

CHAPTER 4

MATERNAL EFFECTS AND PARTITIONING OF THE PHENOTYPIC
VARIANCE FOR GROWTH, FEED INTAKE, FEED EFFICIENCY
AND ESTIMATES OF PARAMETERS OF NONLINEAR GROWTH MODELS

4.1 INTRODUCTION

The maternal influence that a dam has on her offspring may be partitioned into direct genetic effects and indirect components. Direct genetic effects are due to the sample of genes she contributes to her offspring through the eggs. The indirect component is determined by paternal contributions (direct genetic effects from the dam's sire) and the maternal contributions (the maternal environmental effect and the covariance between maternal and genetic effects). Maternal environmental effects can include intra-uterine environmental factors (the prenatal effect) and the dam's mothering ability and milk production (the postnatal environment) (Baker, 1980). These indirect effects are expressed in the phenotype of the offspring as environmental factors in relation to the dam.

Geneticists and animal breeders have been aware for a number of years that maternal effects may bias heritability estimates (Lush, 1945; Dickerson, 1947; Koch and Clark, 1955). Although considerable theoretical research has been undertaken to elucidate the various expectations of the components of variance for maternally affected

characters (Eisen, 1967; Hanrahan, 1976; Hanrahan and Eisen, 1973; Koch, 1972; Willham, 1963, 1972, 1980) little direct application has been attempted to domestic farm species. Recent reviews by Baker (1980), Foulley and Lefort (1978) and Willham (1980) have suggested alternative strategies for utilising maternal components in animal breeding programmes. Of particular importance for consideration in programmes designed to utilise maternal effects, has been the substantial evidence available of a negative genetic correlation between direct genetic and maternal effects. Van Vleck (1976) and Baker (1980) have examined predicted responses to selection when considering the role of a negative genetic correlation between maternal and direct genetic effect. Both concluded there could be considerable long-term advantages in selecting either males or females or both on maternal and direct genetic effects when considering selection for weaning weight. Baker (1980) also suggested that consideration should be given to, when utilising antagonistic selection index procedures, offsetting the undesirable changes associated with negative genetic correlations between the two economically desirable characters, maternal ability and weaning weight.

There have been few reports in the literature of the role of maternal effects on growth, feed intake and efficiency from birth to maturity in either laboratory species or domestic farm animals. No reports appear to be available on the role of maternal effects on parameters of growth models used to describe the weight age relationship or the weight feed intake relationship in animals. As many analyses using growth models include data points prior to weaning, it is essential that some attempt be made to investigate

the extent of variation due to the maternal environment on parameters of growth models. This fact could be of particular importance when considering the rate parameters of the models described in Chapter 3, for example k of the generalised Richards' function and its special cases, or t^* and (AB) of the Parks' function.

The aim of this study was two-fold:

1. to investigate the role of maternal effects on weight, feed intake and feed efficiency from birth to 84 days old in the Quakenbush mouse strain.
2. to study the role of maternal effects on the parameters of Models I to VI considered in Chapter 3.

4.2 MATERIALS AND METHODS

The second group of mice of the three studied was utilised to investigate the role of maternal effects on growth.

4.2.1 Preweaning Growth

The cross-fostering design utilised to enable partitioning of the maternal effects was as suggested by Rutledge *et al.* (1972) and is shown in Table 4.1.

Eighty females and twenty males were taken at random from the unselected line established at the University of New England. Each

TABLE 4.1

CROSS-FOSTERING DESIGN^a

Progeny No.	Cross-foster Dam		
	Dam 1	Dam 2	Dam 3
1	1 ^b	2	3
2	1	2	3
3	2	3	1
4	3	1	2
5	1	2	3
6	1	2	3
7	2	3	1
8	3	1	2

^aAdapted from Rutledge *et al.* (1972).

^bNumbers refer to actual dam number within set.

male was randomly assigned to four females with careful avoidance of full and half sib matings. In no instances were full sib or half sib females allocated to the one sire. Both males and females were 11 - 12 weeks old at joining.

Dams were checked daily and 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 birth weight.

Progeny were sexed and identified by toe-notching. Litters were standardised to 12 for the first 24 hours to help stimulate maximum lactation yields of the dam (Bateman, 1957). Dams were required to have a total of eight offspring after 24 hours to be included in the cross-fostering experiment.

After 24 hours, the litter size was reduced to eight and cross-fostering sets were established between three dams with offspring born in the previous 24 hours. Each dam retained four of her own offspring and received two progeny from each of the other two dams (Table 4.1). Assignment was at random, with the proviso that a male and female were cross-fostered together wherever possible. Of the initial matings, 48 litters satisfied the above design requirements and were arranged into 16 cross-fostered sets. A total of 19 sires were represented in the experiment.

From birth to weaning, litters were housed in individual cages with their natural or cross-foster mother.

Mice were weighed individually at 0, 3, 6, 9, 12, 15, 18 and 21 days of age to the nearest 0.1 gms.

4.2.2 Postweaning Growth

All mice were weaned at 21 days of age and placed in individual cages. Feed was supplied as a finely crushed powder and was available in *ad libitum* quantities at all times. Individual weights and feed intakes were measured at three-day intervals from 21 to 84 days of age to the nearest 0.1 gms.

4.2.3 Statistical Methods

The proposed model and design was based on the assumption that cross-fostering *per se* had no detrimental effect on growth.

Prenatal maternal effects were approximated by comparing body weights at birth; however, separation into environmental and genetic components could not be achieved as they were confounded. The major difference in prenatal environment between litters (as measured by birth-weight) can be attributed to genetic differences between the dams themselves, although these differences are measured as environmental factors in the offspring.

Postnatal maternal effects were calculated by comparing full sib litter-mates with full sib cross-fostered pairs. Since full sib pairs were assigned at random between the three cross-fostered dams, any differences in growth can be regarded as environmental, the dam having the major influence by manipulating the milkflow.

The phenotypic variance can be partitioned in the following manner:

$$\sigma_P^2 = \sigma_{D_A}^2 + \sigma_{D_M}^2 + \sigma_{D_A D_M} + \sigma_c^2 + \sigma_e^2 \quad (\text{Willham, 1963})$$

$\sigma_{D_A}^2$ = the direct additive genetic variance

$\sigma_{D_M}^2$ = the maternal additive genetic variance

$\sigma_{D_A D_M}$ = the direct maternal genetic covariance

σ_c^2 = the common environmental variance = σ_{ec}^2

σ_e^2 = the residual or error variance = σ_{ew}^2

Table 4.2 shows the composition of the genetic covariances between relatives when maternal effects are considered under the above model, and illustrates the expectations.

Due to limitations on degrees of freedom using Harvey's Least Squares and Maximum Likelihood Analysis of Variance (Harvey, 1977), the data were separated into two groups, cross-fostered and non-cross-fostered progeny. The two models utilised to describe the data were:

a) Cross-fostered Model

$$Y_{tijk1} = \mu_t + S_{ti} + C_{tij} + G_{tk} + E_{tijk1}$$

where μ_t is the overall mean for Y_{th} observation in a cross-foster set on the i^{th} individual at time t or over time period t .

