. Although some suckling may have occurred prior to the first weighing, this was considered to have a minimal effect on the initial weight. When litter size exceeded 12 at birth, it was reduced to 12 (where possible, 6 of

each sex). Bateman (1957) has shown that litter sizes of 11 and 12 stimulate maximum lactation in the dam. Where possible, litters of less than 12 were standardised to 12 with fostered mice born within the same 24 hour period. Foster mice were identified by removing 1.5 cm of their tail.

Of the 12 mice (excluding fostered mice), 4 mice of each sex in groups 1 and 2, and 3 mice of each sex in group 3, were identified by toe-notching and weighed (to the nearest 0.1 gm) at birth. Two days after birth, litters were further reduced to 8 mice (4 of each sex, wherever possible) in an attempt to standardise the maternal environment.

The identified mice were weighed at 3-day intervals between birth and 21 days. At weaning (21 days old), mice were placed in individual cages. Individual feed intake was measured using a glass feeding jar designed to eliminate spillage of food (Hetzel, 1978). The feed consisted of a commercially prepared mixture of standard laboratory chow (Table 2.2), ground and offered as a finely crushed powder.

TABLE 2.2

FEED COMPOSITION OF THE LABORATORY CHOW (TAMWORTH FEEDS)

Protein	18.9%
Fat	4.6%
Cellulose	5.5%
Water	8.1%
Energy Content	4.0 Kcal/g feed

Mice were weighed at 3-day intervals between 3 and 12 weeks of age (to the nearest 0.1 gm). At the same time, food remaining at the end of each 3-day period was weighed (to the nearest 0.1 gm) and substracted from the total amount offered.

2.2.3 Characters Studied

The characters studied and analysed in this chapter are presented in Table 2.3.

With the exception of the period between 18 and 24 days of age the characters studied in this chapter were considered at six day intervals. As weaning was at 21 days of age the six day period between 18 and 24 days was split and considered as two 3 day periods, 18-21 and 21-24 days of age.

2.2.4 Statistical Procedures

Means, Standard Deviations and Coefficients of Variation: Progeny that died during the period from birth to 12 weeks were excluded from subsequent analyses. This was based on the premise that individuals that died prior to the conclusion of the experimental period were unlikely to be growing or feeding to their full potential prior to death and inclusion of information on them could bias the results. For traits such as body weight and gain, the mean and variance are related and vary together, and the phenotypic coefficient of variation (the standard deviation expressed as a fraction or percentage of the mean) gives a measure of the relative variability. Estimates of the mean, standard deviation and pheno-

TABLE 2.3

CHARACTERS CONSIDERED FOR GENETIC AND PHENOTYPIC ANALYSES

Characters	Time or Time Periods (Days) at Which Measurements Were Taken
Weights	0, 6, 12, 18, 21, 24, 30, 36, 42, 48, 54, 60, 66, 72, 78, 84.
Weight Gain[1]	0-6, 6-12, 12-18, 18-21, 21-24, 24-30, 30-36, 36-42, 42-48, 48-54, 54-60, 60-66, 66-72, 72-78, 78-84, 0-21, 21-42, 42-63, 63-84.
Fraction of Maturity[2]	Weights at an age (t) divided by 84 day weight.
Feed Intake[3]	Over same time periods as for weight gains except postweaning only (post 21 days)
Feed Efficiency[4]	Over same time periods as for weight gain except postweaning only.
Relative Growth Rate[5]	Same time periods as for weight gain.
Absolute Maturing Rate[6]	Same time periods as for weights.

[1] Weight Gain = $W_{t_2} - W_{t_1}$

[2] Fraction of Maturity = $\mu_t = W_{t/W_{84\ days}}$

[3] Feed Intake = $F.I._{t_2} - F.I._{t_1}$

[4] Feed Efficiency = $(W_{t_2} - W_{t_1}) / (F.I._{t_2} - F.I._{t_1})$

[5] Relative Growth Rate = $(\ln W_{t_2} - \ln W_{t_1}) / (t_2 - t_1)$

[6] Maturing Rate = $(\mu_2 - \mu_1) / (t_2 - t_1)$

typic coefficient of variation were calculated for each character. The number of animals in this experiment may be considered to be sufficient to assume that the phenotypic and genetic means were equal and the environmental mean was zero.

Genetic variances and covariances were estimated from paternal and maternal half sib and full sib covariances using Harvey's (1977) Least Squares procedures. The assumed statistical model for each analysis was

$$Y_{mhijkl} = \mu_m + G_{mh} + S_{mhi} + D_{mhij} + F_{mk} + e_{mhijkl} \text{ where}$$

Y_{mhijkl} = the Y_{th} trait of the l^{th} individual of k^{th} sex from the j^{th} dam mated to the i^{th} sire within the h^{th} group, at a specific age or over an age interval, m.

μ_m = the theoretical overall mean for the Y_{th} trait for a specific age or age interval, m.

G_{mh} = is the effect of the h^{th} group on the Y_{th} trait, at a specific age or over an age interval, m; h = 1, 2, 3.

S_{mhi} = is the effect of the i^{th} sire within the h^{th} group on the Y_{th} trait at a specific age or over an age interval, m; $i = 1, \ldots\ldots, S_h$.

D_{mhij} = is the effect of the j_{th} dam mated to i^{th} sire within the h^{th} group on the Y_{th} trait at a specific age or over an age interval, m; $j = 1, \ldots, D_{hi}$.

F_{mk} = is the effect of the k^{th} sex on Y_{th} trait for a specific age or over an age interval, m; F = 1, or 2, 1 = male, 2 = female.

e_{mhijkl} = the random error, $l = 1, \ldots, n_{hij}$; progeny/dam/sire/group.

The following are assumed: 1. $\sigma^2_{e_{mhijkl}} \sim NID(0, \sigma^2_m)$, $S_{mhi} \sim NID(0, \sigma^2_{sm})$, $D_{mhij} \sim NID(0, \sigma^2_{Dm})$. 2. All effects are mutually uncorrelated for fixed m. 3. There are no interactions between sires and dams; as the dam component was assumed not to include dominance variance. 4. Sires, dams and error were assumed random. Groups and sex were fixed. The form of the analysis of variance for the Y_{th} trait for the m^{th} age or over an age interval is presented in Table 2.4.

TABLE 2.4

THE FORM OF THE ANALYSIS OF VARIANCE FOR THE Y_{th} TRAIT

Source	Sums of Squares	Error Mean Squares
Groups (G)	$R(\mu,G,F)-R(\mu,F)$ From $\hat{\beta}' Z^{-1}\hat{\beta}$	$\sigma^2_e + k_4\sigma^2_{D:SG} + k_5\sigma^2_{S:G} + q^2_G$
Sires within Groups (S:G)	$R(\mu,G,S,F)-R(\mu,G,F)$	$\sigma^2_e + k_2\sigma^2_{D:SG} + k_3\sigma^2_{S:G}$
Dams within Sires/ Groups (D:SG)	$R(\mu,G,S,D,F)-R(\mu,G,S,F)$	$\sigma^2_e + k_1\sigma^2_{D:SG}$
Sex (F)	$\hat{\beta}Z^{-1}\hat{\beta}$ (Adjusted for GSD subclasses)	$\sigma^2_e + kq^2_F$
Error	$y'y - R(\mu,G,S,D,F)$	σ^2_e

where, $\hat{\beta}'Z^{-1}\hat{\beta}$ refers to direct method of sum of squares computation

q^2 = quadratic term (fixed effect)

R, reduction in sums of squares.

During the least squares estimation of the above mixed model, constants were fitted for the means, μ_m, and the two fixed effects, groups and sex. Components of variance and covariance for sire, dam and error terms were determined and used to calculate heritabilities and genetic, phenotypic and environmental correlations for each trait considered by the model.

2.2.5 Expected Direct and Correlated Responses to Selection for Weights, Growth Rates and Feed Efficiency

Within the overall aim of this study expected direct and correlated responses to selection for various growth and feed intake traits were considered. Using information provided by the analyses described in Section 2.2.4 above, expected direct and correlated responses to single trait selection, were determined for traits over the three week periods from birth to 84 days of age. Responses were calculated by assuming a single generation experiment with a standard selection differential of 1.0.

2.3 RESULTS

2.3.1 Means, Standard Deviations and Coefficients of Variation for Body Weights

The least squares means for body weights from birth to 84 days of age are plotted in Fig. 2.1. At all ages, males are heavier than females ($P < 0.001$). The mean male and female weights were still increasing at 84 days of age.

Standard deviations and variances for weights at six day

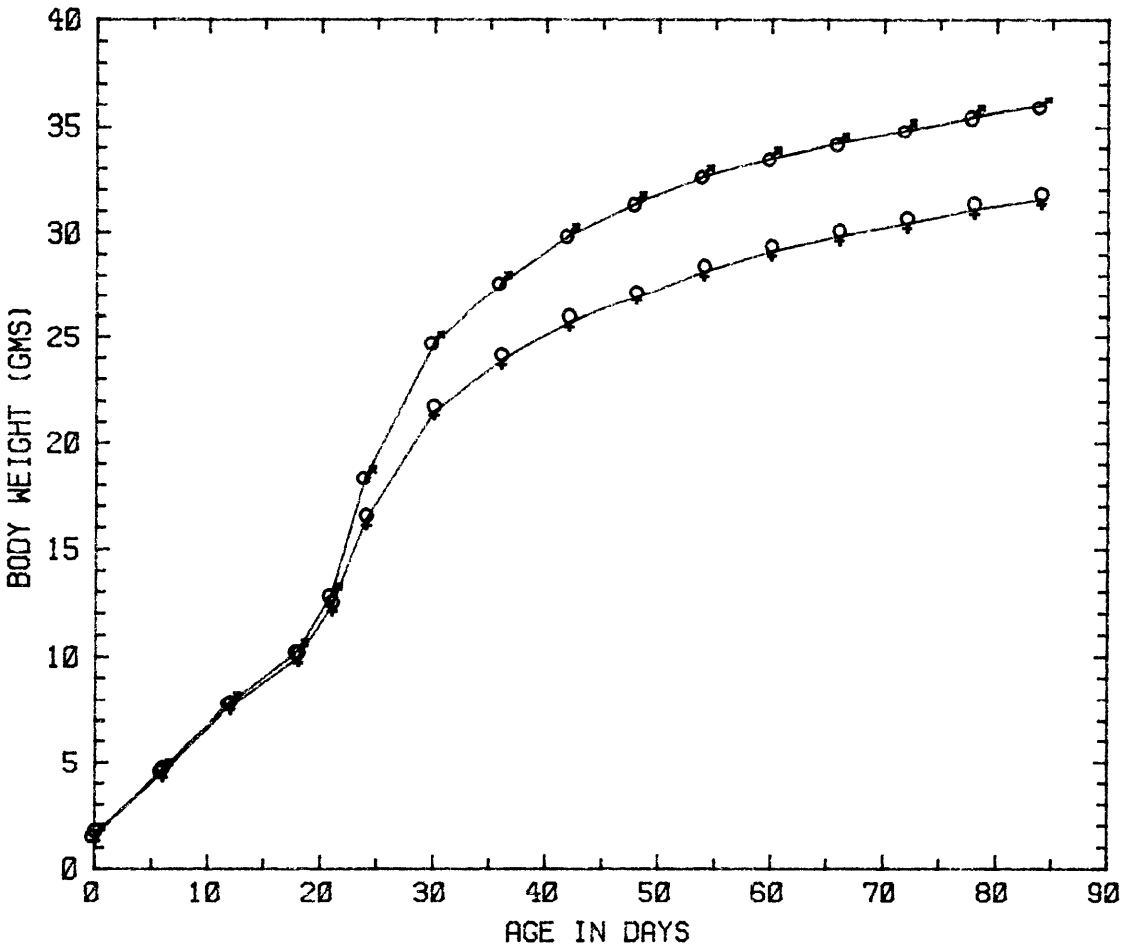

Figure 2.1: Least squares means for body weights from birth to 84 days of age.

intervals are plotted in Fig. 2.2. The mean and, overall, the variance increased over time, both eventually approaching a steady state. There was a marked 4.5-fold increase in phenotypic variance between 18 days (3 days prior to weaning) and 24 days of age (3 days post-weaning), which could be associated with a divergence between individuals due to the differential role of maternal effect pre- and post-weaning. After 24 days of age the variance decreased to 5.5 grammes^2 (females) and 7.0 grammes^2 (males) at 42 days of age. Monteiro and Falconer (1966) discussed the theory of the change in variance of body weight. Simply, the variance at some time t is composed of the variance at time t-1, plus the variance of weight gain plus twice the covariance between weight at t-1 and the weight gain. As the variance of weight gain cannot be negative, reductions in the variance at time t are due to a negative covariance between weight at time t-1 and weight gain between the two weights. Compensatory growth has been associated with a decline in the variance of body weights.

The phenotypic coefficients of variation for body weight (Fig. 2.3) were less than 10% for all weights other than 24 day weight. Initially, the coefficients from birth to 12 days of age decrease, then rise to a maximum at 24 days followed by another decline to 30 days. Thereafter, coefficients of variation fluctuated between six and seven percent.

2.3.2 Heritability Estimates for Body Weight

The estimates of the additive genetic variance were based solely on the sire components of variance. The plot of heritabilities for body weight (Fig. 2.4) shows a five phase pattern.

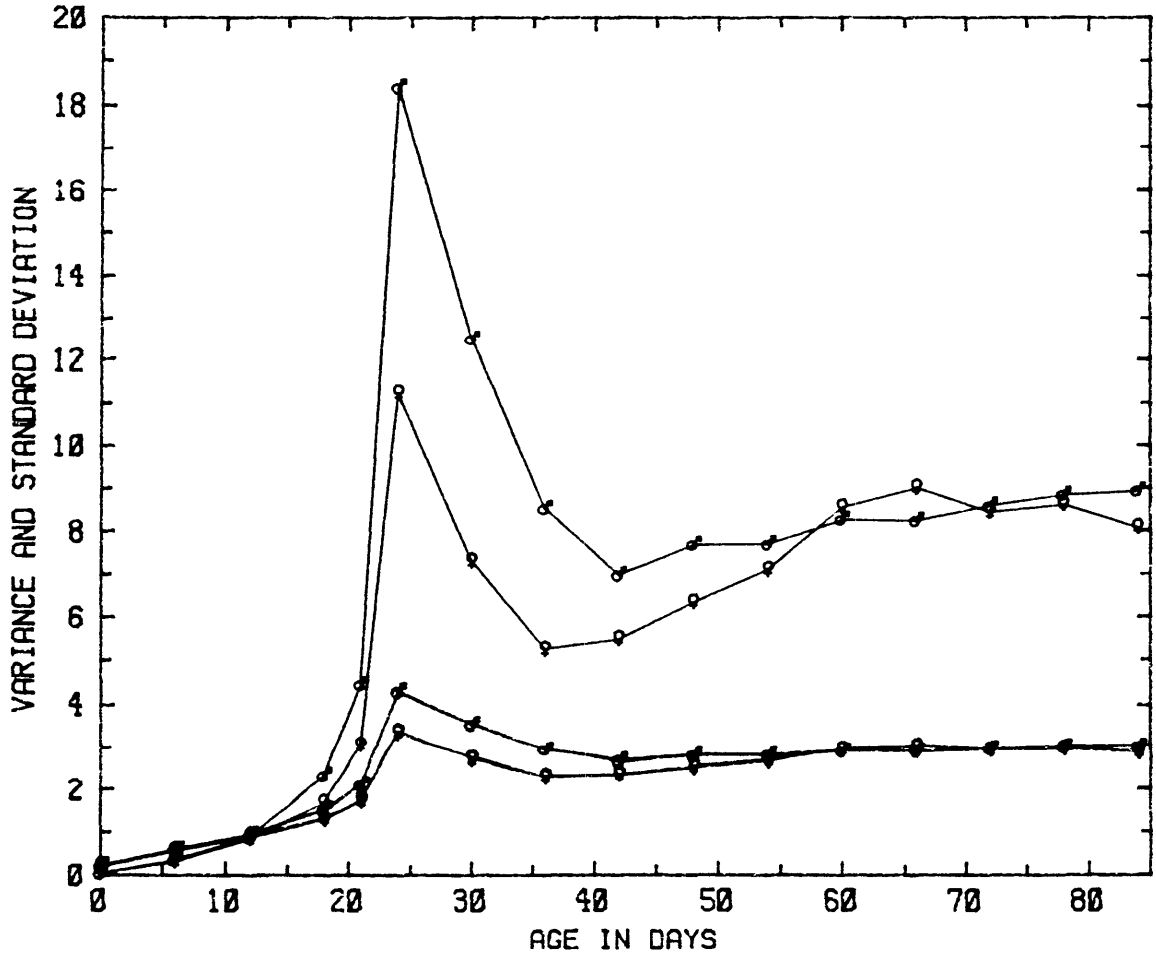

Figure 2.2: Standard deviations and variances for weights at six-day intervals.

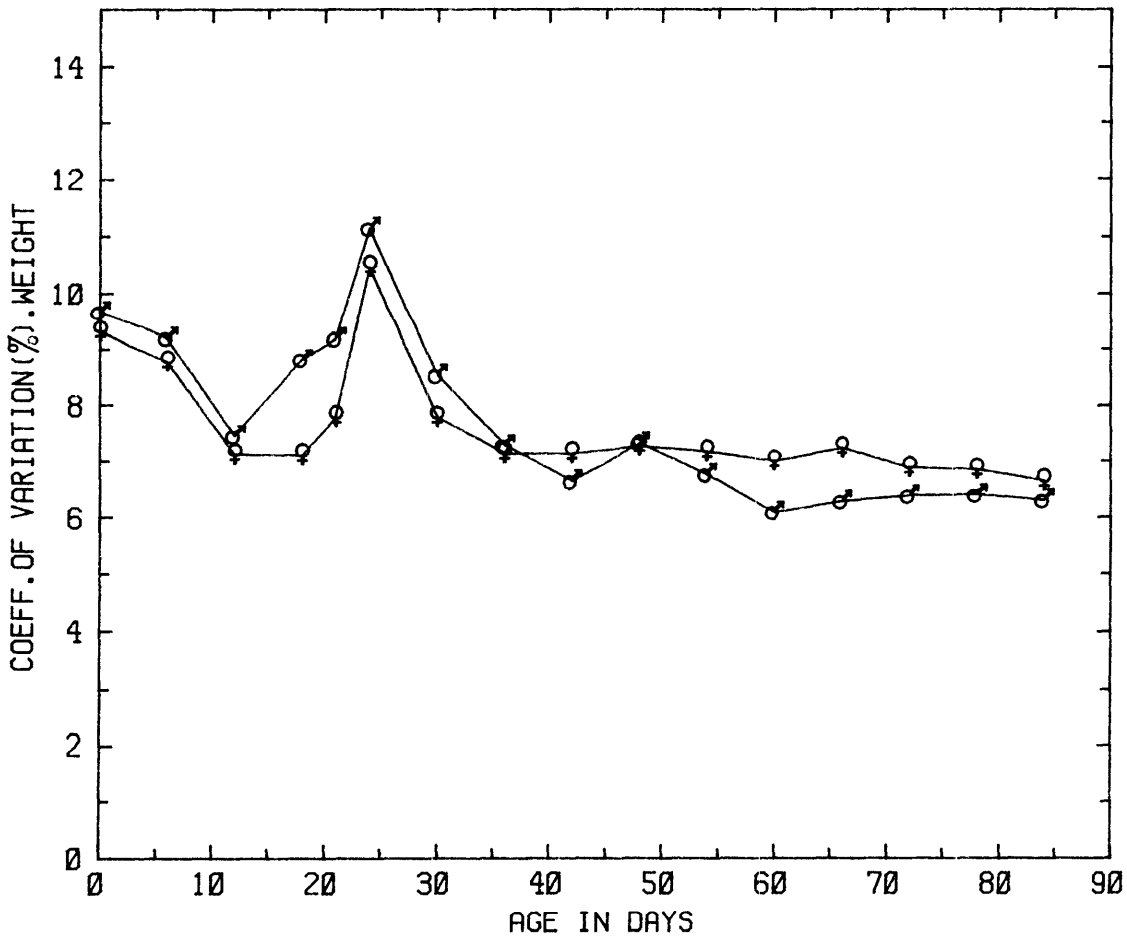

Figure 2.3: Coefficients of variation of body weight for males and females.