S_{ti} is the effect of the i^{th} sire

TABLE 4.2

EXPECTATIONS^a OF CAUSAL COMPONENTS FOR THE
COVARIANCES AMONG RELATIVES CONSIDERED IN THIS STUDY

Relatives Correlated	Causal Components				
	D_A	D_M	$D_A D_M$	c	w
Paternal Half-sibs	$\frac{1}{4}$	0	0	0	0
Full-sibs within sire	$\frac{1}{4}$	1	$\frac{1}{2} + \frac{1}{2}$	1	0
Within Full-sibs	$\frac{1}{2}$	0	0	0	1

^aThe subscripts on the causal components denote

direct additive genetic effects	D_A
additive genetic maternal effects	D_M
covariance of direct additive with	
direct maternal effects	$D_A D_M$
common litter or environmental effects	C
effects not common to full-sibs	W

C_{tij} is the effect of j^{th} cross-foster dam mated to i^{th} sire,

G_{tk} is the effect of the k^{th} sex,

E_{tijk1} is the random error.

b) Non-cross-fostered Model

$$Y_{tijk1} = \mu_t + S_{ti}^* + N_{tij}^* + G_{tk}^* + E_{tijk1}^*$$

the only difference in the terms of two models being that in Model (b) N refers to the natural dam.

As the data were split, to allow the complete analysis, the k coefficients or constants were required to enable the variance components to be equated to their expected mean squares. Grossman and Gall (1968) provides a method for computing the k coefficient matrix. Variance components were obtained by multiplying the inverse of the coefficient matrix by the estimated mean squares.

Substituting the various components of variance into the following equations allowed the partitioning of the total variance into direct genetic, maternal and covariance terms.

$$\sigma_{D_{A+M}}^2 = \sigma_{D_A}^2 + \sigma_{D_M}^2 + 2\sigma_{D_A D_M} \quad (1)$$

where, $\sigma_{D_A}^2$ and $\sigma_{D_M}^2$ are the direct and maternal genetic variances

$\sigma_{D_M}^2$ is estimated from the dam component of variance: cross-fostered progeny

$\sigma_{D_{A+M}}^2$ is estimated from the dam component of variance: non-cross-fostered progeny.

$$\sigma_{D_{A+M}}^2 - \sigma_{D_M}^2 = \sigma_{D_A}^2 + 2\sigma_{D_A D_M} \quad (2)$$

The component of direct genetic effects cannot be separated from the covariance term in equation (2). Assuming equal additive genetic effects are received by the offspring from the sire and dam, four times the sire component of variance ($4\sigma_S^2$) was substituted for $\sigma_{D_A}^2$. Equation (3) provides an estimate of the direct and maternal genetic covariance.

$$\sigma_{D_A D_M} = \frac{\sigma_{D_{A+M}}^2 - \sigma_{D_M}^2 - \sigma_{D_A}^2}{2} \quad (3)$$

$$\text{where, } \sigma_{D_A}^2 = 4\sigma_S^2$$

Substitution of the sire component of variance for the dam component may cause a bias in the estimation of the covariance term, $\sigma_{D_A D_M}$ in equation (3). As the sire component will not exactly equal the dam component, due to the exclusion of the dominance effects, this may result in some bias in the estimates of the covariance. Further problems may arise if we backsolve to obtain an estimate of $\sigma_{D_A}^2$ from equation (2). If the covariance term estimated by equation (3) is negative, then negative estimates of the genetic effects for the dam may be given by equation (2).

The above models and variance/covariance estimations were

applied to weights, feed intake, feed efficiency, and weight gain information collected on the mice between birth and 84 days old. The same models and estimation procedures were applied to the individual parameter estimates obtained for the nonlinear models considered in Chapter 3.

4.3 RESULTS

4.3.1 Comparisons between means of Cross-fostered and Non-Cross-fostered Mice for Weight, Weight Gains, Fraction of Maturity, Feed Intake and Feed Efficiency

Means for bodyweights of cross-fostered and non-cross-fostered mice are presented in Table 4.3. No differences in bodyweights at birth between the two groups ($P < 0.05$) indicated that there had been random allocation of progeny between dams within a cross-foster set. Similar results were found for comparisons between bodyweights at all other ages suggesting there were no significant differences between the groups for maternal influences on individuals pre- and post-weaning.

Comparisons between means for weight gain (Table 4.4) gave one significant result, weight gain of the cross-fostered animals was significantly less ($P < 0.05$) for the period between 42 and 48 days of age. As with bodyweights, no significant differences were observed between fraction of maturity at any age for the cross-fostered and non-cross-fostered (Table 4.5).

Analysis of feed intakes between various ages post-weaning

TABLE 4.3

LEAST SQUARES MEANS AND STANDARD ERRORS FOR WEIGHTS
OF CROSS-FOSTERED AND NON-CROSS-FOSTERED MICE

Age	Non-Cross-Fostered		Cross-Fostered	
	Mean (gms)	Error	Mean (gms)	Error
Birth	1.535	0.022	1.540	0.019
6 day	4.613	0.083	4.510	0.074
12	7.421	0.140	7.315	0.092
18	9.072	0.202	8.973	0.185
21	11.085	0.286	10.975	0.250
24	13.867	0.389	13.693	0.329
30	20.828	0.366	20.778	0.408
36	25.175	0.331	25.417	0.282
42	27.515	0.306	27.657	0.281
48	28.698	0.199	28.522	0.258
54	29.828	0.349	29.806	0.258
60	30.697	0.365	30.788	0.259
66	31.624	0.369	31.550	0.301
72	32.168	0.361	32.104	0.266
78	32.921	0.378	32.845	0.272
84	33.392	0.384	33.278	0.283

TABLE 4.4

LEAST SQUARES MEANS AND STANDARD ERRORS FOR WEIGHT
GAIN OF CROSS-FOSTERED AND NON-CROSS-FOSTERED MICE

Period (Days)	Non-Cross-Fostered		Cross-Fostered	
	Mean (gms)	Error	Mean (gms)	Error
0-6	3.078	0.081	2.969	0.087
6-12	2.808	0.121	2.805	0.062
12-18	1.651	0.126	1.658	0.141
18-21	2.013	0.201	2.001	0.084
21-24	2.781	0.326	2.719	0.123
24-30	6.961	0.216	7.085	0.174
30-36	4.347	0.165	4.640	0.220
36-42	2.340	0.132	2.240	0.136
42-48	1.183	0.136	0.865	0.133
48-54	1.130	0.127	1.285	0.155
54-60	0.869	0.130	0.981	0.084
60-66	0.927	0.108	0.762	0.110
66-72	0.544	0.118	0.554	0.094
72-78	0.753	0.103	0.741	0.091
78-84	0.471	0.081	0.433	0.087

TABLE 4.5

LEAST SQUARES MEANS AND STANDARD ERRORS FOR FRACTION
 OF MATURITY ($\mu = W_t/A$) OF CROSS-FOSTERED AND
 NON-CROSS-FOSTERED MICE

Age	Non-Cross-Fostered		Cross-Fostered	
	Mean (gms)	Error	Mean (gms)	Error
Birth	0.047	0.0009	0.047	0.0009
6	0.138	0.0015	0.139	0.0030
12	0.223	0.0039	0.224	0.0030
18	0.274	0.0056	0.273	0.0067
21	0.335	0.0082	0.335	0.0089
24	0.418	0.0111	0.417	0.0114
30	0.629	0.0093	0.626	0.0139
36	0.763	0.0076	0.759	0.0081
42	0.830	0.0062	0.827	0.0059
48	0.863	0.0062	0.855	0.0068
54	0.899	0.0053	0.890	0.0061
60	0.919	0.0051	0.920	0.0059
66	0.950	0.0046	0.942	0.0052
72	0.963	0.0049	0.960	0.0043
78	0.986	0.0120	0.986	0.0025
84	1.000	0.0000	1.000	0.0000

(Table 4.6) showed significant differences between the two groups for feed intakes over three periods, 60 to 66 days, 72-78 days, and 78-84 days. As the differences in feed intakes were for periods when individuals were nearly at their mature weights and mature feed intakes, these results may reflect random fluctuations in feeding patterns. No significant differences were observed between the cross-fostered and non-cross-fostered mice in feed efficiencies measured over the periods from 21 to 84 days of age (Table 4.7).