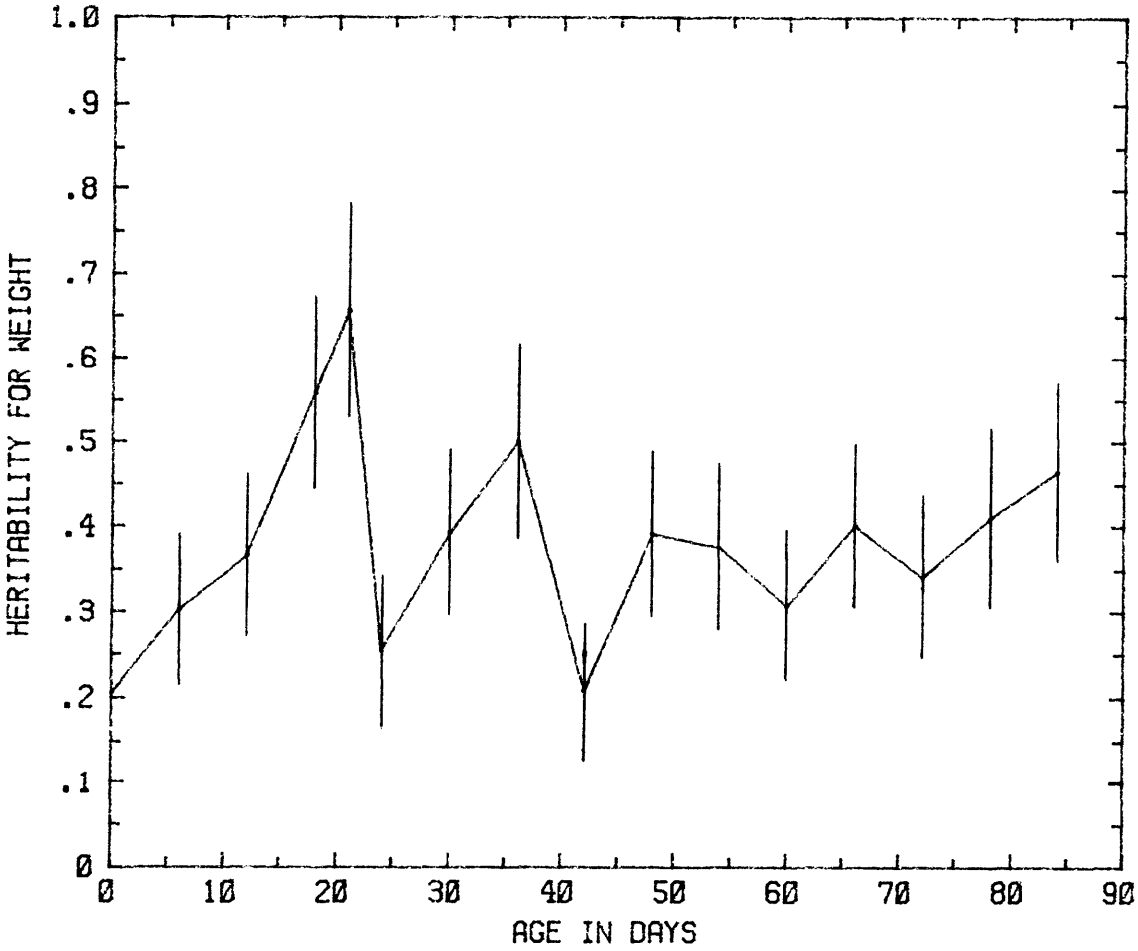

Figure 2.4: Heritabilities (and errors) of body weight.

Heritability increases from birth to weaning (0.2 to 0.66) followed by a sharp decline to 0.25 at 24 days of age and then a gradual increase to 0.5 at 36 days. A further decline occurs to the 42 day heritability of 0.21, while from 42 to 84 days of age, heritabilities fluctuate but gradually rise to give an estimate of 0.46 for 84 day weight. The magnitude of the errors associated with the heritability estimates would suggest that the changing pattern of estimates, particularly after 36 days of age, may not reflect real differences in heritabilities.

2.3.3 Correlations Among Body Weights

Correlations Between Consecutive Body Weights: Correlations between consecutive body weights are shown in Fig. 2.5. Since weight at some previous time (in this case, six days previous) is part of the whole weight at a later time, this type of correlation reflects a part-whole relationship.

The pattern of the phenotypic and genetic correlations are marked by the disjuncture at weaning. This is particularly evident for the genetic correlations. The phenotypic correlations, with the exception of the correlation between 21 and 24 day weight, show a gradual increase with age so that at later ages they have levelled off at about 0.9 to 1.0. The decrease in phenotypic correlations between weights at 21 and 24 days was possibly associated with weaning stress over the period. Observations on the mice during this period showed a number of mothers had imposed a self-weaning on their litters prior to the artificially imposed weaning at 21 days. Also, it was noted that a number of the progeny within litters were eating feed

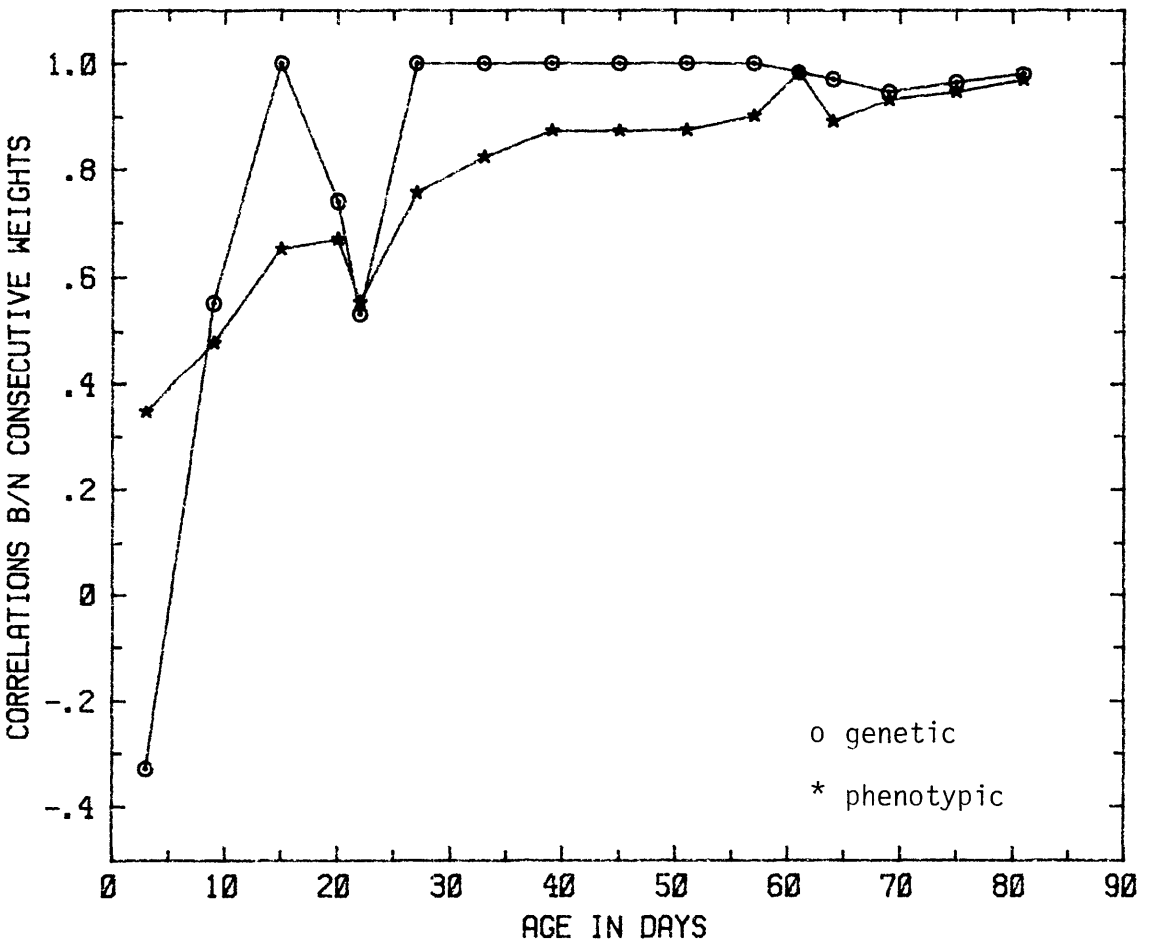

Figure 2.5: Genetic and phenotypic correlations between consecutive body weights.

made available to the dam. As noted previously, the phenotypic variance increased over this period. This possibly reflects the exaggerated differences between individuals due to weaning stress and a decrease in the phenotypic correlation.

There was a sharp decrease in the genetic correlations between weights from 18 to 24 days. The genetic correlations between 12 and 18, 18 and 21, 21 and 24 day weights were respectively 1.0, 0.741 and 0.532. By partitioning the additive genetic variance for a weight at time t in the same way as previously suggested for the phenotypic variance (Section 2.3.1), i.e.

$$V_{Wt} = V_{Wt-1} + V_G + 2 \text{ Cov } (W_{t-1}, G)$$

where G is the weight gain over the period t-1 to t, and substituting the respective variances obtained for body weights and weight gains in this equation, gives covariance terms for the three intervals as 0.591, 0.206 and -2.057. The covariance term then increases to 0.698 for the period 24 - 30 days. A possible explanation for the marked fluctuations in covariances may be varying degrees of interaction between direct genetic, maternal genetic variances and maternal-genetic covariances. This is examined in more detail in Chapter 4. After climbing from the trough, the genetic correlations remain stable and level off in the region of 0.9 to 1.0.

Correlations Between Birth and Later Body Weights: The correlations between weight at birth and weights up to 84 days of age are plotted in Fig. 2.6. The phenotypic correlations decrease

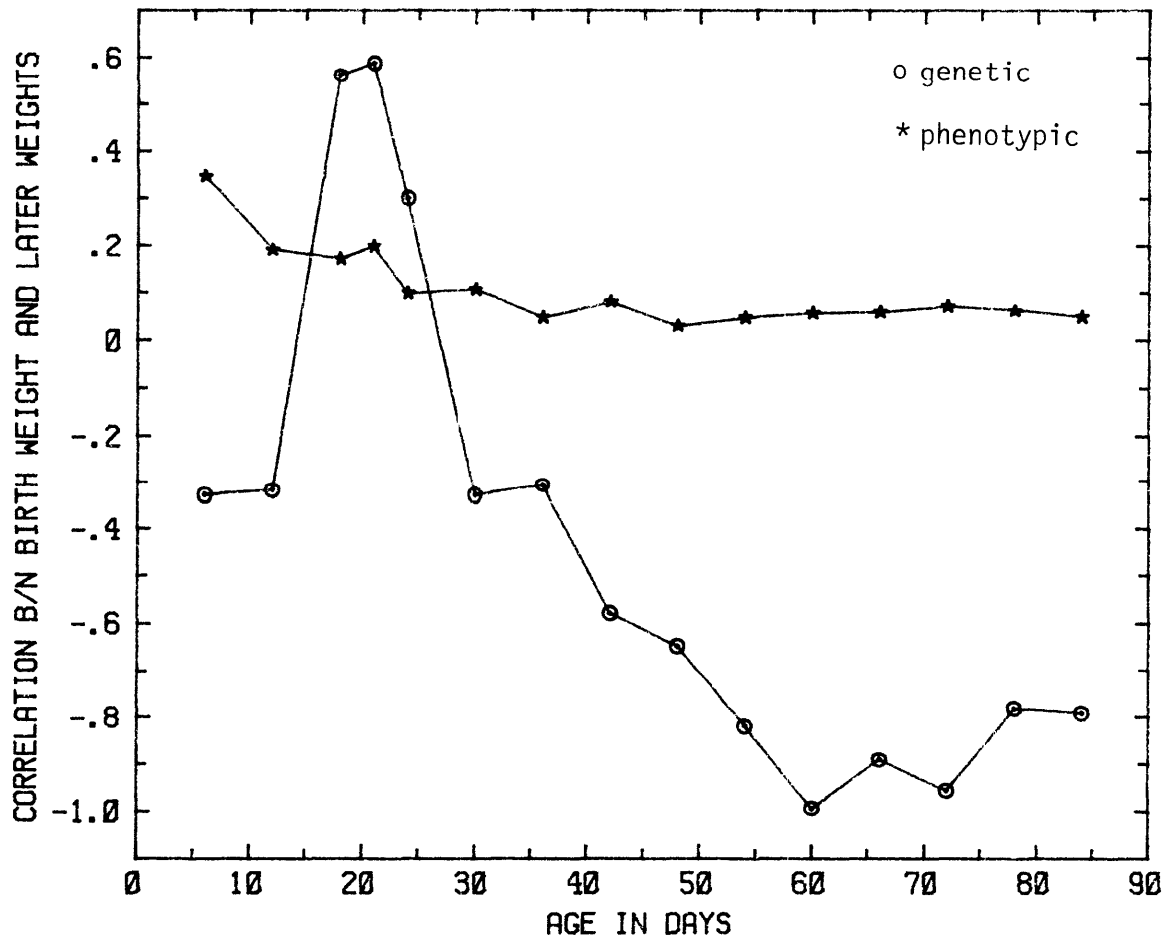

Figure 2.6: Genetic and phenotypic correlations between birth weight and later body weights.

rapidly from 0.346 between birth and 6 day weight to 0.198 between birth and 21 day weight. The relatively constant correlation after 30 days is not surprising since birth weight constitutes only a small part of the observed later weight, that is, there is a part-whole relationship between birth and later weights.

The picture for the genetic associations is again marked by the disjuncture around the 18 - 24 days old period. All other correlations are negative; however, for this short period, the correlations were positive. Animals lighter (heavier) at birth are lighter (heavier) over the weaning period. As a cautionary point, it is important to note that the errors associated with many of the correlations are quite high, this is particularly pertinent for the correlations in the region of $\pm$ 0.3. There is, however, no doubt that there is a distinct negative-positive-negative trend in the genetic correlations between birth weight and later weights.

Correlations Between Final and Preceding Weights: The phenotypic and genetic correlations between final body weight, at 84 days, and previous weights are presented in Fig. 2.7. The pattern for the phenotypic correlations is as expected. Correlations gradually rise from birth to weights at later ages as the time intervals between final weight and early weight become less.

The trend for the genetic correlations is essentially the reverse of that shown in Figure 2.6. Particular note should be made of the fact that genetic and phenotypic correlations are of opposite sign for the correlations between 84 day weight and birth weight and 84 day weight and six day weight. The negative genetic relationship may be masked phenotypically by the buffering effect of the maternal enivronment.

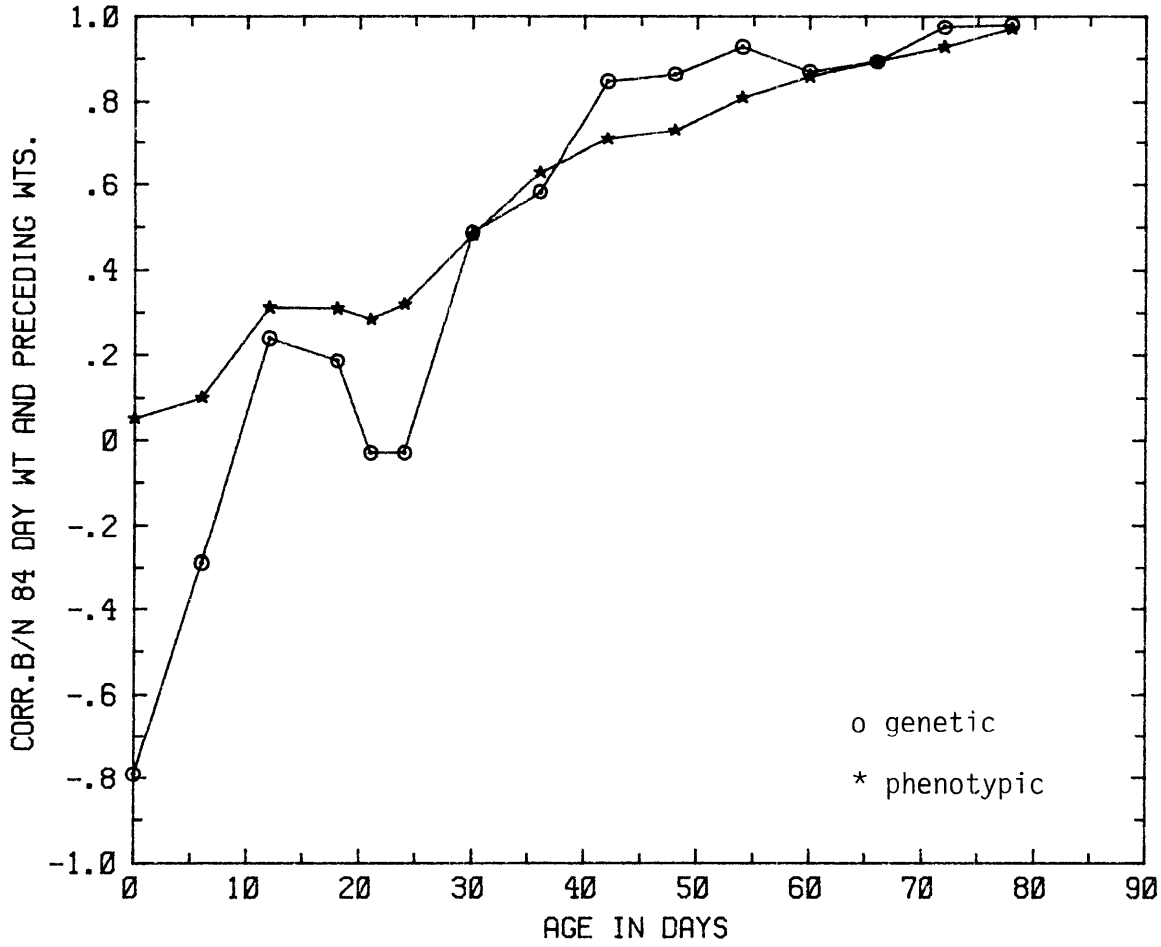

Figure 2.7: Genetic and phenotypic correlations between 84 day weight and preceding body weights.

2.3.4 Means and Coefficients of Variation for Fraction of Maturity.

The least squares means for fraction of maturity are plotted on Fig. 2.8. The specific end-point of body weight at 84 days of age was used and accounts for the value of 1.0 obtained for both sexes at 84 days of age. An important facet of this analysis was the high percentages of maturity attained by both males and females at early ages. The mean male and female values were 35.9% and 29.3% at 21 days, 51.1% and 52.4% at 24 days and by 42 days or halfway through the measurement period, males were 83.6% and females 82.0% of their estimated mature weights.

The coefficients of variation show a gradual decrease over the 84 day period, except for the period about 18 - 24 days of age (Fig. 2.9). The pattern was as expected for measurements with a specific end-point. By definition as the fraction of maturity approaches 1.0 the variance will decrease and must be zero when all animals are 84 days old.

2.3.5 Heritability Estimates for Fraction of Maturity

Heritabilities for fraction of maturity at each age are plotted in Fig. 2.10. Heritability estimates rise to a peak at 21 days of age of 0.86 $\pm$ 0.15 and decline immediately thereafter, fluctuating in the range of 0.2 to 0.5. Given the large errors associated with some of the estimates, it appears that there is a trend to decreasing heritability with age. Certainly, there is sufficient

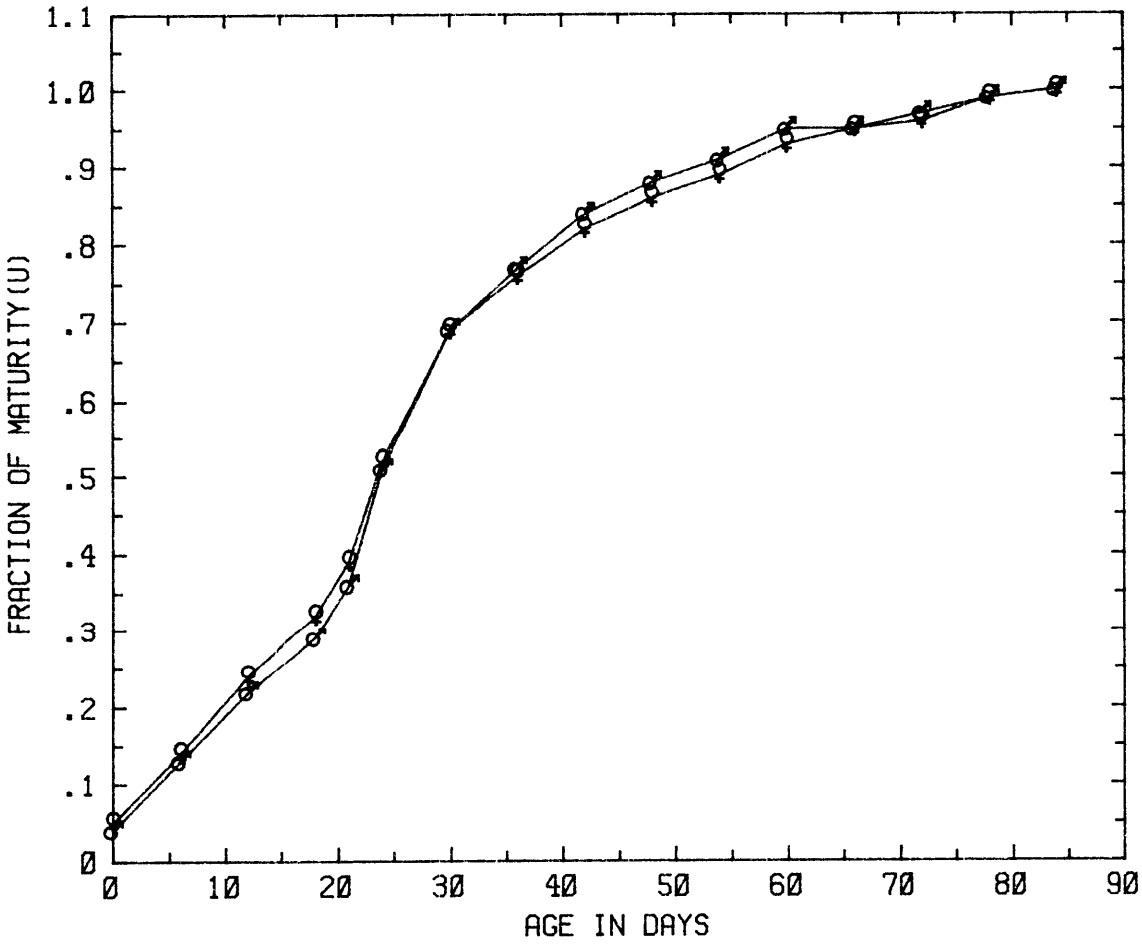

Figure 2.8: Least squares means for fraction of maturity.

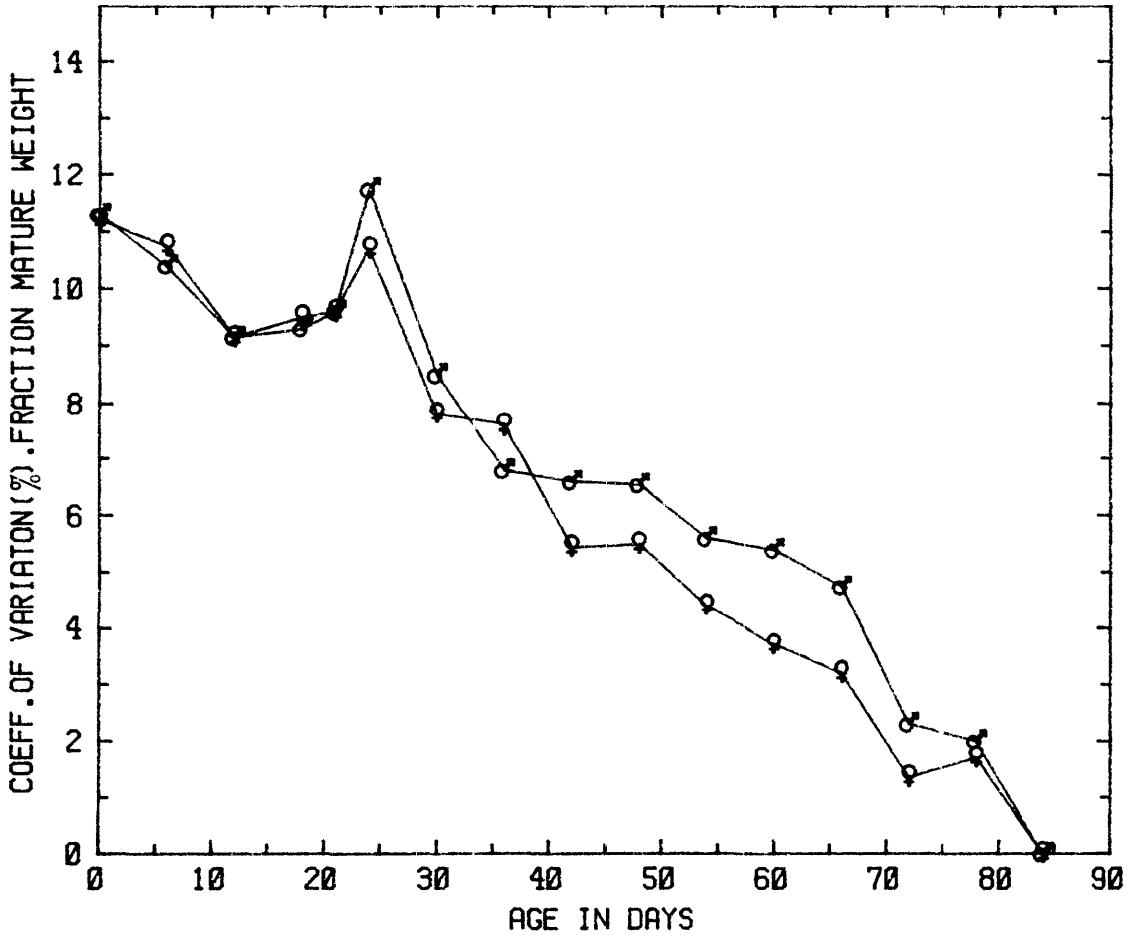

Figure 2.9: Phenotypic coefficients of variation for fraction of mature weight.

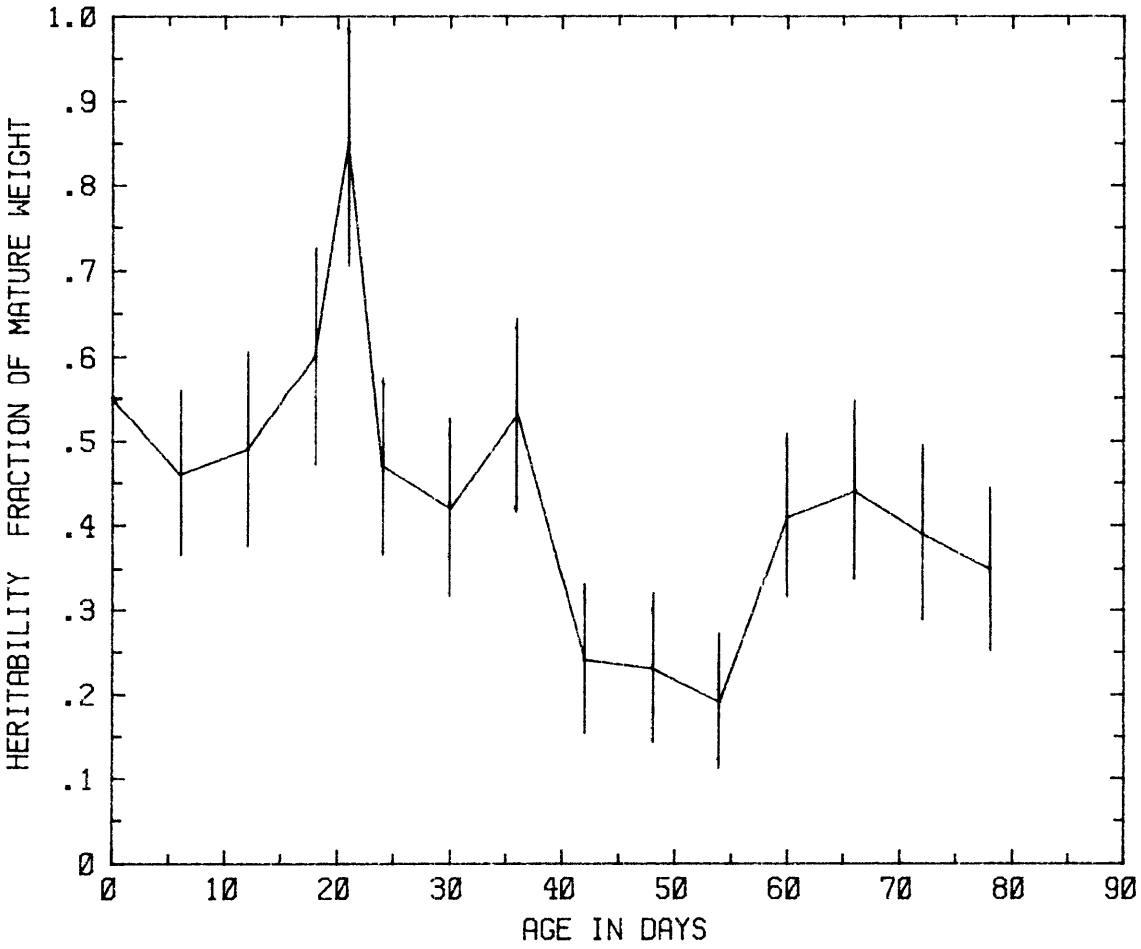

Figure 2.10: Heritabilities (and errors) for fraction of mature weight.

genetic variation to suggest that selection to increase fraction of maturity at a given age would be successful. However, careful consideration would have to be given to the decrease in the variances at later ages (Fig. 2.9).

No heritability is plotted for 84 days as it must be by definition 1.0.

2.3.6 Measures of Growth Rate; Weight Gain, Relative Growth Rate (RGR) and Absolute Maturing Rate (AMR)

On all figures relating to the growth rate measures the value for a particular time interval is plotted at the midpoint of that time interval, for example, weight gain from birth to six days of age is plotted over the three day ordinate.

Means, Standard Deviations and Coefficients of Variation: The means and coefficients of variation for the three measures of growth (Table 2.3) are presented in Figures 2.11 to 2.16.

The plot of weight gains (Fig. 2.11) show that both males and females follow the same trend. Males achieve and maintain higher growth rates than females up to 54 days of age, after which no differences were detectable over the six day intervals. Weight gain declined prior to weaning as the most readily available feed supply becomes depleted. As mentioned previously, many pre-weaned mice appeared to be consuming the laboratory chow made available for their dams; this may account for the ability of many mice to rapidly overcome the immediate post-weaning stress reported in other

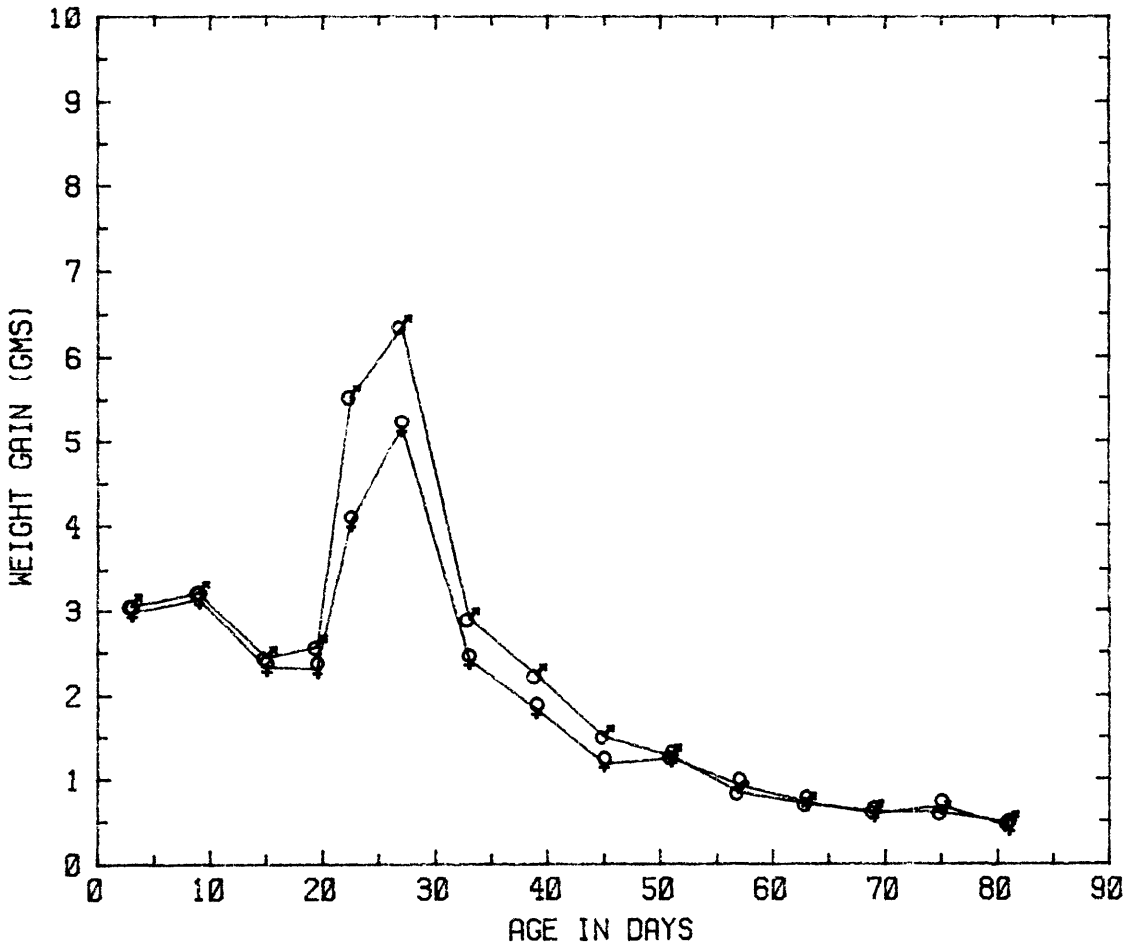

Figure 2.11: Least squares means of body weight gain for males and females.

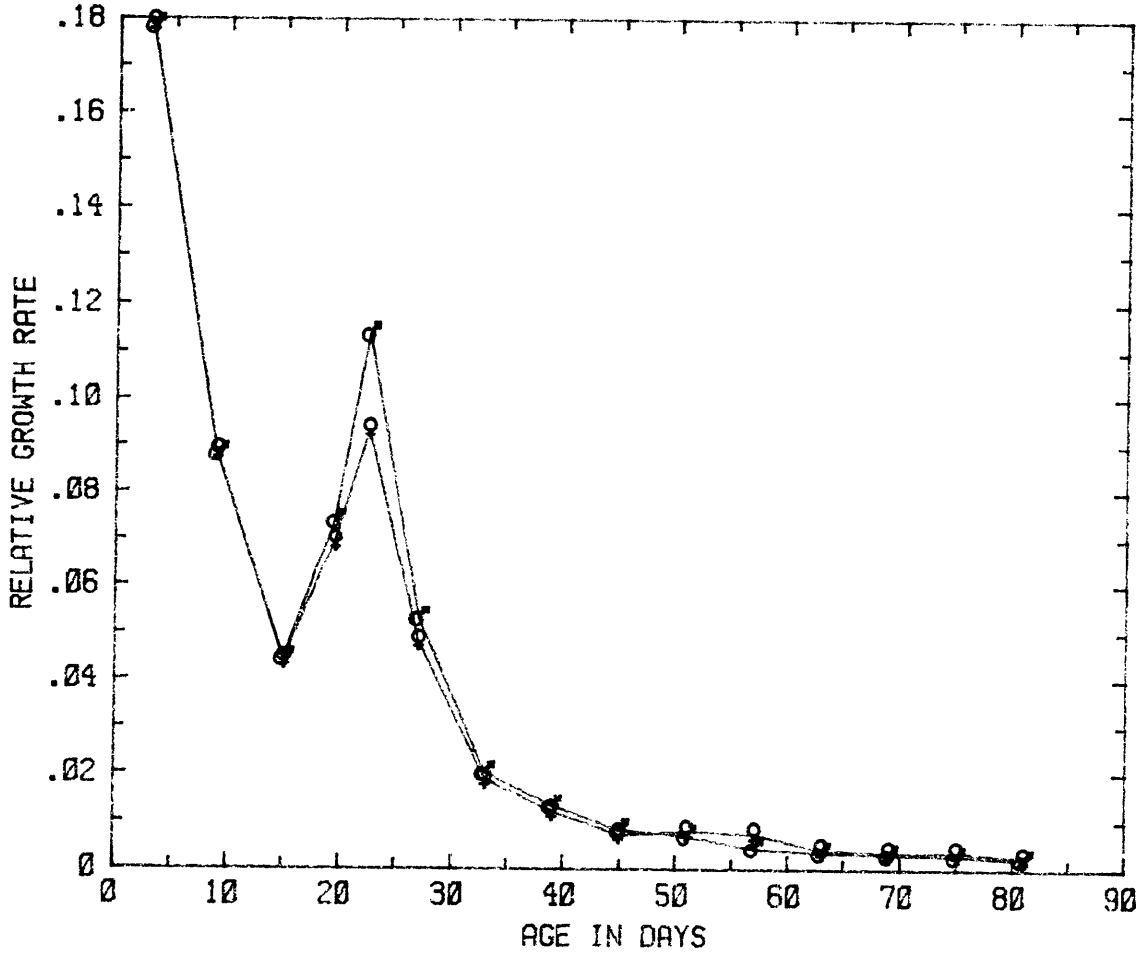

Figure 2.12: Least squares means for relative growth rate.