4.3.2 Comparisons Between Characteristics of Nonlinear Models Estimated for Cross-fostered and Non-Cross-fostered Mice

The two forms of the Logistic and Gompertz equations (Models I, VII, and II, VIII respectively) and the Parks' equations (Models VIa, VIb, and XI) were fitted to individual growth data available on cross-fostered and non-cross-fostered mice. Least squares means of the parameter estimates and points of inflections for the two groups are presented in Table 4.8. Comparisons between the two groups showed age, at the point of inflection for Models I, II and VIII, and weight, at point of inflection for Model II, were significantly different ($P < 0.05$). However, there were no differences between the parameters involved in calculations of the co-ordinates for the point of inflection.

4.3.3 Components of Variance

a) Variance Components for Bodyweight, Weight Gain, Fraction of Maturity, Feed Intake and Feed Efficiency

Components of variance for bodyweights are plotted in Fig. 4.1.

TABLE 4.6

LEAST SQUARES MEANS AND STANDARD ERRORS FOR FEED
INTAKE OF CROSS-FOSTERED AND NON-CROSS-FOSTERED MICE

Period (Days)	Non-Cross-Fostered		Cross-Fostered	
	Mean (gms)	Error	Mean (gms)	Error
21-24	11.65	0.317	11.59	0.284
24-30	34.24	0.658	34.13	0.696
30-36	41.31	0.503	42.15	0.615
36-42	41.01	0.474	41.31	0.580
42-48	41.20	0.658	42.13	0.621
48-54	41.75	0.501	42.34	0.649
54-60	40.69	0.510	40.20	0.601
60-66	37.67	0.557	38.97	0.668
66-72	39.19	0.719	38.92	1.038
72-78	41.14	0.468	37.73	1.544
78-84	34.81	1.531	30.33	2.204

TABLE 4.7

LEAST SQUARES MEANS AND STANDARD ERRORS FOR FEED
EFFICIENCY OF CROSS-FOSTERED AND NON-CROSS-FOSTERED MICE

Period (Days)	Non-Cross-Fostered		Cross-Fostered	
	Mean (gms)	Error	Mean (gms)	Error
21-24	0.256	0.021	0.235	0.017
24-30	0.216	0.008	0.208	0.011
30-36	0.108	0.004	0.110	0.006
36-42	0.057	0.004	0.054	0.003
42-48	0.027	0.004	0.026	0.003
48-54	0.030	0.003	0.030	0.003
54-60	0.021	0.003	0.024	0.003
60-66	0.025	0.003	0.020	0.003
66-72	0.015	0.003	0.014	0.003
72-78	0.018	0.003	0.020	0.003
78-84	0.014	0.002	0.014	0.002

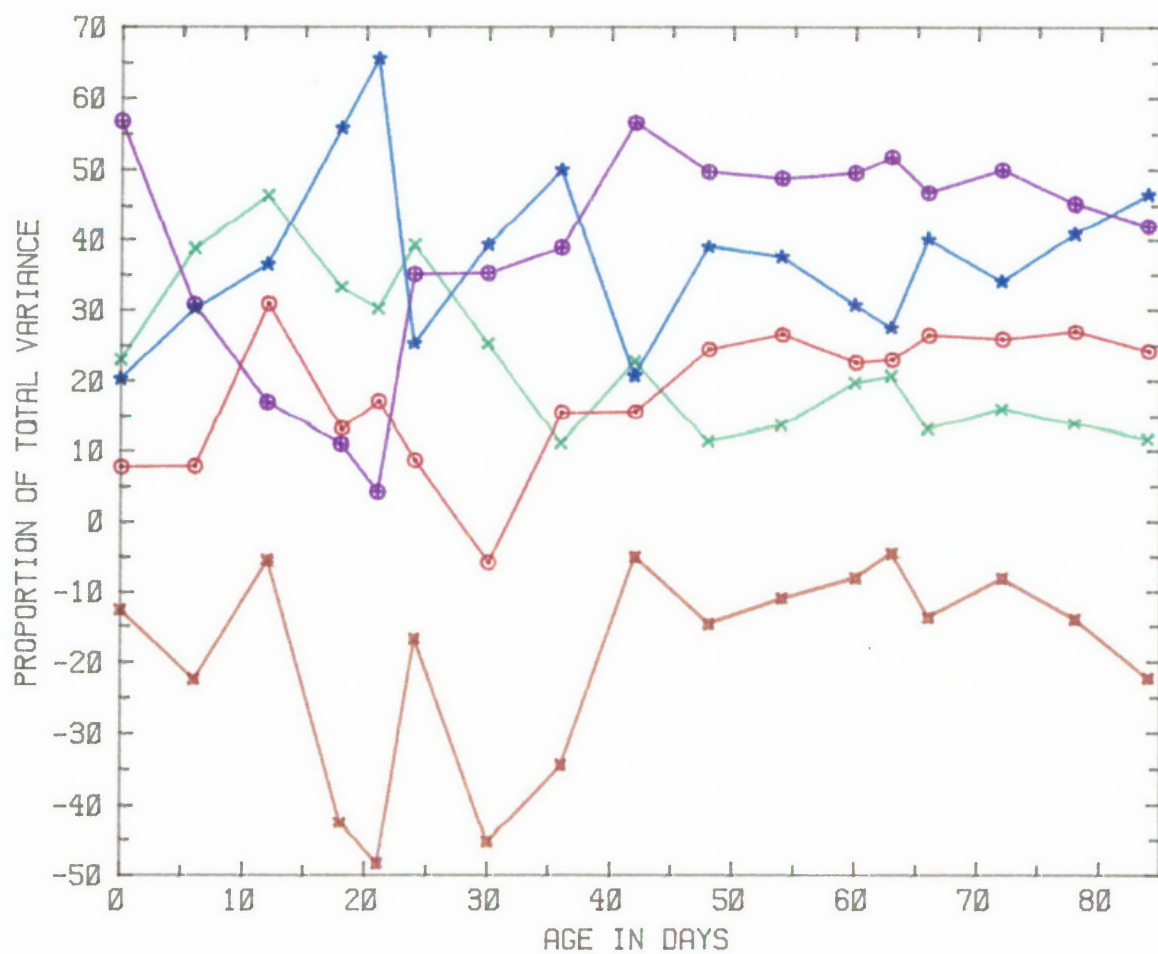
TABLE 4.8

LEAST SQUARES MEANS AND STANDARD ERRORS FOR PARAMETERS
AND POINTS OF INFLECTION OF NONLINEAR MODELS FITTED TO THE
GROWTH DATA OF CROSS-FOSTERED AND NON-CROSS-FOSTERED MICE