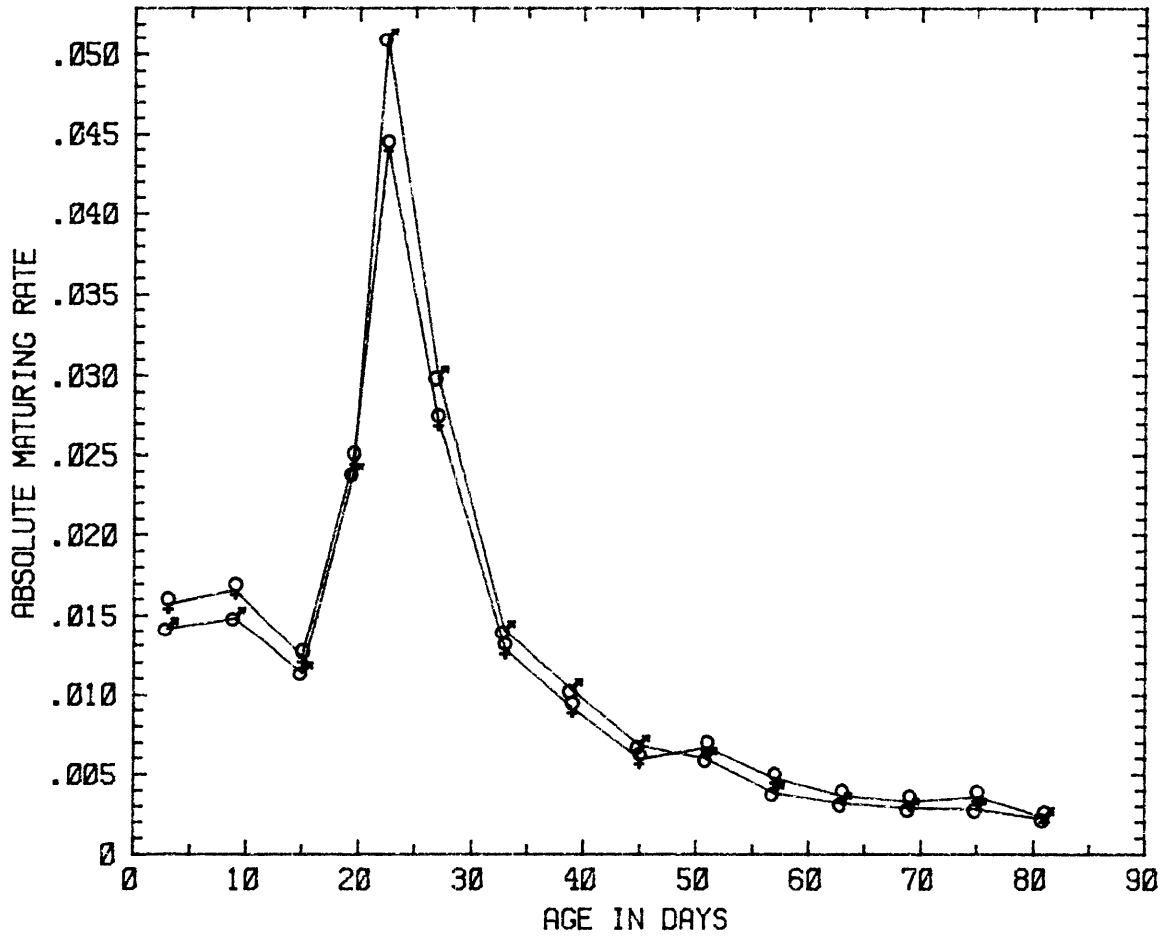

Figure 2.13: Least squares means of absolute maturing rate for males and females.

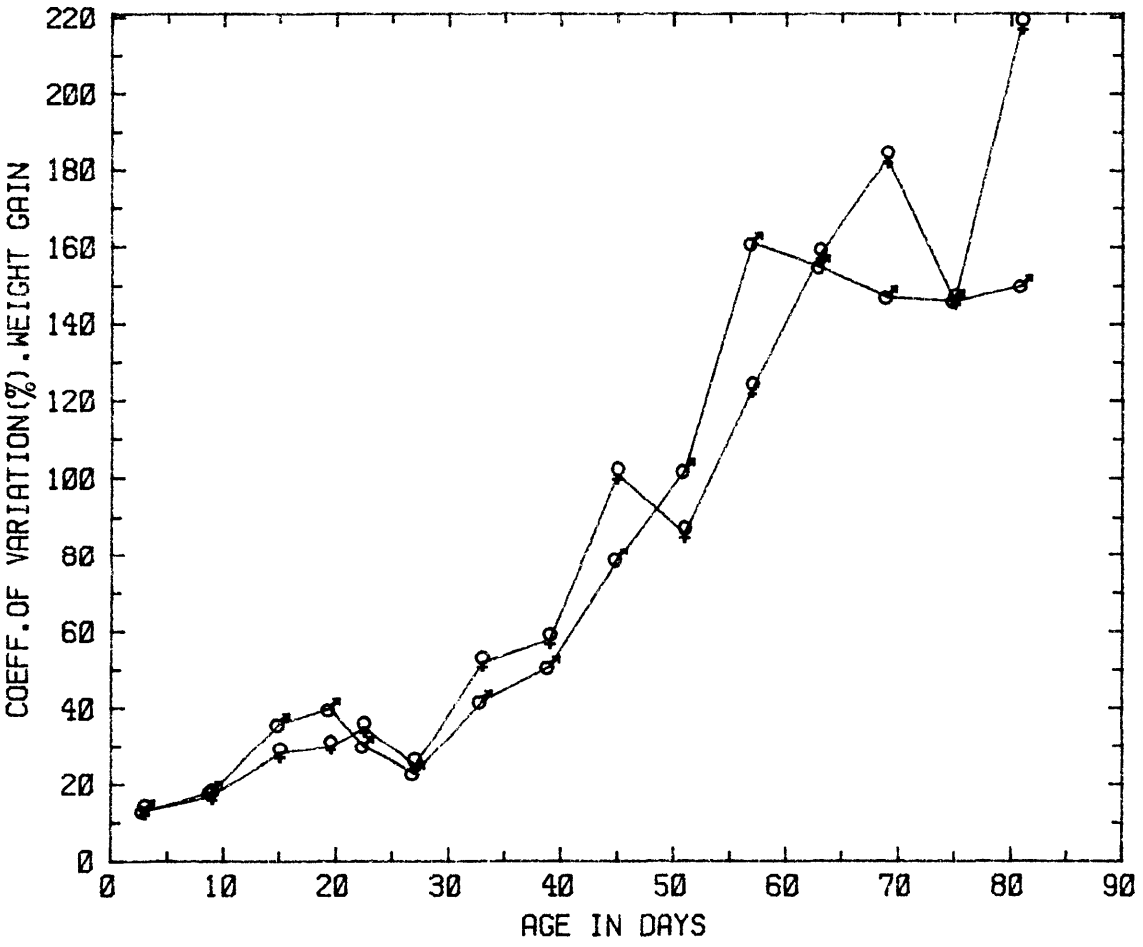

Figure 2.14: Coefficients of variation of body weight gain for males and females.

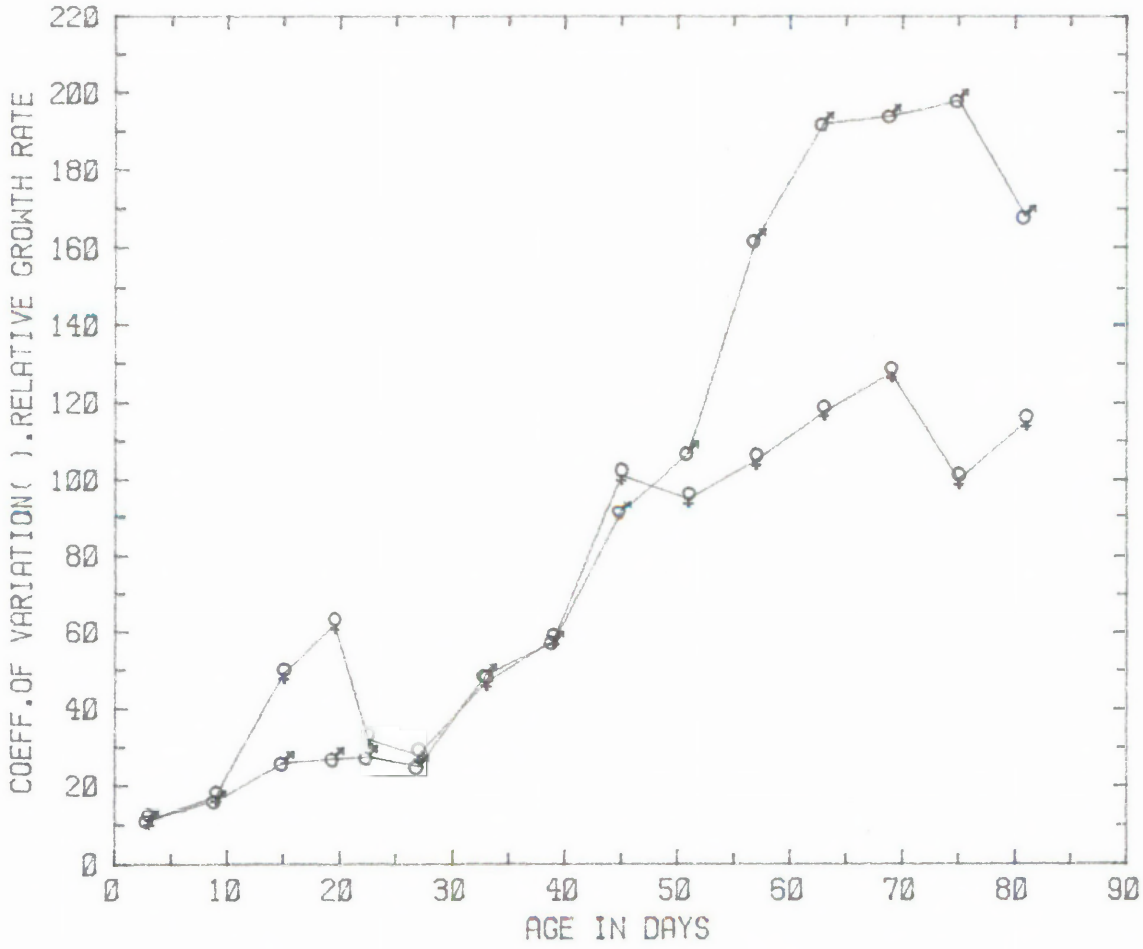

Figure 2.15: Coefficients of Variation of Relative Growth Rate for Males and Females.

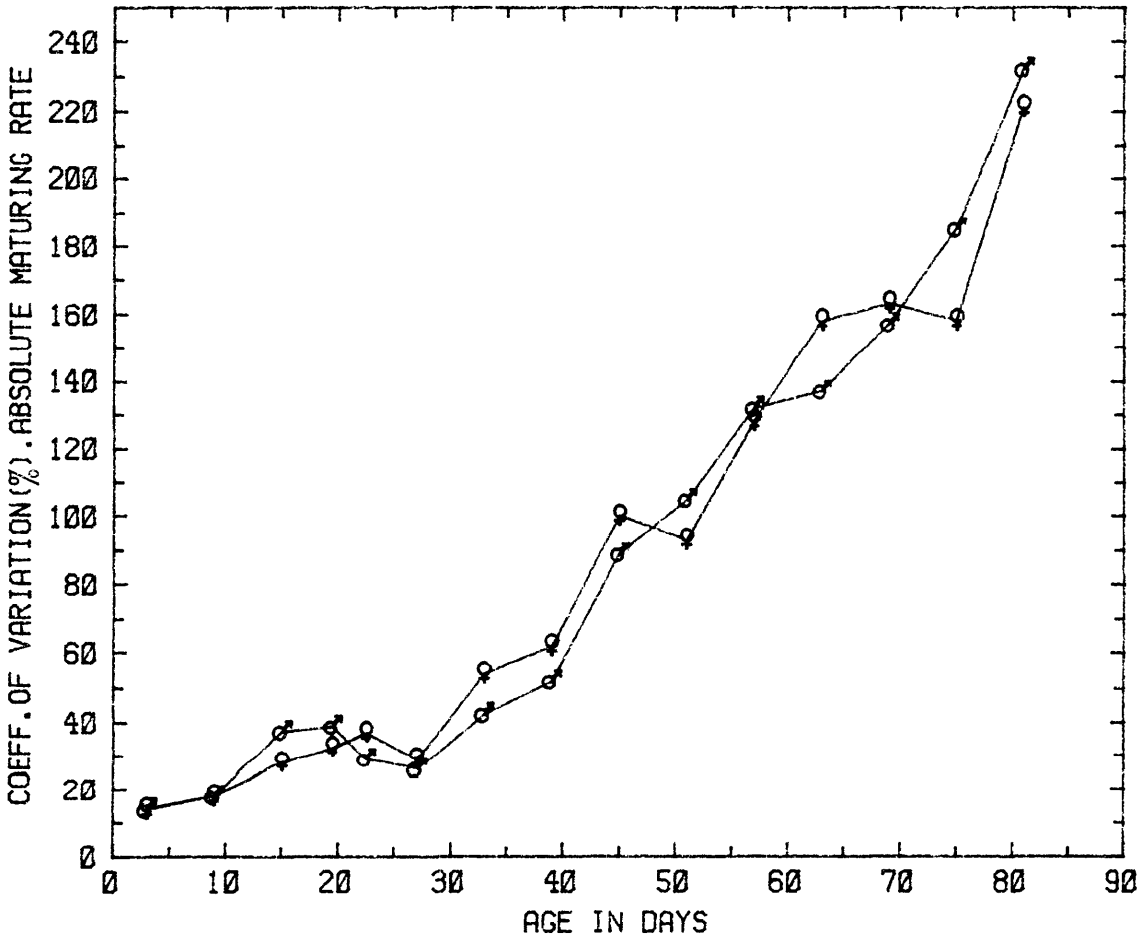

Figure 2.16: Coefficients of variation of absolute maturing rate for males and females.

studies (Hetzel, 1978). Once weaned, growth rates, as measured by weight gain, RGR or AMR, increased rapidly in both sexes.

Relative Growth Rate (Fig. 2.12) declined rapidly prior to 18 days of age for both sexes (0.177 and 0.178 for 0 - 6 days, 0.090 and 0.090 for 6 - 12 days, 0.046 and 0.046 for 12 - 18 days for males and females respectively) and then rose to a post-weaning maximum over the period 21 - 24 days (0.126 for males and 0.108 for females).

The contention that pre-weaned mice had begun to consume laboratory chow prior to weaning is much more evident in the curves of relative growth rate. It is hard to conceive that such a marked change in growth rate pattern could be achieved merely by a change in efficiency of conversion of milk to weight.

The pattern of changes in absolute maturing rate were very similar to that of the previous measures (Fig. 2.13). After 12 days of age, males tended to approach their mature weight at a greater rate than females; however, a further crossover of the curves occurs between 48 and 54 days of age. The higher rate in females prior to 12 days of age was directly related to the higher proportion of mature weight (often referred to as fraction of maturity, μ_t) in females at birth. μ_t for males and females at birth were 0.044 and 0.049 respectively, and 0.129 and 0.143 respectively at 6 days old. It is important to remember that mature weight was estimated by 84 day weight for each individual and thus, measures involving the estimated mature weight have a fixed end-point. This relationship affects interpretations, particularly for those

periods close to the end-point.

The plots of the coefficients of variation show a similar pattern for each of the three growth rate measures (Figures 2.14, 2.15, 2.16). The pattern of variation for the three measures fluctuates considerably, especially when compared to the pattern for body weight (Fig. 2.3). The high degree of variation is similar to that found by Grossman (1969), particularly at later ages. As animals approach a steady state (i.e., mean growth rates fluctuate closely around zero), the variation becomes inflated by animals not yet at their equilibrium mature weights. This increased variation was more pronounced for males, particularly for relative growth rate (Fig. 2.15).

2.3.7 Heritability Estimates for Growth Rate Measures

In all cases, the heritabilities for the growth rate measures (weight gain, relative growth rate and absolute maturing rate) were based solely on sire components of variance (Figures 2.17, 2.18 and 2.19). Although both the additive and phenotypic variance increased prior to weaning, the proportionate increase in additive variance was not as great. Disproportionate increases in the phenotypic variance prior to 18 days may have been due to competition for milk supplies, although the litters had been standardised in an attempt to overcome this problem. Around weaning, the heritabilities increased dramatically, then decreased to about 30 days of age, and stabilised in the region of 0.1 to 0.3.

For each growth rate measure, peaks in heritability occurred

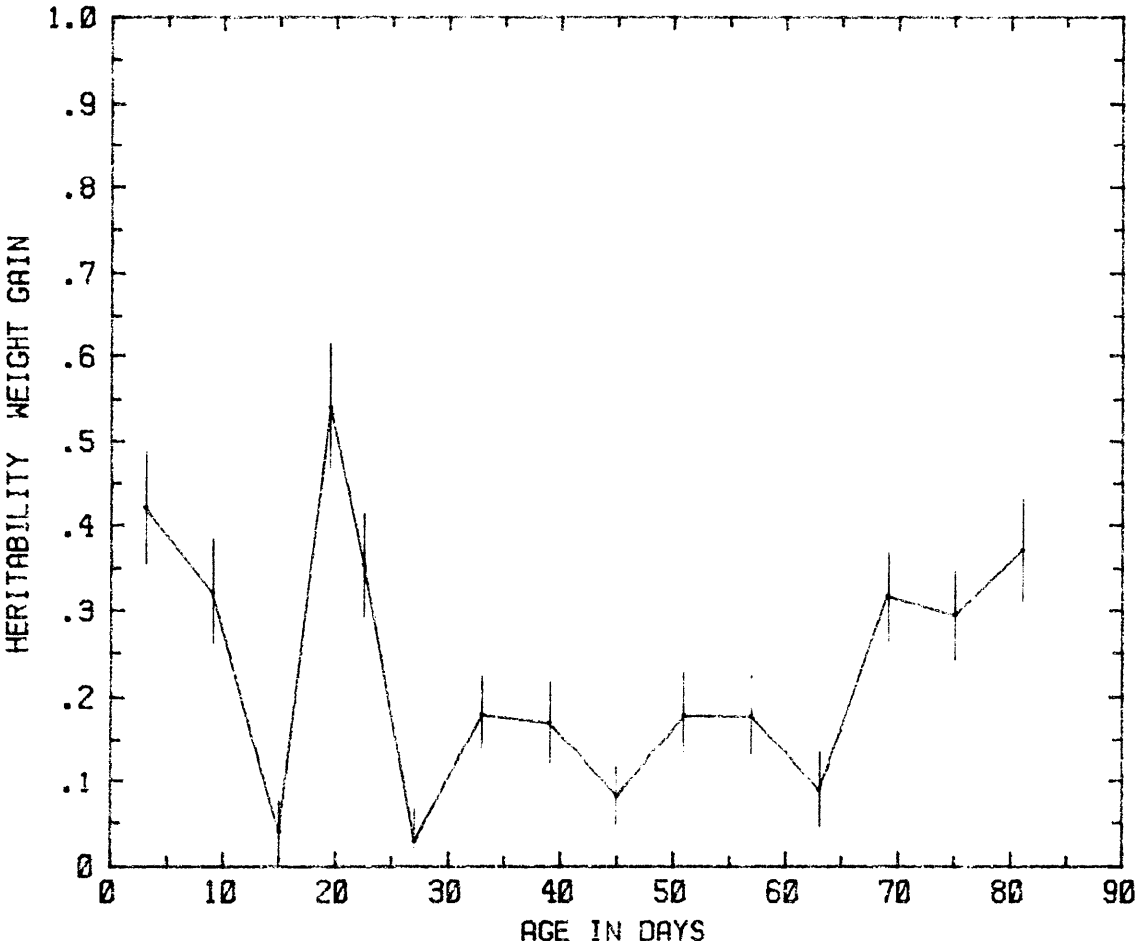

Figure 2.17: Heritabilities (and errors) for body weight gain.