Model	Character	Non-Cross-fostered	Cross-fostered
		Mean \pm S.E.	Mean \pm S.E.
Logistic, I	A (gms)	32.095 \pm 0.326	31.898 \pm 0.331
	b	14.505 \pm 0.269	14.407 \pm 0.268
	k	0.107 \pm 0.001	0.109 \pm 0.001
	POI _{WT} (gms)	16.047 \pm 0.163	15.949 \pm 0.165
	POI _{AGE} (days)	25.057 \pm 0.280	24.474 \pm 0.284
Logistic, VII	A	30.929 \pm 0.314	30.567 \pm 0.320
	k	0.128 \pm 0.002	0.129 \pm 0.002
	POI _{WT}	15.465 \pm 0.157	15.284 \pm 0.163
	POI _{AGE}	20.349 \pm 0.262	20.182 \pm 0.235
Gompertz, II	A	35.096 \pm 0.205	35.011 \pm 0.227
	b	3.294 \pm 0.019	3.265 \pm 0.019
	k	0.054 \pm 0.001	0.055 \pm 0.001
	POI _{WT}	13.213 \pm 0.144	12.880 \pm 0.145
	POI _{AGE}	22.080 \pm 0.299	21.514 \pm 0.226
Gompertz, VIII	A	35.918 \pm 0.390	35.666 \pm 0.373
	k	0.057 \pm 0.001	0.058 \pm 0.001
	POI _{WT}	12.880 \pm 0.127	13.121 \pm 0.137
	POI _{AGE}	20.460 \pm 0.300	19.827 \pm 0.316
Parks, VIa	A	37.544 \pm 0.793	37.212 \pm 0.699
	k	0.033 \pm 0.002	0.035 \pm 0.002
	t*	4.709 \pm 0.086	4.700 \pm 0.081
Parks, VIb and XI	A	33.796 \pm 0.381	33.112 \pm 0.327
	(AB)	0.297 \pm 0.029	0.288 \pm 0.031
	C	6.801 \pm 0.113	6.772 \pm 0.126
	t*	4.386 \pm 0.430	4.275 \pm 0.412
	T ₀	5.018 \pm 0.112	4.969 \pm 0.110

Figure 4.1: Components of variation as the percent they represent of the total variance for bodyweight.

V_A = blue V_{ew} = purple
 V_M = red Cov_{AM} = brown
 V_{ec} = green



By definition, the variance due to direct genetic effects (V_A), variance due to common environment (V_{ec}) and the within group error component of variance (V_{ew}) sum to 100%. The maternal variance (V_M) and the covariance between maternal and genetic effects (Cov_{AM}) were estimated by the methods presented earlier. The additive variance after reaching a peak at 21 days of age remained relatively stable throughout the measurement period. Maternal environmental effects, measured by V_{ec} , rose to a peak at 12 days of age. After weaning V_{ec} decreased steadily and accounted for less than 20% of the total variation for most post-weaning traits. This concurred with results reported in a number of other studies. Eisen (1976) reviewed results from several experiments suggesting that postnatal maternal effects accounted for between 50 and 70% of the total variation in bodyweight between 12 and 14 days of age. The results presented here suggest that the variance due to direct maternal effects (V_M) was 31% for weight at this age. However, as discussed earlier, since the covariance term was negative throughout the measurement period, caution must be used in the interpretation of the role of the maternal genetic variance. Except for the 12 day and 30 day weight measurements, maternal genetic variances remained between 5 and 25%.

The residual expressed as the within litter component (V_{ew}) decreased pre-weaning as the additive genetic component increased. After weaning the V_{ew} component increased rapidly so as to represent 56% of the total variance by 42 days of age. For the period from 42 to 84 days of age V_{ew} remained high and always represented more than 40% of the total variation.

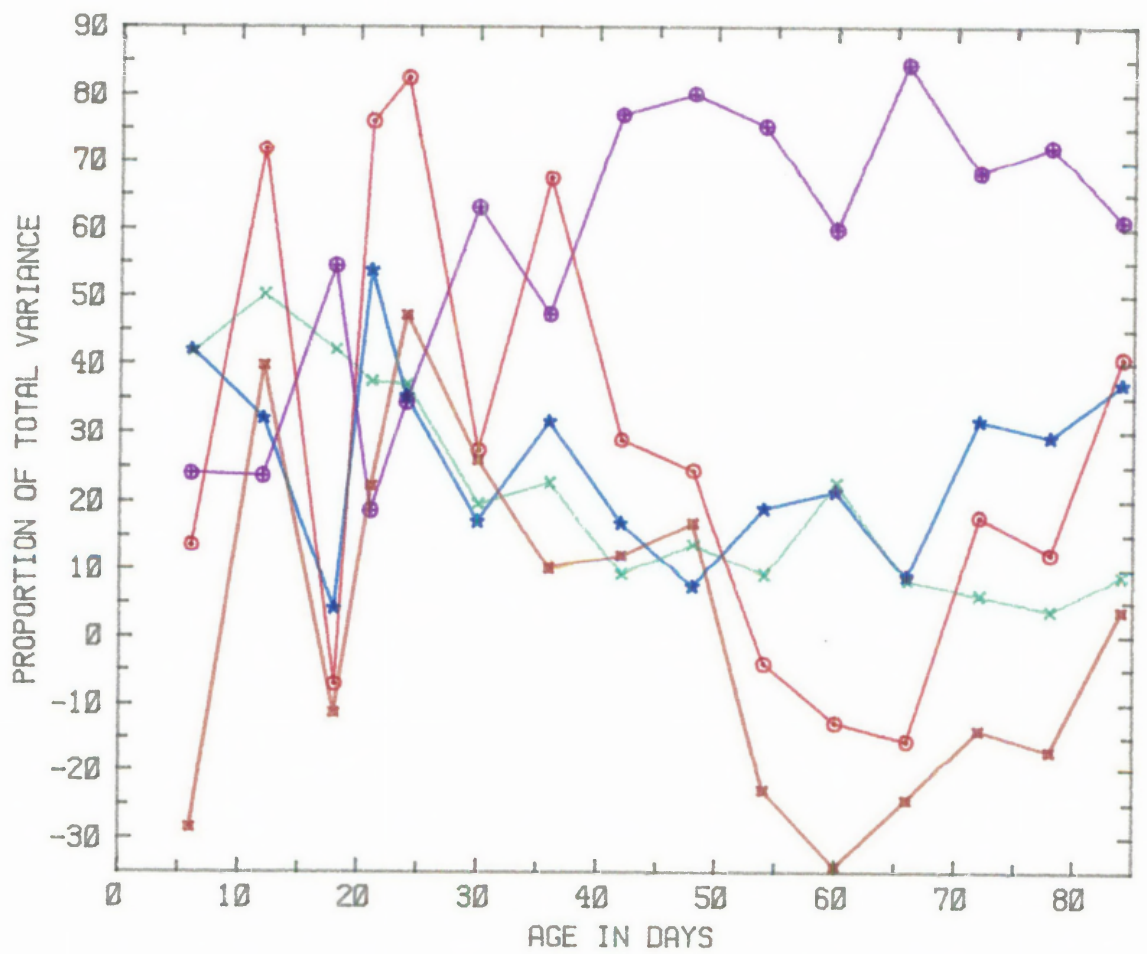
The pattern for components of variation for weight gain is presented in Fig. 4.2. Both negative and positive estimates for the covariance between direct genetic and maternal genetic effects were observed for weight gain. The estimated maternal influences on weight gain between 6 and 12 days of age were high; $V_M = 71.9\%$, $V_{ec} = 50.3\%$, and $Cov_{AM} = 39.8\%$. Negative covariance estimates were obtained for weight gain intervals between 48 days and 78 days of age. Hanrahan and Eisen (1973) reported a negative covariance estimate for 3 - 6 week weight gain in males. Young and Legates (1965) reported positive covariances for 3 week and 6 week weights and weight gain over the same time interval. Hanrahan and Eisen (1973) also reported considerable additive maternal effects on body weights and weight gains; however, their results were obtained by assuming $V_{ec} = 0$.

The negative variances obtained for additive maternal effects for gain between 12 - 18, 54 - 60, 60 - 66 and for 30 day weight were theoretically impossible. This indicates the possible biases introduced into the analyses by assuming that the additive genetic variance for dams can be estimated by the sire component of variance. This may also be a reflection of the fact that quadratic unbiased estimators of variance components can be negative.

The amount of variation associated with the components V_{ec} and V_{ew} combined was high for all weight gain periods, only for the period from 18 - 21 days did the variation attributable to these sources fall below 55%. The variation due to common environmental effects between full-sibs decreased in importance throughout the measurement period, so that only two values greater than 10% were recorded after 36 days of age. Residual error (V_{ew}) accounted for sixty or more per cent of the total variation in weight gain after 36 days of age.

Figure 4.2: Components of variation as a percent they represent of the total variance in weight gains.

V_A = blue V_{ec} = green
 V_M = red V_{ew} = purple
 Cov_{AM} = brown



Variance components for fractions of maturity expressed as percentages of the total variance are presented in Fig. 4.3. As was found for body weight, the covariance term was negative throughout the measurement period. The variation due to common environmental influences remained low throughout. With the exception of the value obtained for 78 days of age, V_{ec} was less than 10% after 30 days of age. Similarly, the maternal variance (V_M) was low as compared with values obtained for body weight, a value of -27% was recorded for the 30 day measurement. V_{ew} continued to increase throughout the growth period and accounted for more than 40% of the variation in measurements after 24 days of age, again the exception being the value for 78 days of age.

The components of variation for feed intake, as presented in Fig. 4.4, were marked by the 'see-sawing' pattern in all components. The additive genetic variance tended to account for significant proportions of total variance, usually being between 30% and 70%, never below 20% and rising to a peak of over 85% for 36 - 42 day food intake. The proportion of the variance due to maternal influence (V_{ec}) remained at or below 20% for the periods from 21 to 84 days. In contrast to this result, the variance due to direct maternal effects was mostly above 20%, this was against a back-drop of negative covariance terms throughout. Because direct additive genetic effects (V_A) tended to be high for most feed intakes, residual error rarely accounted for more of the variation in feed intake than genetic effects.

The components of variation for feed efficiency (Fig. 4.5) show that, unlike those for feed intake, direct genetic effects (V_A)

Figure. 4.3: Components of variation as the percent they represent of the total variance for fraction of maturity.

V_A = blue V_{ew} = purple
 V_M = red Cov_{AM} = brown
 V_{ec} = green

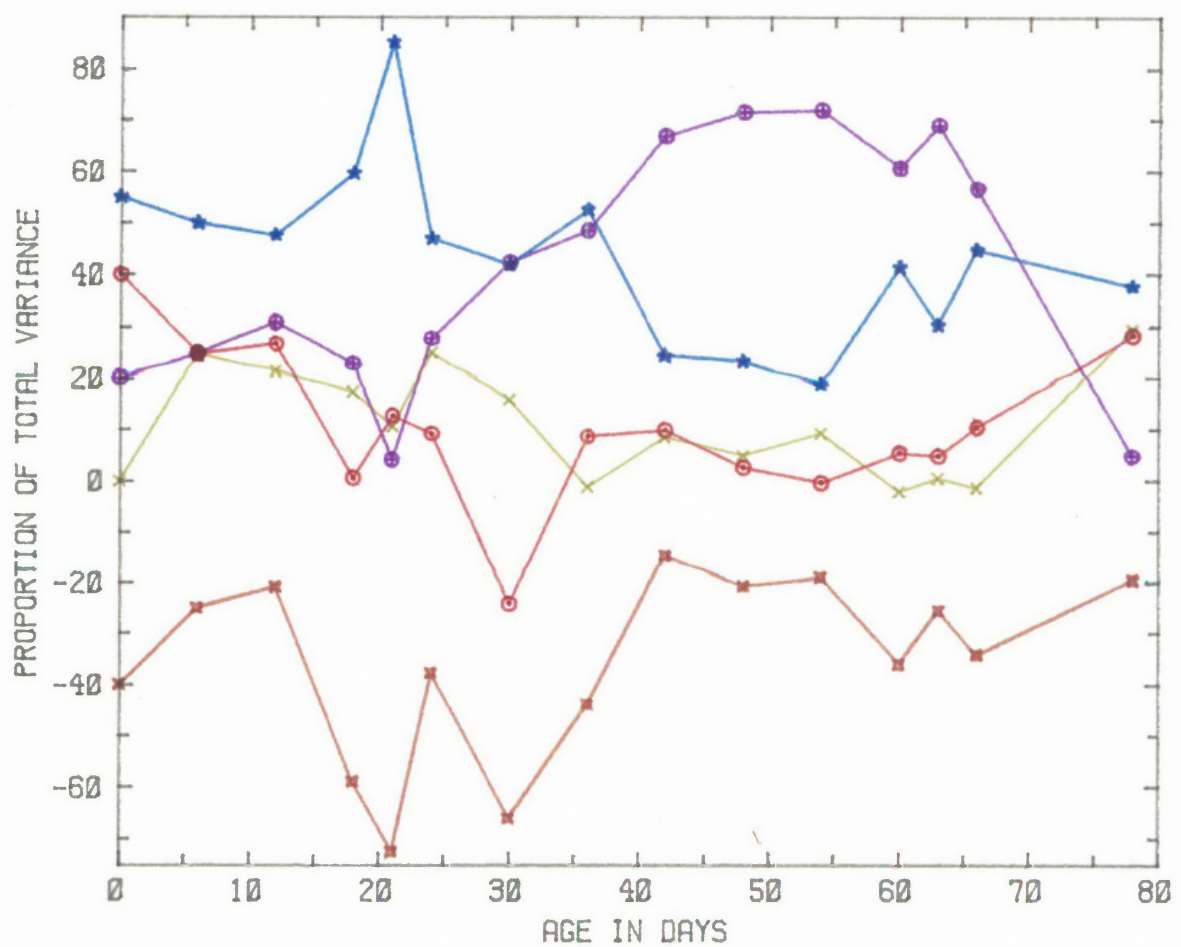


Figure 4.4: Components of variation as a percent they represent of the total variance for feed intake.