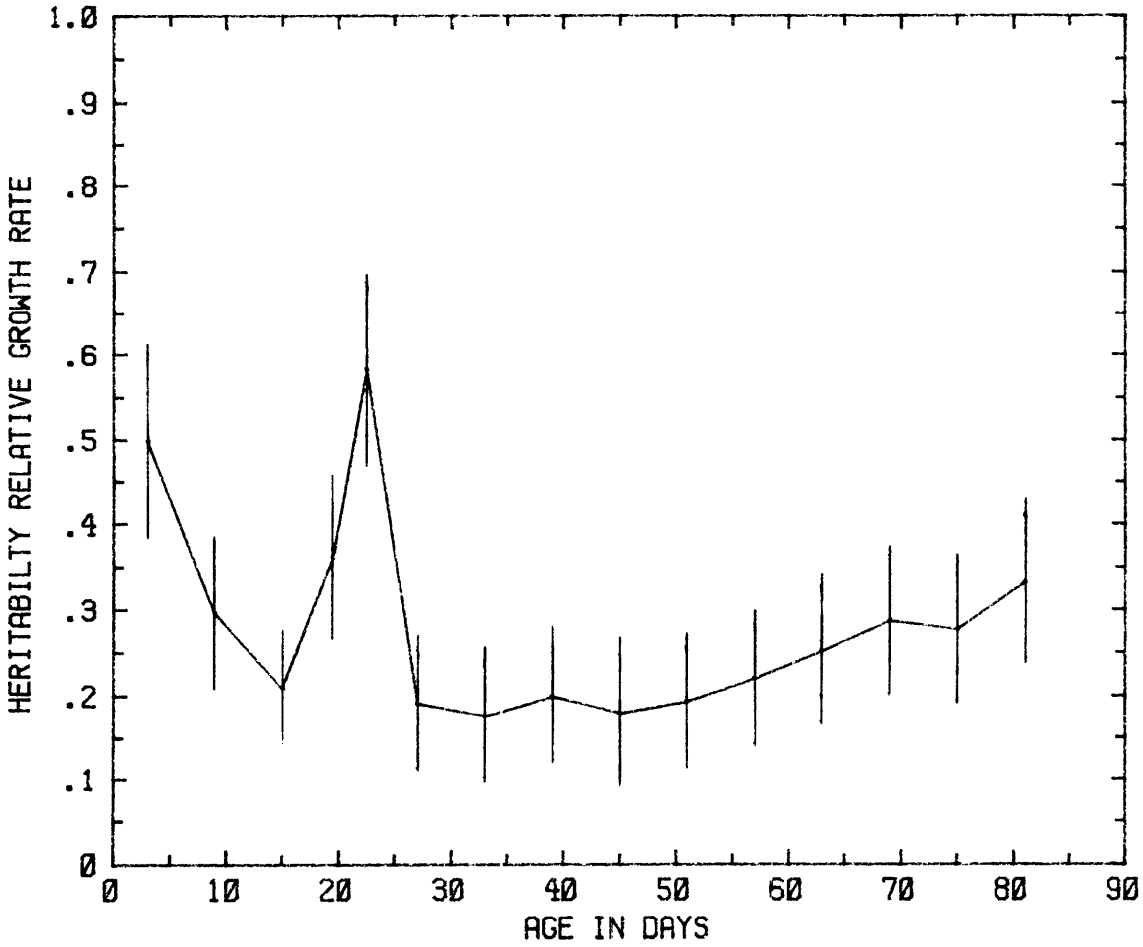

Figure 2.18: Heritabilities (and errors) for relative growth rates.

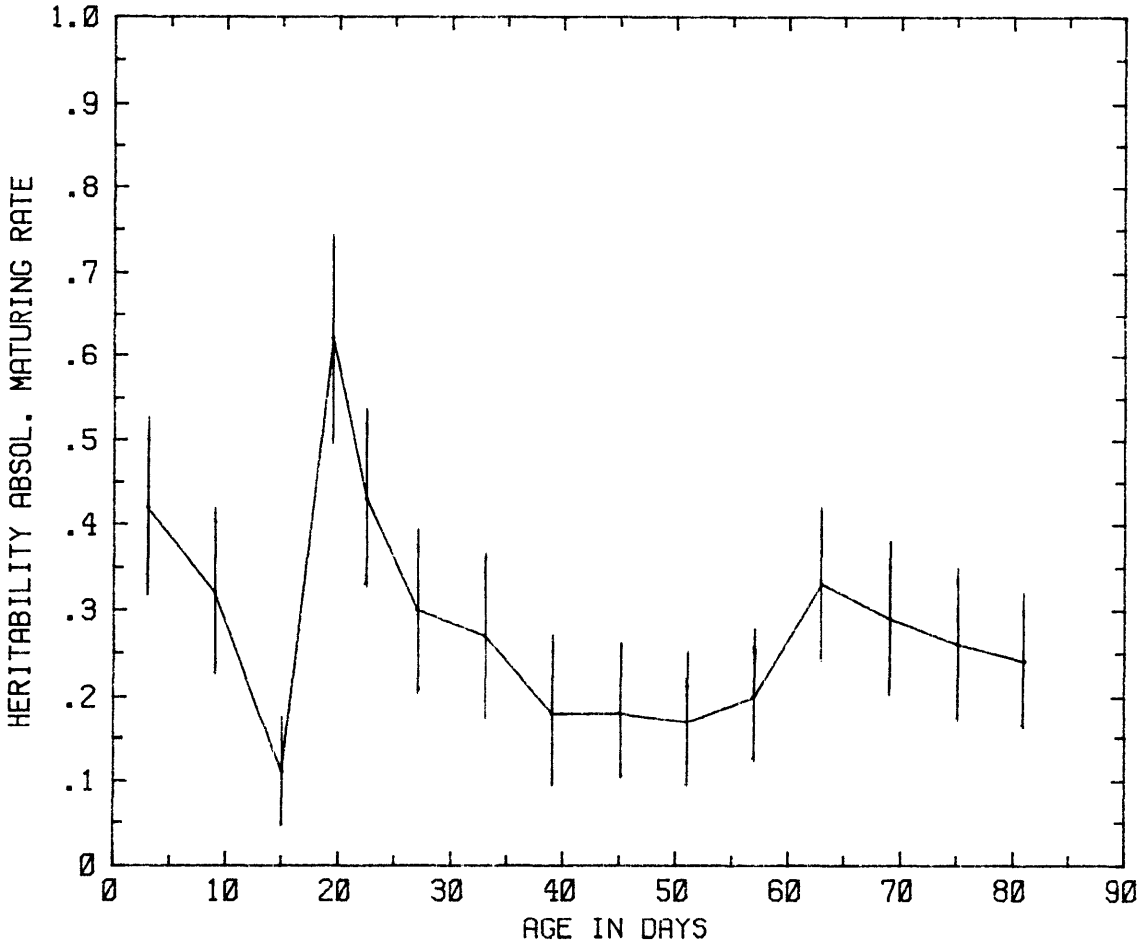

Figure 2.19: Heritabilities (and errors) for absolute maturing rate.

over the periods 18 - 21 and 21 - 24 days of age. The relevant measures being 0.539 $\pm$ 0.12 and 0.353 $\pm$ 0.1 respectively for weight gain, 0.35 $\pm$ 0.09 and 0.52 $\pm$ 0.14 for relative growth rate, and 0.615 $\pm$ 0.127 and 0.43 $\pm$ 0.108 for absolute maturing rate. The decline of heritability estimates after this period suggests that a large amount of the variance in growth rates was probably due to random environmental variation.

2.3.8 Means and Coefficients of Variation for Feed Intake and Feed Efficiency

Feed intake rose rapidly postweaning in both sexes (Fig. 2.20). After 36 days of age, feed intake had reached a plateau, oscillating between 6.0 and 7.0 grams per day. The variation in feed intake was high for the period 21 - 24 days, then decreased for the following two periods (24 - 30 and 30 - 36 days), and rose again after 36 days (Fig. 2.21).

The pattern for feed efficiency is as one expects, high just postweaning and declining throughout the 21 - 24 day period (Fig. 2.22). The greater efficiency of males over the earlier periods was directly attributable to the greater weight gains. They were eating more and converting the extra food to tissue more efficiently than the females. This pattern continued up to 36 days of age, but thereafter no differences in feed efficiency were discernible between the two sexes.

The coefficients of variation for feed efficiency for both sexes increase, with some fluctuations, throughout the 63 day period

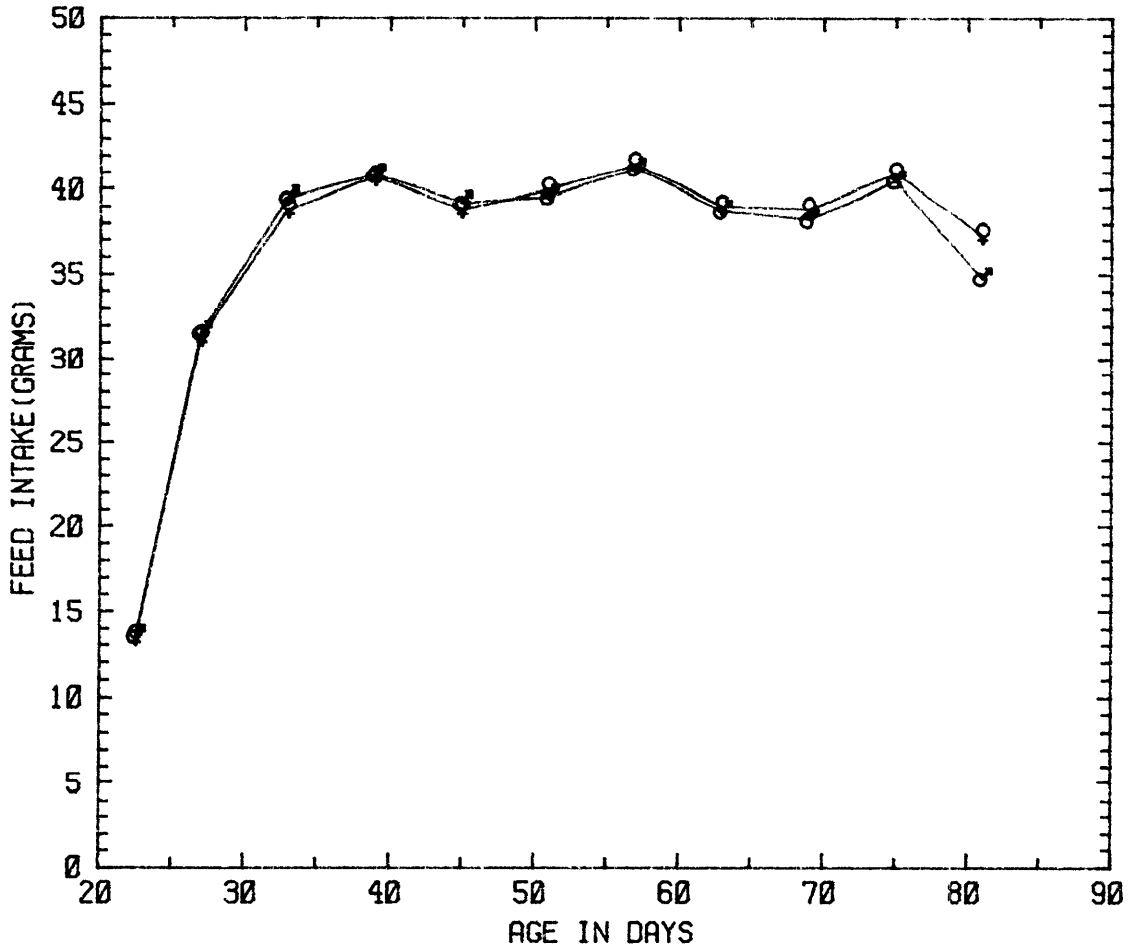

Figure 2.20: Feed intake from 21 - 84 days.

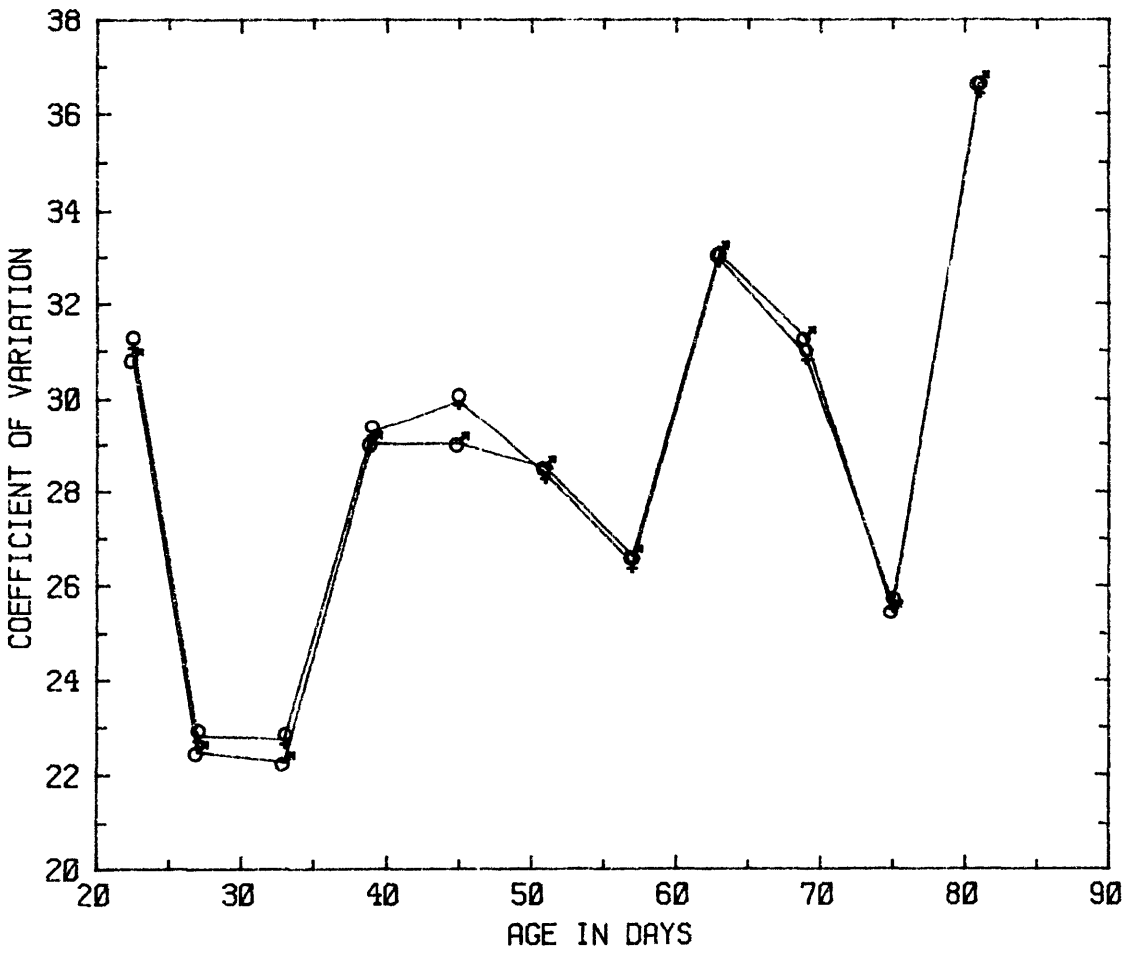

Figure 2.21: Coefficients of variation for feed intake.

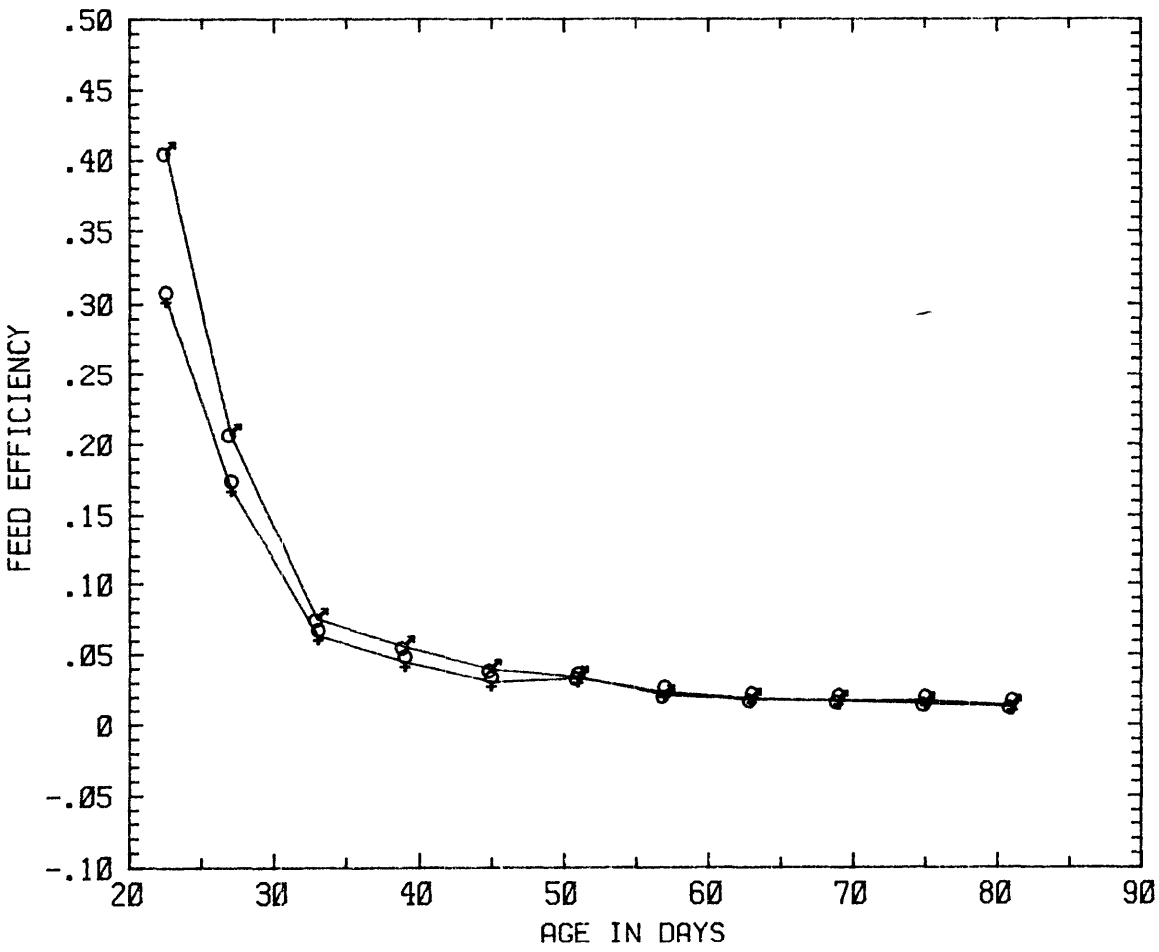

Figure 2.22: Feed efficiency from 21 - 84 days.

(Fig. 2.23). These coefficients rose from 32% in males and 38% in females for the period from 21 - 24 days of age, up to 150% in males and 158% in females for the 66 - 72 day period.

2.3.9 Heritability Estimates for Feed Intake and Feed Efficiency

The heritabilities for feed intake (Fig. 2.24) show considerable fluctuation over the 21 to 84 day time period. The heritabilitity for the period 21 - 24 days was 0.595 $\pm$ 0.126, it then decreased to a minimum of 0.218 $\pm$ 0.08 for the subsequent period between 24 - 30 days, and then increased to a maximum of 0.882 $\pm$ 0.15 for the period 36 - 42 days. After this period, heritabilities for feed intake continued to oscillate. The additive genetic variance from 36 days as measured by the sire component of variance, remains relatively stable, ranging from a low of 0.096 for the period 72 - 78 days to a high of 0.336 for the period 78 - 84 days. However, as can be seen from the plot of the coefficients of variation (Fig. 2.21), the phenotypic variance fluctuated considerably. Environmental and appetite fluctuations over the period from 36 to 84 days of age considerably affect the proportion of the phenotypic variance that has additive genetic origins.

The heritability of feed efficiency as plotted in Fig. 2.25 shows a much more stable pattern than for either feed intake or weight gain. Heritabilities range from a minimum 0.126 $\pm$ 0.07 for the period 24 - 30 days of age to a maximum of 0.332 $\pm$ 0.102 for the following period from 30 to 36 days.