V_A = blue	V_{ec} = green
V_M = red	V_{ew} = purple
	Cov_{AM} = brown

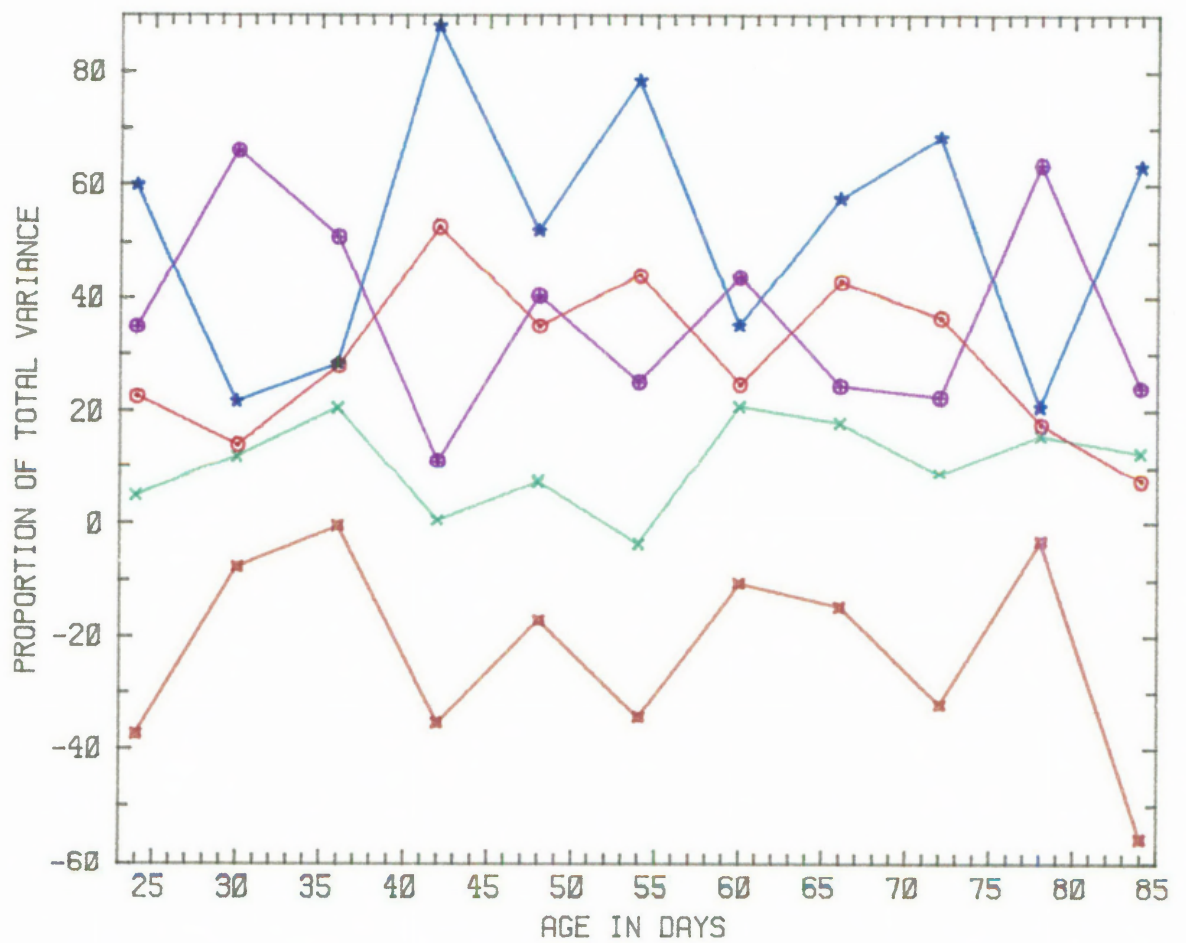
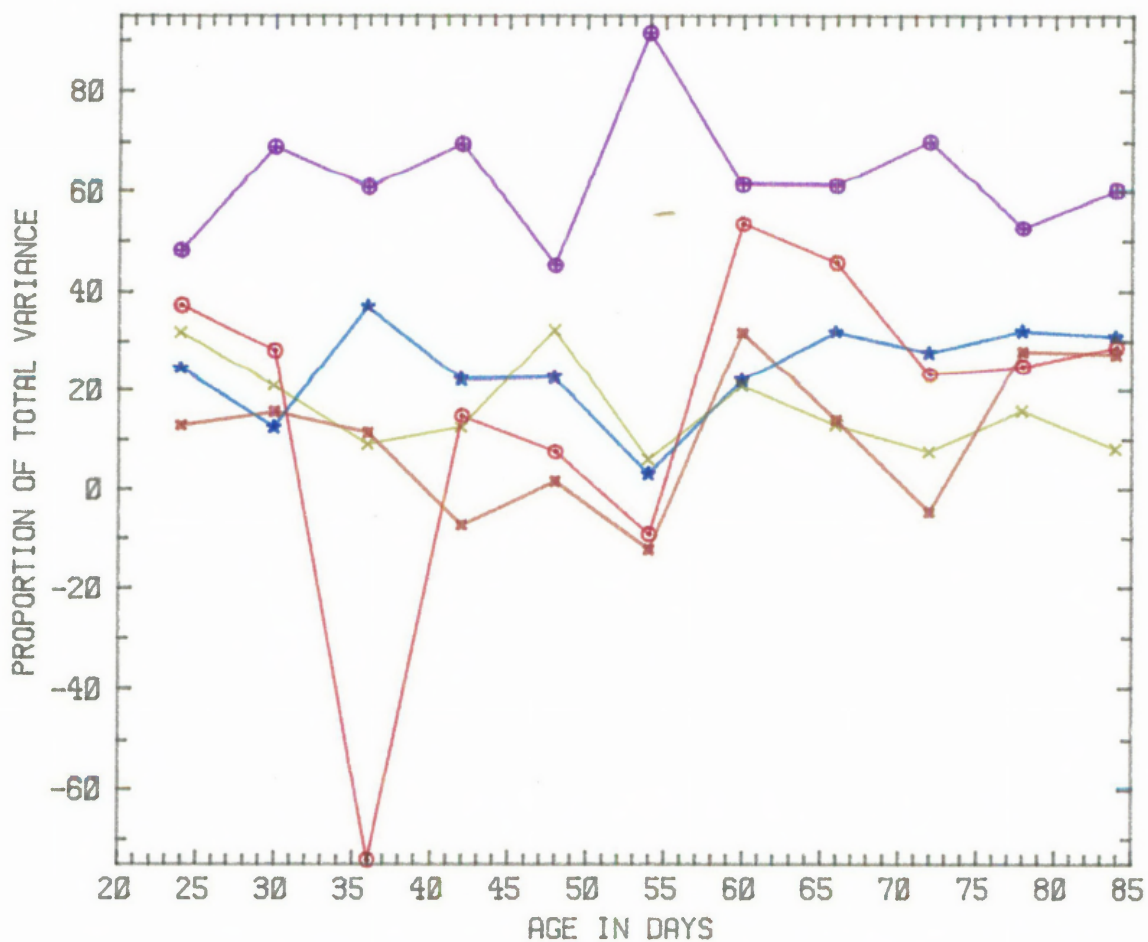


Figure 4.5: Components of variation as a percent they represent of the total variance in feed efficiencies.

V_A = blue V_{ec} = green
 V_M = red V_{ew} = purple
 Cov_{AM} = brown



accounted for much lower proportions of the total variance. The additive genetic component estimated from the sire variances ranged from 3.08% for efficiency between 48 - 54 days of age, to 37.11% for the period from 30 - 36 days.

The maternal genetic variances (V_M) for feed efficiency were initially high, represented by 37.18% for 21 - 24 day period, then declined through to the period from 54 - 60 days of age where estimates again accounted for a large proportion of the variation. If the maternal influence is estimated simply by the variance due to common environmental effects (V_{ec}), its role was much less important than that suggested by V_M , accounting for less than 20% of the total variation for all but two periods (31.9% and 32.3% for the periods 21 - 24 days and 42 - 48 days respectively). The V_{ew} component represented more than 45% of the total variation for all measured periods.

b) Variance Components for Parameters and Points of Inflection of Nonlinear Growth Models

As the estimates for direct maternal effects and covariances between additive genetic and maternal effects were consistently biased, by using the sire component of variance to estimate the dam's direct genetic effects for the analyses involving weights and feed intakes, the total variance for the parameter estimates was not partitioned into the V_M and Cov_{AM} components.

Components of variation as the percent they represent of the total variance for the parameters and characteristics of the non-

linear models are presented in Table 4.9. The proportion of the total variance due to additive genetic effects for a parameter were consistent for alternative parameterisations of the Logistic and Gompertz models. For instance, the percentage value for the additive variance of the asymptotes for Models I and VII were 38.43% and 34.04% respectively. The role of the maternal environment, as estimated by V_{ec} , was low for all estimates of mature weight. The V_{ec} estimates for the maturing rate parameter (k) were greater than those for mature weight (values ranged between 16.52% for Model VIa and 35.67 for Model VIII). Eisen *et al.* (1969) reported intraclass correlations for k , estimated by the Logistic and Gompertz equations (Models I and II), of 0.24 and 0.38 respectively. Rutledge *et al.* (1972) reported heritabilities of 0.18 and 0.00 for the asymptote and rate parameter of the Logistic equation (Model I), for both parameters the within component of variance accounted for more than 80% of the total variance.