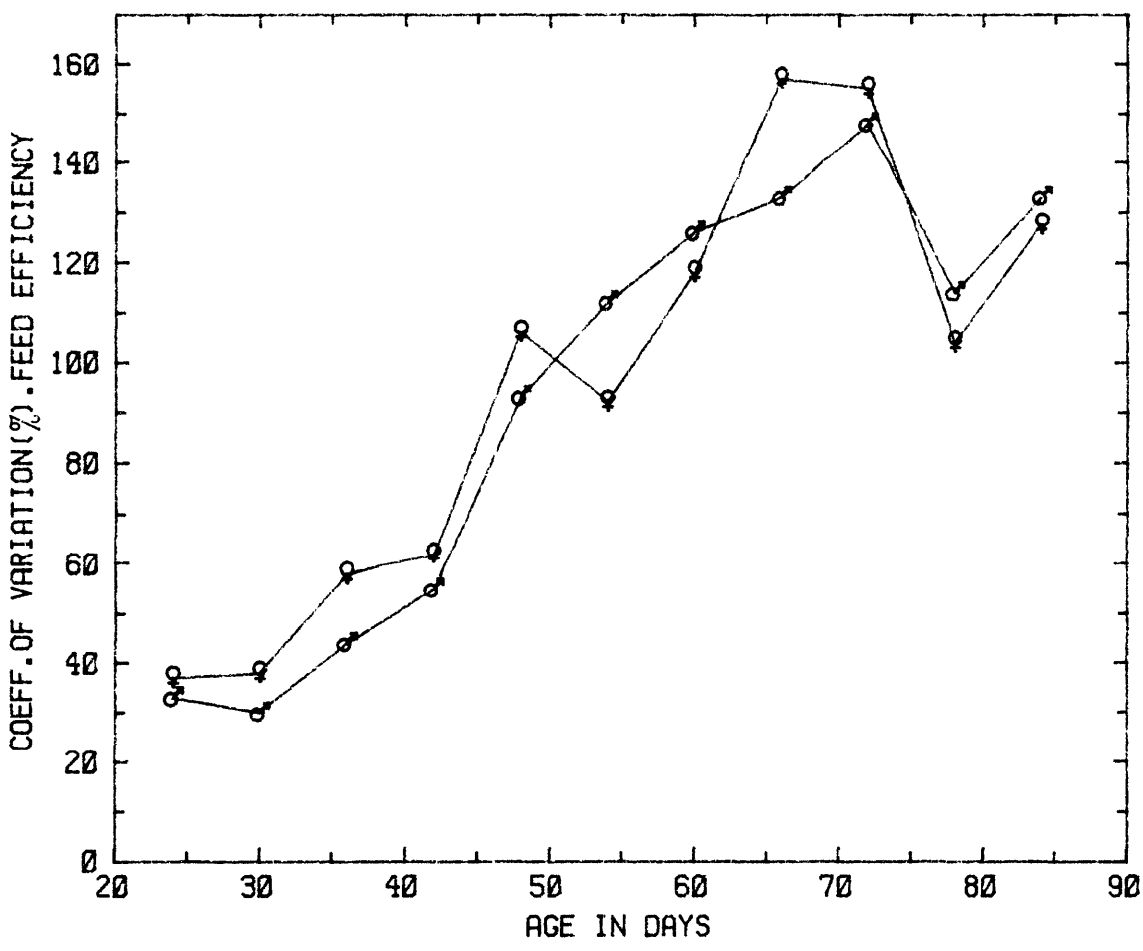

Figure 2.23: Phenotypic coefficients of variation for feed efficiency.

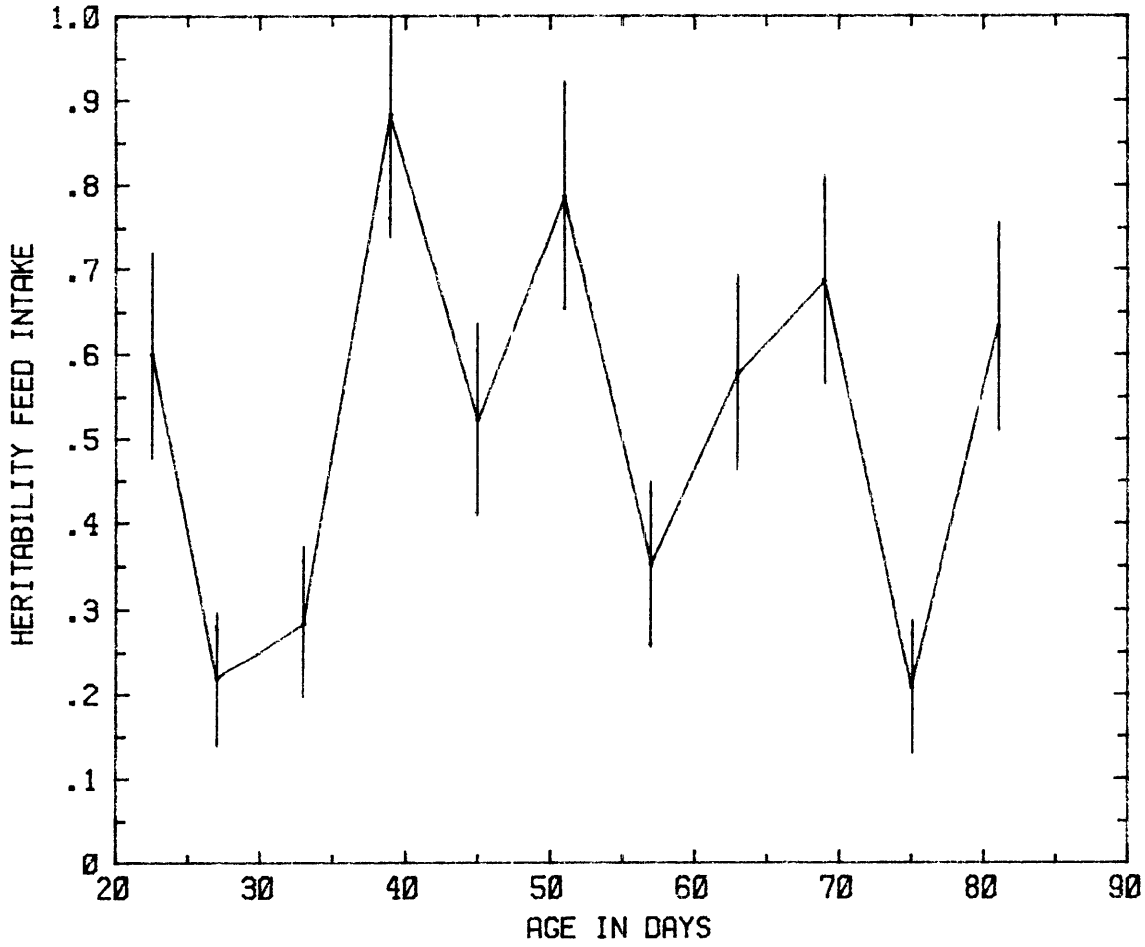

Figure 2.24: Heritabilities (and errors) for feed intake from 21 - 84 days.

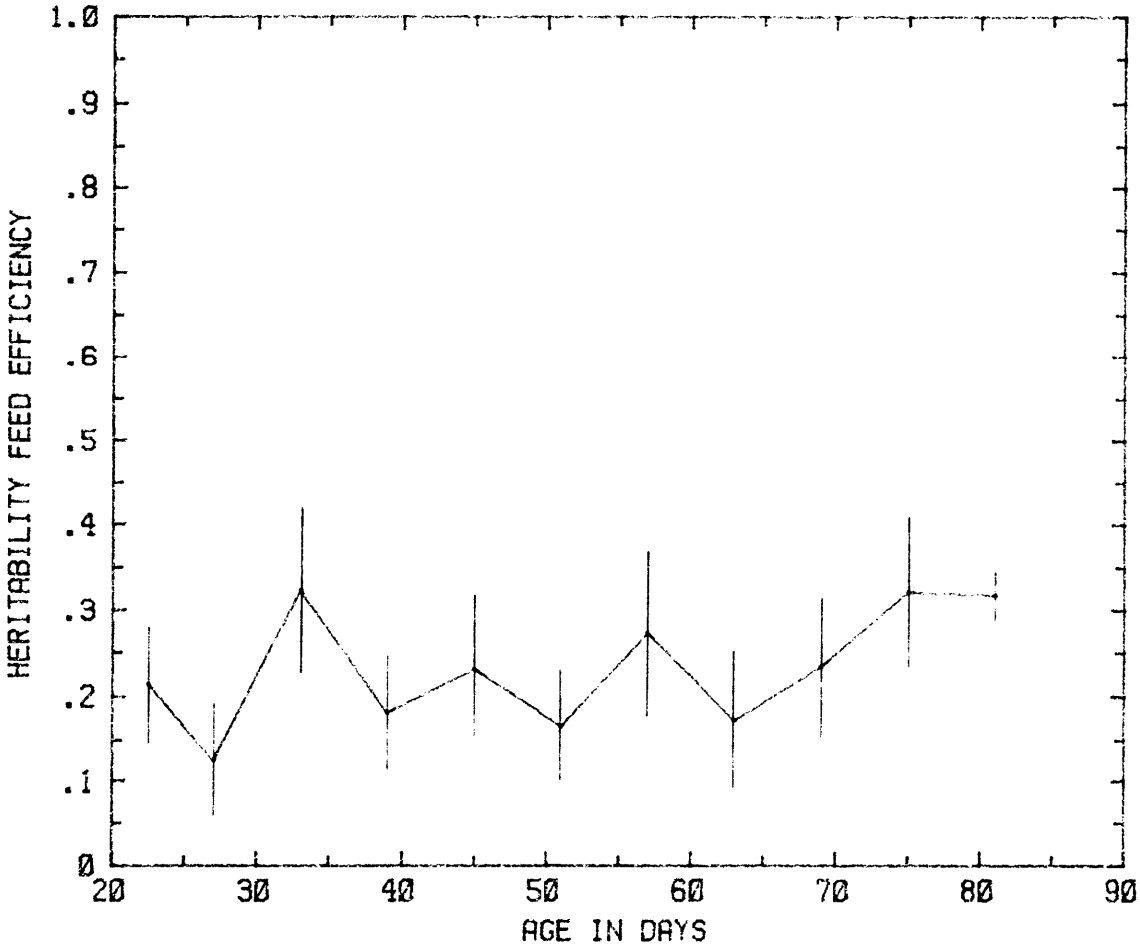

Figure 2.25: Heritabilities (and errors) for feed efficiency.

2.3.10 Associations Between Weight, Cumulative Food Consumed and Feed Efficiency

In Fig. 2.26, feed efficiency and body weight are plotted together. The male mice are more efficient than the females at all comparable body weights. Feed efficiency as a function of body weight declines as body weight increases, as is expected. When feed efficiency is plotted against fraction of maturity (Fig. 2.27), the pattern is similar but the dichotomy is not as great. This is partly due to the problem of a specific end-point in fraction of maturity calculations. But, the plot does illustrate that when compared at similar fractions of maturity, and therefore presumably similar physiological ages, males are mostly more efficient than females and never less efficient.

In Fig. 2.28, weights for males and females are plotted against cumulative food consumed. The graph illustrates the 'law of diminishing returns', or a negative exponential relationship between the two variables. The graph clearly indicates that males are better converters of food, because at any fixed level of food consumption, males have attained a higher weight. Females have higher maintenance costs than males. This may be related to higher protein turnover or heat loss, or the onset of fat deposition at an earlier fraction of maturity. Webster (1977) has suggested that when compared on a weight basis, one unit of fat is five to seven times more expensive energetically than lean tissue to deposit, possibly indicating that females were depositing more fat than males.

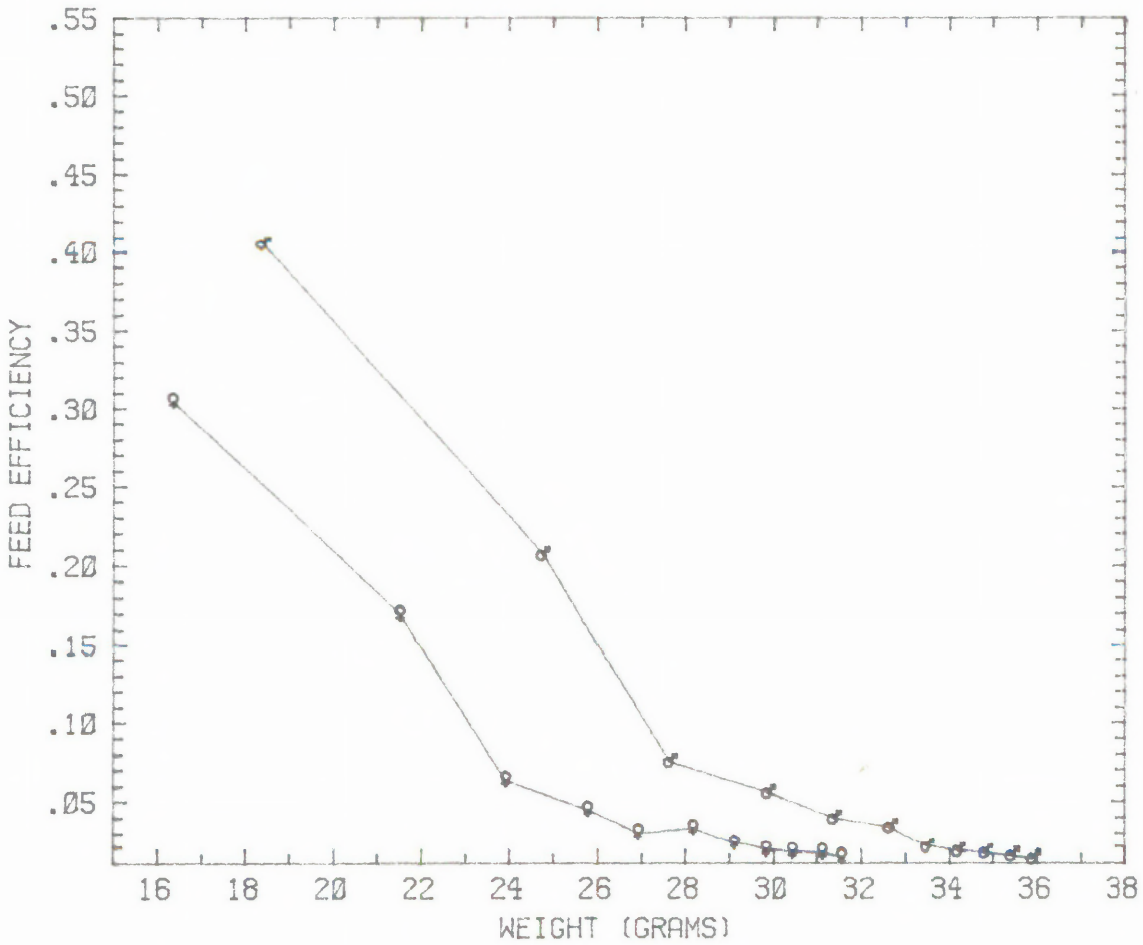

Figure 2.26: Feed Efficiency Versus Body Weight for Males and Females.

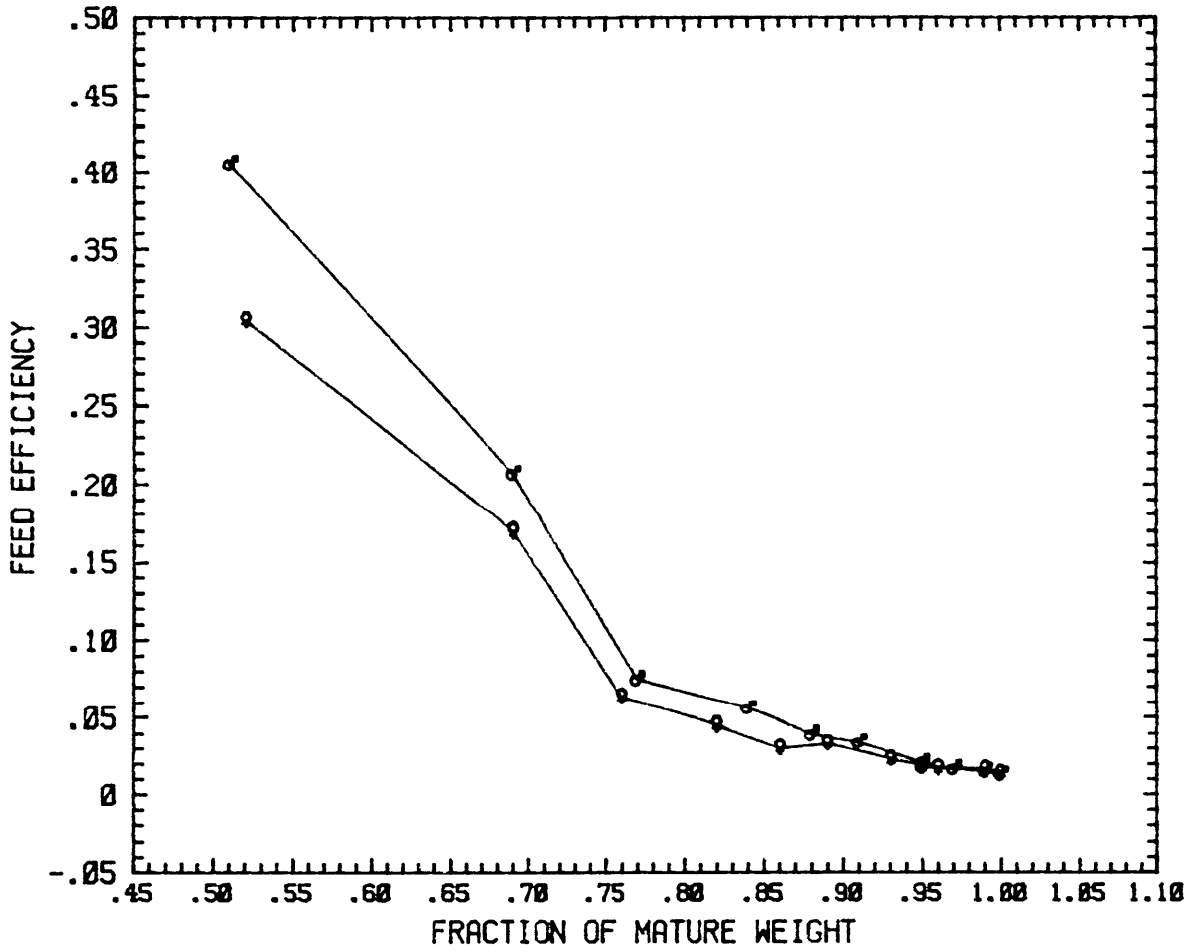

Figure 2.27: Feed efficiency versus fraction of maturity for males and females.

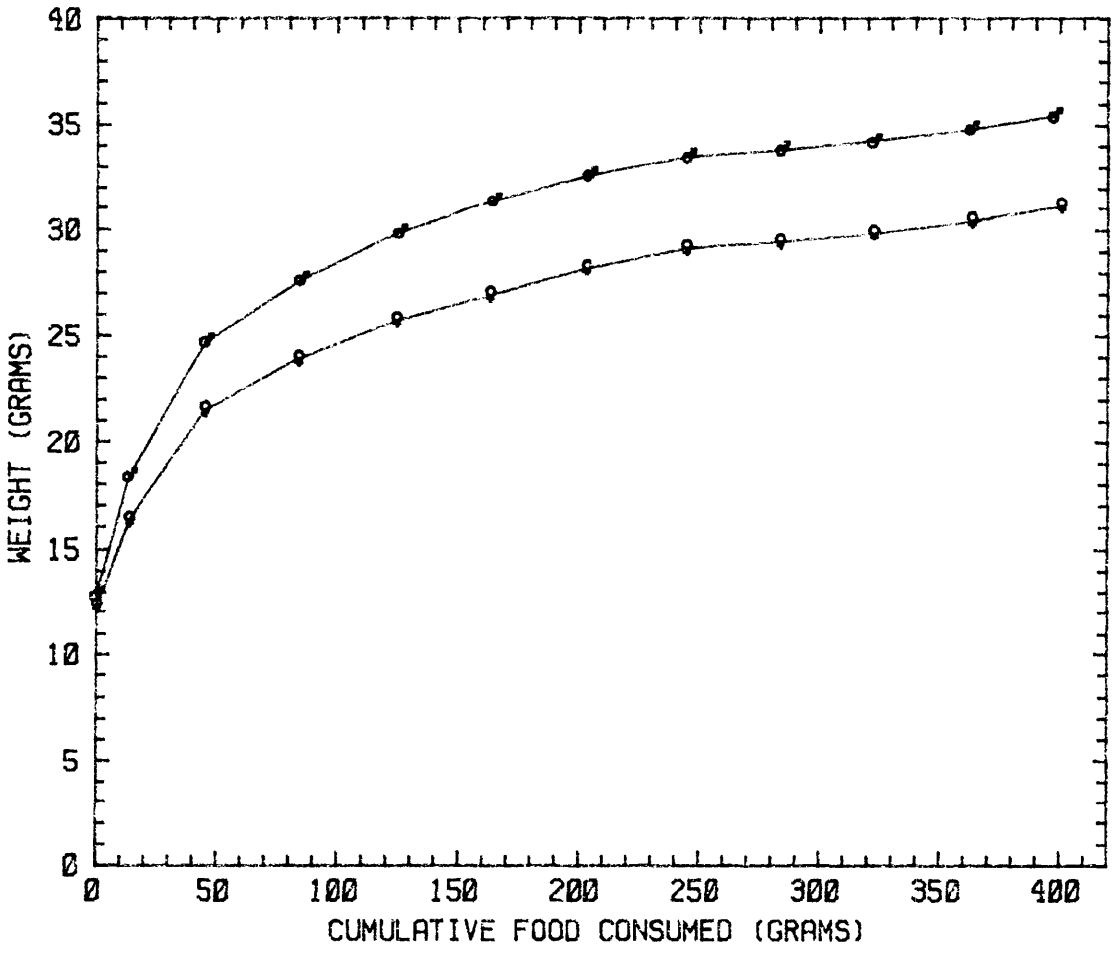

Figure 2.28: Weight plotted against cumulative food consumed, 21 - 84 days.