The proportion of the variation attributable to the residual error, V_{ew} , was consistent when comparing the same parameter across Models I, II, VII and VIII. Percentage V_{ew} estimates for parameter A were between 48.91% and 53.30%, between 23.42% and 37.08% for parameter k and 55.75% and 43.75% for the two b parameter estimates. In most cases, the V_{ec} component accounted for less than 15% of the total variation for the parameters of the Parks' models, thus necessarily, the residual variance was closely allied to the variation due to additive genetic effects. The two exceptions were for parameters k and t^* estimated by Model VIa. If the negative value of -2.62% for k is considered as being equal to zero the variance for this parameter was governed predominantly by additive genetic effects

TABLE 4.9

COMPONENTS OF VARIATION AS A PERCENT THEY REPRESENT
OF THE TOTAL VARIANCE FOR CHARACTERS OF THE NONLINEAR MODELS

Model	Character	Variance Components			
		V_A	V_{D+M}	V_{ew}	V_{ec}
Logistic, I	A	38.43	89.07	48.91	12.66
	b	15.56	130.31	55.75	28.69
	k	33.18	162.23	34.54	32.27
	POI _{WT}	38.43	89.06	48.91	12.66
	POI _{AGE}	58.96	147.00	19.03	22.01
Logistic, VII	A	34.04	91.53	51.59	14.37
	k	27.49	170.16	37.08	35.67
	POI _{WT}	34.04	91.53	51.59	14.37
	POI _{AGE}	61.74	149.63	16.29	21.98
Gompertz, II	A	35.61	83.21	52.49	11.90
	b	43.18	95.55	43.75	13.07
	k	49.04	159.19	23.42	27.54
	POI _{WT}	35.61	83.21	52.49	11.90
	POI _{AGE}	62.03	118.62	23.82	14.15
Gompertz, VIII	A	34.33	83.80	53.30	12.37
	k	41.09	174.14	25.65	33.26
	POI _{WT}	34.34	83.80	53.30	12.37
	POI _{AGE}	52.48	157.55	21.25	26.27
Parks, VIa	A	53.86	102.46	33.99	12.15
	k	86.11	152.22	-2.62	16.52
	t*	33.18	117.72	45.69	21.14
Parks, VIb and XI	A	12.83	29.47	83.01	4.16
	(AB)	80.00	84.76	18.81	1.19
	c	53.72	97.04	35.45	10.83
	t*	19.86	45.52	73.72	6.41
	T ₀	45.47	67.70	48.98	5.56

(86.11%) and maternal influences ($V_{ec} = 16.52\%$).

The dam component of variation which involves direct genetic, maternal genetic and covariance terms was always greater than the additive genetic variance, estimated from the sire component of variance, and in several instances values of more than 100% were observed.

4.4 DISCUSSION

Due to inadequacies in the data set and in the computer programmes available at the time this study was undertaken, it was not possible to estimate direct maternal variances and direct genetic and maternal covariances free from biases due to dominance components of variance. By assuming that the sire component of variance was an adequate indicator of the dam's additive genetic variance, the variance due to maternal genetic effects and the covariance between the two were estimated. The results presented suggest that for all traits considered, there were both negative and positive correlations between the direct and maternal genetic effects operating at various ages throughout the growth period from birth to twelve weeks of age.

From the analyses on body weights at various ages, it was apparent the maternal influences were greatest prior to weaning and that they decreased throughout the measurement period. If the negative covariance term was in fact accurate, the resultant negative correlation estimates between direct genetic and maternal genetic effects could decrease expected responses to selection for body weights, weight gains or fraction of maturity at a specific

age. However, the extremely erratic nature of the estimates for the maternal variances, in some instance these being negative, and covariances for weight gain cast doubts on the accuracy of the results for weight gain. There appears to be conflicting evidence in the literature on both the direction and magnitude of the covariances between maternal genetic effects (Young and Legates, 1965; Hanrahan and Eisen, 1973). Results presented here appear to be consistent with other estimates in the literature when examining estimates at different stages of growth.

As no values for the role of maternal effects on feed intake and feed efficiency post-weaning were found in the literature, the results presented herein should be treated with caution. Analyses of feed intake variances showed that the combined maternal influences, measured by the common environmental variance, fluctuated at low proportions of the total variance throughout the measurement period. Results obtained for the portions of the total variance attributable to the various components for feed efficiency suggested that random environmental fluctuations were the most significant causes of variation between individuals. Both additive genetic and maternal effects accounted for less than 40% of the variation over all measurement periods.

The partitioning of components of variation for the parameters of the growth models suggested that maternal genetic variance and the covariance between direct and maternal genetic effects would have important implications on breeding programmes involving the parameters of any model considered in this study. This is particularly true for the rate para-

meters k and to a lesser extent, t^* of the Parks' models. The low combined estimate of the maternal component, V_{ec} , obtained for the parameters of Parks' weight-feed intake models, VIb and XI, suggests that selection, based on the genetic and phenotypic correlations (reported in Chapter 3) between these parameters and pre-weaning weights, would produce correlated responses free of the confounding influences of the maternal environment.

The results found during this study would suggest that, in accordance with statements by Willham (1980) and Baker (1980), there appear to be negative genetic correlations between the direct maternal and additive genetic components of several growth traits. Careful consideration should be given to incorporating the variable role of maternal effects on growth in animal breeding programmes, particularly to pre-weaning weight or growth to weaning.

CHAPTER 5

DISTRIBUTIONAL AND STATISTICAL PROPERTIES
OF NONLINEAR GROWTH MODELS

5.1 INTRODUCTION

Two distinct approaches dominate the growth curve literature, the 'biological' and the 'statistical'. Until now, the 'statistical' approach has been almost purposely avoided in the preceding chapters. The premise has been to develop an awareness and understanding of the growth process, particularly in relation to the application of nonlinear models. There is certainly no lack of biologically-based models in the literature. However, the works of Brody (1945), Kleiber (1961) and more recently, Parks (1982), suggest that our knowledge of growth is uncertain, and constantly unfolding. With the increasing use and application of nonlinear models, we are constantly asking questions about the distributional and statistical properties of the models and the estimated parameters.

Geneticists particularly should be concerned with problems associated with the application of parameter estimates and derived characteristics from the parameters to analysis of variance techniques. Grossman (1969) found the intrinsic growth rate constant, k of the logistic equation, to 'appear near enough to normal

to warrant analysing the data without transformation'. This was the only study cited where the distributional properties of the parameters were considered when nonlinear models were applied to animal data and subsequently used in genetic analyses.

In linear regression, the least-squares estimators of the parameters, with an independently and identically distributed error term, $N \sim (0, \sigma)$, have the desired properties of being unbiased, normally distributed and achieving minimum variance bound (MVB), whereas nonlinear regression models may only achieve these properties asymptotically. Until recently, there have been no objective guidelines to determine the extent of bias, non-normality, or the extent to which the variance may exceed the MVB. The magnitude to which these properties remain unfilled differs with the model under consideration and its parameterisation, and may decrease with increasing sample size. If a choice amongst several nonlinear models is to be made, particularly between those suitable for biological interpretation, one should choose a model whose behaviour closely approximates that of a linear model.

A number of statistical tools are now available to aid in the choice of nonlinear models.

a) Box (1971): Bias in nonlinear parameters: M.J. Box (1971) suggested bias in the least-squares estimates of the parameters in a nonlinear regression model, given a specific data set, can be estimated by,

$$E(\phi) = -\frac{\sigma^2}{2} \left(\sum_{v=1}^n F_v^T F_v \right)^{-1} \sum_{\mu=1}^n F_{\mu}^T \text{tr} \left\{ \left(\sum_{v=1}^n F_v^T F_v \right)^{-1} H_{\mu} \right\} \quad (5.1)$$

where, F is the $1 \times p$ vector of first derivatives and

H is the $p \times p$ matrix of second derivatives, of the model with respect to each of the p parameters, evaluated at the conditions of the μ th observations, $\mu = 1, 2, \dots, n$.

v is the index determining the order of the variance - covariance matrix of the parameter set.