2.3.11 Phenotypic and Genetic Correlations

a) Weights from Birth to 84 Days.

The phenotypic and genetic correlations (and standard errors) are shown in Table 2.5. All phenotypic correlations between weights are positive, although the more removed two weights are chronologically the closer to zero is the correlation; for example, the phenotypic correlations between birth weight and weights at ages older than 30 days are all less than 0.1. This pattern has already been shown in Figures 2.5 and 2.6.

The genetic correlations between weights at various ages follow a similar course. A schematic representation of the relationships between weights at various ages is shown below:

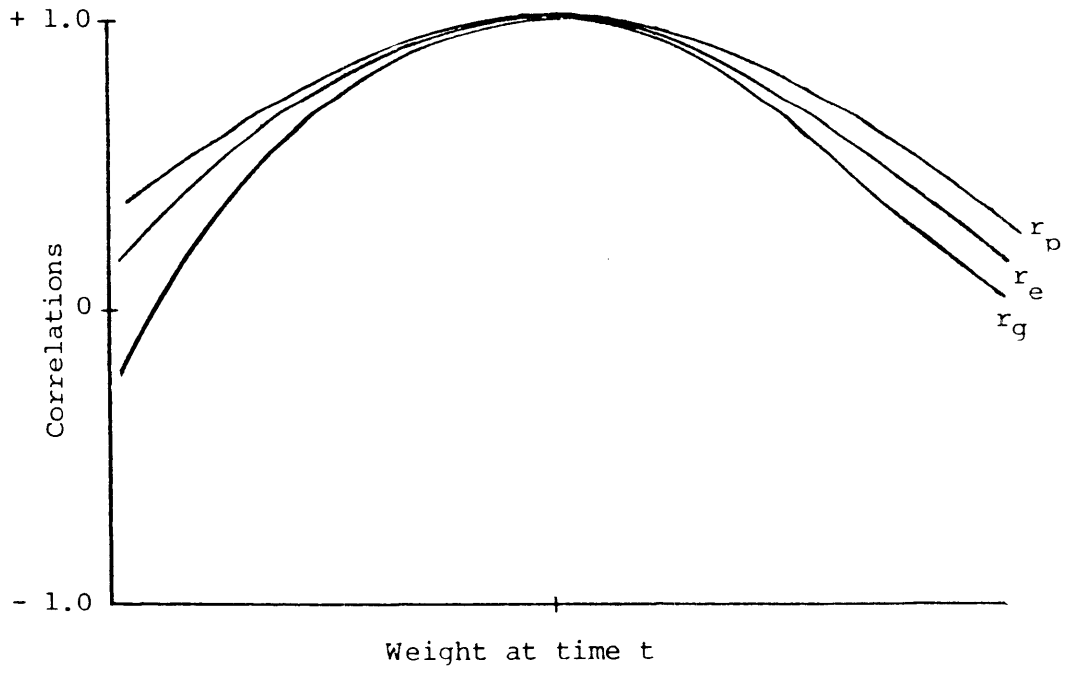

TABLE 2.5

PHENOTYPIC (ABOVE DIAGONAL) AND GENETIC (BELOW DIAGONAL) CORRELATIONS BETWEEN WEIGHTS FROM BIRTH TO 84 DAYS OF AGE

	Age in Days															
	0	6	12	18	21	24	30	36	42	48	54	60	66	72	78	84
0		0.35	0.19	0.17	0.18	0.10	0.11	0.05	0.08	0.03	0.05	0.06	0.06	0.07	0.06	0.05
6	-0.33(.22)		0.48	0.36	0.28	0.24	0.20	0.15	0.16	0.13	0.11	0.12	0.12	0.13	0.13	0.10
12	0.32(.22)	0.55(.15)		0.65	0.54	0.48	0.44	0.40	0.40	0.35	0.33	0.33	0.33	0.32	0.32	0.31
18	0.56(.18)	0.14(.19)	1.12(.04)		0.67	0.54	0.46	0.42	0.41	0.36	0.35	0.32	0.32	0.31	0.31	0.31
21	0.59(.17)	0.44(.16)	0.83(.08)	0.74(.08)		0.55	0.44	0.42	0.40	0.34	0.32	0.31	0.30	0.30	0.30	0.28
24	0.30(.25)	0.16(.23)	0.65(.14)	0.60(.14)	0.53(.14)		0.76	0.62	0.52	0.46	0.42	0.39	0.37	0.32	0.33	0.32
30	-0.33(.22)	0.37(.19)	0.79(.11)	0.76(.10)	0.37(.15)	1.00(.04)		0.82	0.71	0.63	0.60	0.56	0.56	0.50	0.49	0.48
36	-0.31(.21)	0.35(.18)	0.55(.14)	0.61(.12)	0.32(.15)	0.89(.08)	1.01(.02)		0.87	0.78	0.75	0.71	0.70	0.65	0.64	0.63
42	-0.58(.26)	0.48(.22)	0.53(.18)	0.54(.16)	0.25(.19)	0.74(.15)	1.04(.06)	1.03(.04)		0.87	0.83	0.79	0.78	0.74	0.72	0.71
48	-0.65(.21)	0.13(.21)	0.24(.19)	0.15(.17)	-0.01(.18)	0.45(.17)	0.81(.08)	0.86(.06)	1.05(.03)		0.87	0.83	0.82	0.78	0.76	0.73
54	-0.82(.20)	0.12(.21)	0.35(.18)	0.27(.17)	0.07(.18)	0.30(.20)	0.67(.11)	0.79(.07)	0.95(.05)	1.01(.02)		0.90	0.88	0.85	0.82	0.81
60	-0.99(.20)	0.01(.22)	0.08(.21)	0.12(.19)	-0.10(.18)	0.11(.23)	0.54(.15)	0.69(.10)	0.97(.05)	1.04(.03)	1.03(.02)		0.93	0.90	0.87	0.86
66	-0.89(.19)	0.07(.21)	0.27(.18)	0.19(.17)	0.00(.18)	0.28(.20)	0.67(.11)	0.76(.08)	1.01(.05)	1.02(.02)	1.02(.02)	0.99(.01)		0.93	0.91	0.89
72	-0.96(.19)	-0.07(.21)	0.14(.20)	0.05(.19)	-0.07(.18)	-0.06(.23)	0.52(.15)	0.63(.12)	0.89(.08)	0.87(.06)	0.95(.03)	0.94(.03)	0.95(.02)		0.95	0.93
78	-0.78(.19)	-0.12(.20)	0.29(.18)	0.11(.18)	-0.01(.17)	0.01(.22)	0.53(.14)	0.61(.11)	0.89(.08)	0.88(.06)	0.95(.03)	0.93(.03)	0.91(.03)	0.96(.02)		0.97
84	-0.79(.19)	-0.29(.19)	0.24(.18)	0.19(.17)	-0.03(.17)	-0.03(.21)	0.49(.14)	0.58(.12)	0.85(.09)	0.86(.06)	0.92(.04)	0.87(.05)	0.89(.04)	0.97(.02)	0.95(.01)	

This pattern is illustrated by the phenotypic, genetic and environmental correlations between weights at all ages and 42 day weight (Fig. 2.29). The curves all follow a similar pattern, reflecting the basic part-whole relationship between weights at various ages. The phenotypic expression of a weight at a particular age is governed in part by weights at previous ages. The closer (further) weights are chronologically together (apart) the less (more) genetically and environmentally independent they will be from one another. This has obvious repercussions for any attempt to genetically alter the growth pattern of a population when selection criteria are weights closely allied chronologically.

b) Feed Intakes from 21 to 84 Days of Age.

Phenotypic and genetic correlations between feed intakes over the 21 to 84 day period are shown in Table 2.6, including relationships between the three-week periods.

The genetic correlations between one six-day feed intake period and subsequent periods tend to fluctuate markedly. For example, the genetic correlations between 24 - 30 feed intake and feed intakes from 30 - 36, 36 - 42, 42 - 48, 48 - 54 days were 0.31, 0.43, -0.86 and 0.16 respectively. Similar results for other groups of genetic correlations can be found in Table 2.6. This fluctuating pattern could be related to variation in appetite or simply a function of gut fill and the short measurement periods involved. Examination of the covariance components from the genetic analyses showed considerable fluctuation in both the non-additive genetic covariance and additive genetic covariance between measurements taken over six-day periods.

Figure 2.29: Phenotypic, genetic and environmental correlations between weights at all ages and 42 day weight.

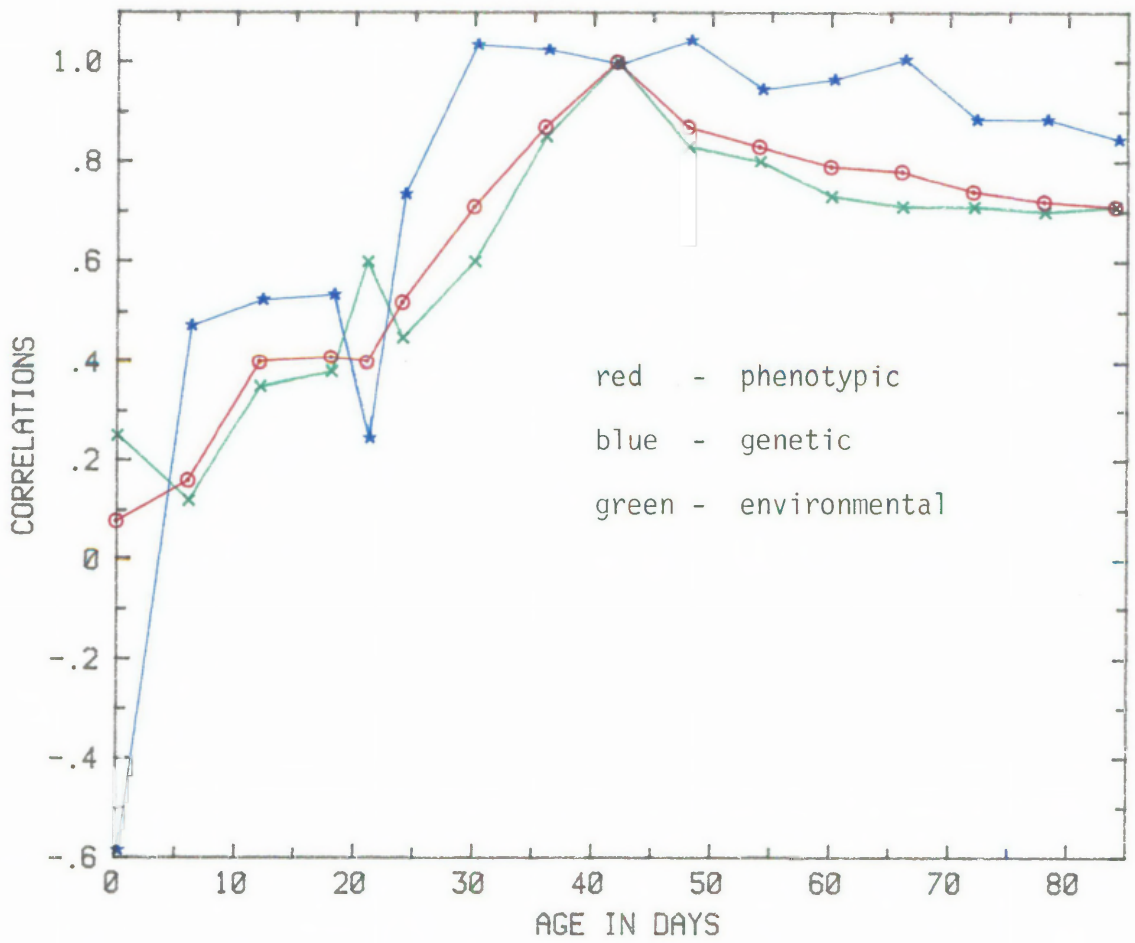

TABLE 2.6

PHENOTYPIC (ABOVE DIAGONAL) AND GENETIC CORRELATIONS (BELOW DIAGONAL) BETWEEN FEED INTAKES FROM 21 TO 84 DAYS OF AGE

Feed Intake Interval	21-24	24-30	30-36	36-42	42-48	48-54	54-60	60-66	66-72	72-78	78-84	21-42	42-63	63-84
21-24		0.69	0.13	0.26	-0.03	0.16	0.21	-0.06	0.17	0.07	0.00	0.62	0.11	0.08
24-30	-0.74(.11)		0.17	0.20	-0.03	0.08	0.09	-0.12	0.15	-0.01	-0.03	0.67	0.03	0.01
30-36	0.60(.16)	0.31(.23)		0.36	0.44	0.40	0.25	0.36	0.38	0.10	[illegible]	0.68	0.48	0.35
36-42	0.84(.08)	0.43(.17)	1.00(.09)		0.23	0.52	0.47	0.18	0.39	0.28	0.16	0.74	0.49	0.36
42-48	-0.17(.17)	-0.86(.18)	-0.16(.19)	-0.27(.15)		0.41	0.31	0.54	0.26	0.24	0.28	0.28	0.77	0.42
48-54	0.69(.11)	0.16(.20)	1.11(.08)	0.82(.06)	0.34(.14)		0.58	0.38	0.57	0.35	0.29	0.47	0.81	0.55
54-60	0.94(.10)	-0.28(.23)	0.77(.15)	0.88(.07)	0.45(.16)	0.79(.08)		0.23	0.41	0.52	0.18	0.40	0.75	0.48
60-66	0.10(.16)	-0.82(.19)	0.23(.18)	-0.01(.15)	0.57(.12)	0.30(.14)	0.11(.18)		0.29	0.25	0.49	0.18	0.63	0.61
66-72	0.43(.14)	0.37(.19)	0.86(.10)	0.75(.08)	-0.34(.15)	0.82(.06)	0.47(.14)	-0.03(.16)		0.30	0.38	0.43	0.51	0.71
72-78	0.60(.19)	-0.88(.25)	0.52(.23)	0.62(.16)	0.87(.15)	0.73(.14)	0.85(.12)	0.28(.20)	0.25(.19)		0.33	0.18	0.46	0.70
78-84	0.31(.15)	0.08(.21)	0.37(.17)	0.11(.15)	0.08(.16)	0.30(.14)	-0.03(.18)	0.53(.12)	0.42(.13)	0.04(.21)		0.16	0.38	0.79
21-42	0.63(.10)	0.40(.16)	0.97(.05)	1.03(.02)	-0.40(.14)	0.88(.06)	0.78(.10)	-0.10(.16)	0.78(.08)	0.39(.19)	0.23(.15)		0.46	0.34
42-63	0.52(.14)	-0.51(.19)	0.68(.12)	0.50(.12)	0.77(.07)	0.84(.05)	0.82(.07)	0.58(.11)	0.35(.14)	0.94(.11)	0.26(.15)	0.43(.13)		0.66
63-84	0.53(.14)	-0.21(.22)	0.77(.13)	0.56(.12)	0.25(.16)	0.79(.08)	0.46(.15)	0.56(.12)	0.73(.08)	0.47(.17)	0.83(.06)	0.55(.13)	0.67(.10)	

c) Genetic and Phenotypic Correlations Between Longer Periods of Growth.

As part of the genetic analyses undertaken in this study, relationships between growth, growth rates, feed intakes and feed efficiency for 3 week intervals were also examined.

The results presented in Table 2.7 suggest that the relationships between these measures are more stable than for shorter 6 day periods reported above. For example, the genetic correlations between feed intake for 21 - 42 days with 42 - 63 days and 63 - 84 days are 0.43 and 0.55 respectively, and between 42 - 63 days and 63 and 84 days is 0.67. There is surprisingly little information available from studies on mouse populations for periods of growth outside the 21 - 42 day range. Genetic relationships between pre-weaning (including 21 day weight) and post-weaning traits tended either to be opposite in sign or, not different from zero when compared with genetic relationships between post-weaning (excluding 21 day weight) traits.

Utilising information from analyses on longer periods of growth expected direct and correlated responses to selection were calculated. Genetic correlations with errors either greater than the estimate itself or close to zero were assumed to be zero (Table 2.8). With this in mind, some results presented in Table 2.9 are

TABLE 2.7

PHENOTYPIC (ABOVE DIAGONAL) AND GENETIC (BELOW DIAGONAL) CORRELATIONS FOR WEIGHTS, AVERAGE GROWTH RATE, FEED INTAKE AND EFFICIENCY

	Weights					Average Growth Rate				Feed Intake			Feed Efficiency		
	0	21	42	63	84	0-21	21-42	42-63	63-84	21-42	42-63	63-84	21-42	42-63	63-84
0		0.18	0.08	0.07	0.05	0.08	-0.05	-0.01	-0.03	0.02	0.04	-0.04	-0.06	-0.03	0.05
21	0.59(.17)		0.40	0.31	0.28	1.00	-0.34	-0.07	-0.03	0.10	0.08	0.05	-0.35	-0.10	0.11
42	-0.58(.26)	0.25(.19)		0.77	0.71	0.40	0.73	-0.16	-0.10	0.23	0.16	0.14	0.50	-0.17	-0.01
63	-1.05(.21)	-0.13(.19)	0.90(.07)		0.87	0.30	0.56	0.51	-0.23	0.10	0.19	0.17	0.43	0.41	-0.01
84	-0.79(.19)	-0.03(.17)	0.85(.09)	0.92(.04)		0.28	0.51	0.40	0.28	0.13	0.20	0.20	0.38	0.33	-0.07
0-21	0.39(.20)	1.00(.001)	0.26(.19)	-0.07(.19)	0.03(.17)		-0.34	-0.06	-0.03	0.10	0.08	0.06	-0.35	-0.10	0.10
21-42	-0.86(.20)	-0.73(.15)	0.51(.15)	0.73(.11)	0.58(.12)	-0.70(.15)		-0.11	-0.07	0.17	0.11	0.11	0.80	-0.10	-0.09
42-63	-1.18(.30)	-0.61(.22)	0.19(.30)	0.64(.18)	0.57(.18)	-0.67(.25)	0.88(.28)		-0.22	-0.15	0.08	0.07	-0.01	0.86	-0.01
63-84	0.06(.24)	0.19(.18)	0.33(.23)	0.34(.22)	0.70(.13)	0.17(.18)	0.12(.20)	0.22(.30)		0.06	0.01	0.10	-0.10	-0.14	-0.11
21-42	-0.56(.19)	0.22(.15)	0.99(.12)	0.47(.17)	0.52(.14)	0.26(.15)	0.50(.14)	-0.61(.23)	0.37(.16)		0.46	0.34	-0.45	-0.27	-0.04
42-63	-0.17(.21)	-0.12(.16)	0.31(.19)	0.13(.19)	0.25(.16)	-0.13(.16)	0.32(.16)	-0.23(.22)	0.36(.17)	0.43(.13)		0.66	-0.16	-0.19	0.02
63-84	-0.81(.20)	-0.05(.16)	0.33(.20)	0.22(.19)	0.42(.15)	-0.01(.16)	0.27(.16)	-0.07(.22)	0.57(.15)	0.55(.13)	0.67(.10)		-0.06	-0.07	-0.15
21-42	-0.49(.24)	-0.96(.16)	-0.18(.23)	0.48(.17)	0.25(.18)	-0.95(.16)	0.72(.09)	1.25(.25)	-0.26(.21)	-0.25(.19)	0.05(.19)	0.06(.19)		0.03	0.05
42-63	-0.97(.24)	-0.34(.19)	0.26(.26)	0.69(.15)	0.53(.16)	-0.30(.19)	0.48(.19)	0.99(.04)	0.02(.21)	-0.50(.19)	-0.44(.19)	-0.12(.20)	0.87(.22)		-0.03
63-84	0.24(.25)	0.19(.18)	0.30(.24)	0.30(.22)	-0.33(.20)	0.19(.18)	0.04(.20)	0.13(.27)	-1.26(.18)	-0.18(.19)	0.35(.18)	-0.46(.19)	-0.14(.18)	-0.14(.20)	

TABLE 2.8

HERITABILITIES AND GENETIC CORRELATIONS BETWEEN GROWTH TRAITS AND FEED EFFICIENCIES

		Birth to 3 Weeks					3 Weeks to 6 Weeks					6 Weeks to 9 Weeks					9 Weeks to 12 Weeks				
		AGR	AMR	RGR	Bth Wt	3 Wk Wt	AGR	AMR	RGR	6 Wk Wt	Feed Eff.	AGR	AMR	RGR	9 Wk Wt	Feed Eff.	AGR	AMR	RGR	12 wk Wt	Feed Eff.
Birth to 3 weeks	AGR	0.65	0.91	0.93	0.39	1.00	-0.70	-0.88	-0.95	0.26	-0.95	-0.56	-0.56	-0.68	-0.22	-0.30	0.19	0.23	0.24	0.0	0.19
	AMR		0.81	0.67	0.69	0.93	-0.87	-0.82	-0.97	0.0	-0.95	-0.76	-0.7	-0.82	-0.43	-0.51	0.0	0.0	0.0	-0.38	0.0
	RGR			0.39	0.0	0.91	-0.35	0.93	-0.73	0.64	-0.79	0.0	0.0	0.0	0.48	0.0	0.24	0.0	0.0	0.47	0.0
	Bth Wt				0.19	0.43	-0.86	-0.54	-0.66	-0.68	-0.49	-1.18	-0.92	-0.96	-1.12	-0.97	0.0	0.0	0.0	-0.79	0.0
	3 wk Wt					0.66	-0.73	-0.89	-0.96	0.25	-0.96	-0.72	-0.60	-0.72	0.0	-0.34	0.19	0.23	0.24	0.0	0.19
3 to 6 weeks	AGR						0.48	0.85	0.90	0.49	0.80	0.13	0.55	0.61	0.73	0.48	0.0	0.0	0.0	0.58	0.0
	AMR							0.43	0.93	0.0	0.73	0.51	0.50	0.55	0.32	0.28	-0.43	-0.50	0.51	0.0	0.0
	RGR								0.71	0.0	0.87	0.71	0.67	0.76	0.40	0.45	0.0	0.0	-0.21	0.25	0.0
	6 wk Wt									0.22	-0.18	0.0	0.0	0.61	0.87	0.26	0.33	0.0	0.0	0.81	0.30
	Feed Eff.										0.32	1.25	1.21	1.08	0.48	0.93	-0.26	-0.30	-0.35	0.25	0.23
6 to 9 weeks	AGR											0.48	0.97	0.97	0.64	0.99	0.0	0.0	0.0	0.57	0.0
	AMR												0.13	0.98	0.50	0.99	0.0	0.0	0.0	0.37	0.0
	RGR													0.12	0.46	0.99	0.0	0.0	0.0	0.42	0.0
	9 wk Wt														0.28	0.69	0.34	0.0	0.0	0.94	0.30
	Feed Eff.															0.27	0.0	0.0	0.0	0.53	0.0
9 to 12 weeks	AGR																0.36	1.00	1.00	0.70	-1.26
	AMR																	0.33	1.00	0.88	-1.09
	RGR																		0.29	0.86	-1.06
	12 wk Wt																			0.47	-0.33
	Feed Eff.																				0.29

TABLE 2.9

EXPECTED DIRECT AND CORRELATED RESPONSES TO SELECTION FOR WEIGHTS AND GROWTH AND MATURING RATES

Responses, % of Initial Mean

Selection Criteria	Birth to 3 weeks AGR	AMR	RGR	Birth Wt.	3 wk.wt.	3 to 6 weeks AGR	AMR	RGR	6 wk.wt.	F. Effic.
Birth to 3 weeks										
AGR, gms d^{-1}	6.25	5.97	2.9	0.61	5.35	-2.71	-3.07	-5.49	0.47	-2.47
AMR, % A	7.78	9.55	2.73	1.40	6.53	-4.42	-3.75	-7.34	0.0	-3.24
RGR	2.63	2.12	2.18	0.0	2.12	-0.59	1.4	-1.83	0.5	-0.89
Birth Wt, gms	1.30	2.56	0.0	1.81	1.17	-1.70	-0.96	-1.94	-0.63	-0.65
3 to 6 weeks										
3 wk.wt. gms	5.88	6.11	4.12	1.37	5.93	-2.55	-2.8	-5.0	0.36	-2.25
AGR	-6.99	-9.71	-2.69	-4.67	-7.36	8.57	4.54	7.96	1.35	3.19
AMR	-5.81	-6.04	4.70	-1.94	-5.93	4.81	5.37	5.45	0.0	1.92
RGR	-4.58	-5.22	-2.71	-1.73	-4.67	3.72	3.66	5.05	0.0	1.67
6 wk. wt.gms	1.07	0.0	2.00	-1.51	0.91	1.72	0.0	0.0	2.4	-0.29
Feed efficiency	-8.02	-9.16	-5.15	-2.30	-8.37	5.93	5.13	7.87	-0.91	6.08
6 to 9 weeks										
AGR	-13.98	-20.82	0.0	-13.33	-15.09	2.74	10.16	18.14	0.0	17.26
AMR	-7.08	-0.89	0.0	-6.32	-7.66	5.97	5.15	8.8	0.0	8.90
RGR	-8.58	-11.55	0.0	-6.58	-9.16	6.60	5.65	10.05	6.46	8.88
9 wk. wt.gms	-0.97	-2.12	1.63	-2.41	0.0	2.77	1.15	1.86	0.0	1.5
Feed efficiency	-5.12	-9.73	0.0	-9.00	-9.00	7.04	3.82	8.05	3.0	11.2
9 to 12 weeks										
AGR	5.80	0.0	5.64	0.0	5.86	0.0	-10.7	0.0	5.91	-5.59
AMR	6.94	0.0	0.0	0.0	7.00	0.0	-12.28	0.0	0.0	-6.37
RGR	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
12 wk. wt.gms	0.0	-2.28	1.94	-2.40	0.0	2.68	0.0	1.41	2.55	0.95
Feed efficiency	8.17	0.0	0.0	0.0	8.24	0.0	0.0	0.0	7.58	6.96
Initial Mean	0.523	0.016	0.099	1.559	12.55	0.728	0.022	0.038	27.85	0.123

Responses for a single generation of selection with a standardised selection differential of 1.0

Average Growth Rate (AGR), Absolute Maturity Rate (AMR) and Relative Growth Rate (RGR) were computed as average daily change in weight, degree of maturity and ln weights over the specific time period.

TABLE 2.9 (cont.)

Selection Criteria	6 to 9 weeks AGR	AMR	RGR	9 wk.wt.	F.Effic.	9 to 12 weeks AGR	AMR	RGR	12 wk.wt.	F.Effic.
Birth to 3 weeks										
AGR	-2.21	-0.6	-0.68	-0.49	-0.66	0.55	0.60	0.56	0.0	0.44
AMR	-3.86	-0.98	-1.07	-1.26	-1.48	0.0	0.0	0.0	-1.87	0.0
RGR	0.0	0.0	0.0	0.47	0.0	0.3	0.0	0.0	0.77	0.0
Birth Wt, gms	-1.98	-0.5	-0.49	-1.15	-1.10	0.0	0.0	0.0	-1.57	0.0
3 to 6 weeks										
3 wk. wt. gms	-2.13	-0.58	-0.65	0.0	-0.68	0.49	0.54	0.50	0.00	0.40
AGR	0.77	0.90	0.93	2.51	1.63	0.0	0.0	0.0	3.34	0.0
AMR	2.00	0.54	0.55	0.73	0.62	-1.25	-1.33	1.20	0.0	0.0
RGR	2.02	0.53	0.56	0.66	0.74	0.0	0.0	-0.36	0.69	0.0
6 wk.wt. gms	0.0	0.0	0.55	0.00	0.00	0.6	0.0	0.0	1.91	0.44
Feed efficiency	5.13	1.41	1.32	1.44	2.73	-0.99	-1.04	-1.08	1.25	0.70
6 to 9 weeks										
AGR	21.05	3.89	3.63	5.41	8.25	0.0	0.0	0.0	8.06	0.0
AMR	10.53	0.0	1.93	4.29	4.17	5.5	0.0	0.0	2.71	0.0
RGR	10.50	5.68	5.49	1.99	4.24	0.0	0.0	0.0	3.05	0.0
9 wk. wt. gms	2.43	1.96	0.88	2.89	1.04	0.67	0.0	0.0	2.32	0.47
Feed efficiency	14.51	7.47	7.35	7.71	11.09	0.0	0.0	0.0	5.22	0.0
9 to 12 weeks										
AGR	0.0	13.6	0.0	6.85	0.0	22.58	12.32	10.80	12.37	-10.84
AMR	0.0	0.0	0.0	0.0	0.0	22.29	21.33	10.78	8.53	-10.70
RGR	0.0	0.0	0.0	0.0	0.0	21.32	20.60	19.40	10.07	-10.34
12 wk. wt. gms	2.63	0.9	0.98	3.20	1.85	2.79	1.86	2.14	4.55	-0.63
Feed Efficiency	0.0	0.0	0.0	8.43	0.0	-31.77	-30.4	-28.62	-12.00	28.52
Initial Mean	0.180	.005	.006	31.64	0.028	.098	.003	.003	33.686	0.044

Responses for a single generation of selection with a standardised selection differential of 1.0

Average Growth Rate (AGR), Absolute Maturity Rate (AMR) and Relative Growth Rate (RGR) were computed as average daily change in weight, degree of maturity and ln weights over the specific time period.

to be treated with caution but may offer a guide to further discussion.

DISCUSSION

Pre-Weaning Growth

Information from the analyses of weight and measures of growth rate, presented here and in Chapter 4, indicated there could have been considerable maternal influences on pre-weaning growth. A decline in the phenotypic variances up to 12 days of age could have been associated with the attempted standardisation of the maternal environment. However, after 12 days, differences between individuals had become large and the phenotypic variance rose rapidly prior to weaning. In some instances, litter numbers were very large (greater than 18 per litter). Standardisation of these litters may have allowed for a brief period of compensation as smaller mice (born in large litters) gained weight faster than heavier mice. Noticeably, growth rates over the 12 day period from birth decreased, suggesting that the food supply, milk, may have been limited. As mentioned previously, a number of mice were observed eating feed made available to the dam prior to weaning. This could have caused large differences in the role of the maternal environment and possible carryover effects post-weaning between full-sibs. This suggestion was borne out in the growth rate measures. Relative growth rates, particularly for males, had begun to increase rapidly prior to weaning.

The additive genetic variance, as a proportion of the phenotypic variance, continues to increase throughout the pre-weaning

growth phase. This was against the background of fluctuating phenotypic variances resulting in increasing estimates of heritability of body weight up to 21 days of age. The extremely high estimate for 21 day body weight (0.66) is difficult to reconcile with estimates from other studies. Frahm and Brown (1975) gave a figure of 0.17 $\pm$ 0.01 and Hetzel (1978) a value of 0.11 $\pm$ 0.08 for 21 day body weight.

Post-Weaning Growth

The pattern of growth post-weaning appeared to follow the 'classical sigmoidal curve'. Body weight continued to increase, but at a decreasing rate as animals tended toward their respective asymptotes. Following the erratic pattern of growth prior to 30 days of age, biometric relationships between weights and weight gains stabilised. This was reflected in the correlations between consecutive weights after 30 days of age, where phenotypic correlations were all greater than 0.9.

The period of growth from 21 to 30 days of age may be associated with compensatory growth according to the criteria described by both Monteiro and Falconer (1966) and Grossman (1969). Monteiro and Falconer suggested that compensation could be associated with a decrease in variance as was reported. Grossman suggested that compensation could be characterised by either a decrease in variance or a negative correlation between body weights and gain to subsequent body weight, i.e. the necessary condition for a negative correlation being;

$$r_{W_{t-1}, W_t} \sigma_{W_t} < \sigma_{W_{t-1}}$$

where W_t = 30 day weight

W_{t-1} = 24 day weight

r_{W_{t-1}, W_t} = correlation between 24 and 30 day weights

σ_{W_t} = standard deviation of weight at 30 days

$\sigma_{W_{t-1}}$ = standard deviation of weight at 24 days.

Substituting the respective values into the relational equation we have

$$(0.757)\ (3.5443) < 4.01223$$

$$2.6830 < 4.01223$$

Thus, as the condition for a negative correlation between weight at 24 days and subsequent gain exists, and the variance also decreased for weights at the two ages, it is reasonable to conclude that compensatory growth had occurred. The negative correlation indicates that lighter (heavier) individuals gain more (less) weight during the six day period. The term compensatory growth can be considered misleading when examining the total growth pattern of an individual. Rather than animals undergoing a compensatory growth phase relative to other individuals, they may be merely following a different growth trajectory to obtain similar mature weights. This may be particularly relevant when selection is to be undertaken to achieve increased weight gains or body weights at

particular ages. However, compensatory growth should be considered to be a descriptor of a group of individuals, not a single individual, when all animals are being fed *ad libitum*.

Using standardised growth measures, such as degree of maturity, showed that the mice considered in this study attained very high degrees of maturity at young ages, especially when compared with results from selected populations. For instance: Roberts (1981) and Parratt *et al.* (1982) reported results for the Q selection lines established by Falconer at Edinburgh. Male mice in the high, low and control lines had achieved estimated percentages of mature weight of 37.0%, 36.0%, 35.6% for 21 day weight, but only 63.9%, 57.3% and 52.2% for 42 day weight. Mature weight was estimated by the mean asymptote from fitting a Gompertz equation to each individual's weekly weights from 3 to 52 weeks of age. If 84 day weights were used as the estimated mature weight, the fraction of maturity for the three lines at 21 and 42 days of age were 40.2% and 69.9% for the large line, 42.2% and 67.33% for the small line, and 46.1% and 67.5% for the control line.

Re-analysis of Hetzel's (1978) data from a sample of the same mouse population as used in this study shows the same maturity pattern. Weights up to 13 weeks of age were available on a limited data set originally used for body composition studies. Fractions of maturity at 21 and 42 days, after seven generations of selection on *ad libitum* feed for weight gain between 3 and 6 weeks, were 38.6% and 82.0% respectively. Values for the control line were 44.8% and 85.1% at 21 and 42 days.

The higher fractions of maturity attained, by the individuals

in this study, may explain the lack of consistency between the heritabilities, and the genetic and phenotypic correlations for characters reported here when compared with estimates on similar characters in the literature. Comparisons of individuals at different levels of maturity could lead to erroneous interpretations of physiological and biochemical phenomena. Parks (1982) and Taylor (1982) have suggested alternative approaches for standardising the growth curves of species, breed and individuals when making phenotypic and genetic comparisons. Better approaches rely upon estimates of mature age body weight and for Parks' approach an estimate of mature feed intake.

Most selection studies in mice have concentrated on the period from 21 to 42 days of age. Phenotypic correlations were similar in direction but not in magnitude to those observed in other studies (Frahm and Brown, 1975; Eisen, 1977; Hetzel, 1978). As with Hetzel's original study on this base population, genetic correlations differed in both sign and magnitude from other studies over this 3-week growth period. More interesting, however, is the fact that some results for this study differ from those reported by Hetzel. Genetic correlations between gain and either feed intake or 42 day weight were both opposite in sign to Hetzel's results, but similar in size and magnitude to those reported by Jara-Almonte and White (1973), Frahm and Brown (1975) and Eisen (1977). But, as with the study by Hetzel, there was a large negative genetic correlation between 21 day weight and 21 - 42 weight gain. However, a realised genetic correlation of 0.83 was obtained after seven generations of selection for weight gain by Hetzel (1978), compared with his base population experiment value of 0.71.

Genetic correlations between weight gains from 21 - 42 days and 42 - 63 days with feed efficiency over the same periods are consistent with results from other experiments (Sutherland *et al.*, 1970; Timon and Eisen, 1970; Hetzel, 1978; Yuskel, 1978).

Heritabilities for traits post-weaning were not consistent with those found in other studies. This heritability for six week weight (0.22) reported here is exactly half of the value given by Hetzel (1978). Heritability values for average growth rate and feed efficiency, over the period from 3 to 6 weeks, were higher than other estimates reported in the literature for other mouse populations. Within this study, genetic correlations and heritabilities for the three growth rate measures examined were similar when compared for the same time period. Heritabilities generally decreased with age. This is contrary to results from other studies where there have been indications of increases in heritabilities, as animals approach mature weight equilibria and as the environmental variance as a proportion of the total variance decreases. The result found here may be simply an artefact of the variable approaches to estimated mature weights associated with an increased variation in growth rates and fluctuating weights. Grossman (1969) suggested that his results, similar to those here, were due particularly to the specific end-point of the measurement period.

In relation to the combined McCarthy-Roberts model presented in Chapter 1 (Fig. 1.1), the genetic and phenotypic relations between weights, growth rate measures, feed intake and efficiency suggest that selection for weight or weight gain would produce responses similar to the predicted model. Correlated responses (Table 2.9)

for selection on weight gain would result in increased weights at later ages, increased growth rate up to nine weeks and increased efficiency up to nine weeks of age. In unison with increases in growth rate and feed efficiencies, there would be an increase in food consumption. Certainly, in terms of the proposed model, selection at early ages would place emphasis on animals less mature than their chronological contemporaries. Selection at later ages, or over later age intervals, would place an emphasis on increasing mature weights thus decreasing fraction of maturity at earlier ages. Interestingly, if the negative correlations between weights and other growth rate measures with feed efficiency are real, over the period from 9 - 12 weeks, selection for increased growth would decrease feed efficiency. This result would fit within the framework of the proposed model as selection over this age interval would be for individuals that have begun to deposit increasing amounts of fat.

It is apparent from an examination of Table 2.9, if we assume that the genetic correlations between characters are at least of the right sign, that no single trait selection would elicit the desirable changes in the total growth curve discussed in the General Introduction (Chapter 1), with the possible exception of relative growth rate between three and six weeks of age. Because of the part-whole relationships between a number of the variables examined in this chapter, desired changes in the growth curve are often counterbalanced by undesired responses. For instance, with selection to increase 3 to 6 week average growth rate (AGR), the period of highest growth, expected correlated increases would occur in 6, 9 and 12 week weight, but decreases would occur in birth weight and three week weights.

Clearly, there is a need to explore alternatives to selection criteria based on weight or weight gains over restricted time periods if animals with growth patterns of an economically desired form, suggested in Chapter 1, are to be obtained.