σ^2 is the error variance and assumed to be constant.

The calculated $p \times 1$ vector ϕ is the bias, representing the discrepancy between the estimate of the parameter and its true value. Gillis and Ratkowsky (1978) and more recently Ratkowsky (1979, and unpublished 1981), have examined a number of models using Box's measure of bias. They concluded that the formula gave predictions of bias to the correct order of magnitude and was also able to give a good indication of the nonlinearity of the models considered. Large bias has generally been associated with excess variance and a high degree of non-normal behaviour, and Ratkowsky (1979) suggests this is a measure of the nonlinear behaviour of the model.

It should be noted from the actual formula 5.1, that there is a dependence on the variance, and thus a dependence on the sample size. Box (1971) also noted that the bias estimated is directly proportional to the experimental variance and the standard errors of the least squares parameter estimates will be an order of magnitude greater than the bias of each estimate.

b) Bates and Watts (1980): Relative Curvature Measures of Nonlinearity: Bates and Watts (1980) have suggested two measures of nonlinearity of a model based on the geometric concept of curvature. They have shown that the nonlinearity of a

model can be separated into two components of curvature, an 'intrinsic' curvature resulting from approximating the curved solution locus by a plane, and a 'parameter-effects' curvature resulting from replacement of the curved parameter lines on the approximating tangent plane by a grid of straight, equispaced and parallel lines. Bates and Watts have shown that Box's (1971) bias measure is closely associated with their measure of parameter effects curvature. They also demonstrate in studies of 24 model-data set combinations that the parameter-effects curvature was greater than the intrinsic curvature. This finding supports Gillis and Ratkowsky's (1978) evidence from a simulation study that nonlinearity due to the parameterisation is more important than intrinsic nonlinearity and also that the bias measure of Box (1971) can serve as a useful indicator of overall nonlinearity of a model.

The measures of curvature are standardised by the scaling factor of the standard radius, $\rho = s\sqrt{p}$ where p is the number of parameters and s is estimate of the standard deviation.

Multiplying both intrinsic and parameter effects curvatures by the standard radius relates both measures to the solution locus. To determine the impact of the nonlinearity upon the confidence region of the solution locus, the scaled curvatures must be compared with $1/\sqrt{F}$, where $F = F(p, v; \alpha)$, and is obtained from a table of the F distribution with numerator degrees of freedom equal to the number of parameters p , and the denominator degrees of freedom equal to the residual degrees of freedom v , and significance level α . If the intrinsic curvature is small compared to the critical value, the solution locus is relatively flat over the confidence

region area and the assumption of planarity can be accepted. If the parameter-effects curvature is small compared to the critical value, then the uniform co-ordinate assumption is considered good over the region of interest.

5.2 MATERIALS AND METHODS

A detailed description of the mouse population, management practices used and measurements recorded were given in Chapter 2.

5.2.1 Distribution Properties of the Model Parameters and Derived Characters

Means, variances and measures of normality, skewness and kurtosis, for function parameters and characters, previously utilised and described in Chapter 3, were calculated using Biomedical Computer Programmes Package (Dixon and Brown, 1979).

The effect of reducing the number of data points used in the nonlinear estimation process was examined. However, as the number of analyses required to examine all models would be extremely large only two models were considered, the Logistic (Model I) and Gompertz (Model II). The data structures examined are presented in Table 5.1. The choice of the data sets described in Table 5.1 was arbitrary. The aim was to assess the minimum number of data points required to obtain accurate estimates of model parameters.

TABLE 5.1

NUMBER AND STRUCTURE OF DATA POINTS FOR
REDUCED DATA SETS

Data Set	Number of Data Points	Ages (day) for Included Data Points
I (0-84)	29	0, 3, 6, 9, 12, 15, 18, 21, 24, 27, 30, 33, 36, 39, 42, 45, 58, 51, 54, 57, 60, 63, 66, 69, 72, 75, 78, 81, 84.
II (0-84)	15	0, 6, 12, 18, 24, 30, 36, 42, 48, 54, 60, 66, 72, 78, 84.
III (0-78)	27	0, 3, 6, 9, 12, 18, 21, 24, 27, 30, 33, 36, 39, 42, 45, 48, 51, 54, 57, 60, 63, 66, 69, 72, 75, 78.
IV (0-78)	14	0, 6, 12, 18, 24, 30, 36, 42, 48, 54, 60, 66, 72, 78.
V (0-72)	25	0, 3, 6, 9, 12, 15, 18, 21, 24, 27, 30, 33, 35, 39, 42, 45, 48, 51, 54, 57, 60, 63, 66, 69, 72.
VI (0-72)	13	0, 6, 12, 18, 24, 30, 36, 42, 48, 54, 60, 66, 72.
VII (21-84)	22	21, 24, 27, 30, 33, 36, 39, 42, 45, 48, 51, 54, 57, 60, 63, 66, 69, 72, 75, 78, 81, 84.
VIII (21-84)	11	21, 27, 33, 39, 45, 51, 57, 63, 69, 75, 81.

5.2.2 Correlation Structure Between Parameters of the Same Model

The mean and range of the correlations between parameters of the same model obtained during the least-squares estimation and iteration of the model fitting were examined. Many criticisms of nonlinear analyses have been directed toward the lack of independence between parameters of the same model. The extent of the correlations between parameters estimated during the regression process is an indication of the dependence.

5.2.3 Bias and Nonlinearity Measures on the Models Investigated and Their Structural Parameters

A simulation study was undertaken to examine the properties of the models and their structural parameters, (partial derivatives for each model are given in Appendix 1.). One thousand pseudo-random samples of size $n = 29$ were generated with the variance of weight, assumed constant on the log scale, i.e. the error structure was assumed multiplicative. Therefore, the data set was of the form

$$Y_t = \log W_t + \varepsilon_t$$

where, for example $W_t = A (1 + be^{-kt})^{-1}$

for $t = 0, 3, 6, \dots, 84$.

The random variables, ε_t , were generated as stochastically

independent and normally distributed with mean zero and variance σ^2 , thus

$$Y_t \sim N(\log W_t, \sigma^2).$$

The parameter values, for functions involving weight and time, were estimated as the mean values obtained for the logistic function from the analyses described in Section 5.2.1. Similarly, the error variances used in the simulation study were estimated from the analyses described in Chapter 3. As only the asymptotic relationships were under consideration and the same 1000 data sets were used for each equation, direct comparisons between the five models involving weight versus time data points can be made.

The bias can be simply estimated as

$$b = \bar{\phi}^* - \hat{\phi}$$

where $\hat{\phi}$ is the parameter value supplied as the 'true' value

$$\bar{\phi}^* = (1/N) \sum_{i=1}^N \phi_i^*$$

where, $\bar{\phi}^*$ is the mean of the sampling distribution, and

ϕ_i^* is the parameter value obtained from the sample.

In addition to the parameter biases, estimated by simulation, estimates of Bates and Watts' (1980) relative curvatures measures of nonlinearity were calculated. Information on a random sample of

10 individuals drawn from the analysed population was used to obtain estimates of "intrinsic" and "parameter effects" curvature. A programme supplied by Dr. D. Ratkowsky (Division of Mathematics and Statistics, CSIRO, Tasmania) and modified to the U.N.E. computer system, provided the above measures of nonlinearity.

5.3 RESULTS

5.3.1 Distribution Properties of the Model Parameters and Derived Characters

The results of the analyses for the six models are presented in Table 5.2. The large number of individuals involved in these analyses should provide a representative sample of the population. The means and variances shown for each parameter and derived characters were not corrected for sex or group effects.

For each model the measures of deviation from normality, skewness and kurtosis, indicate distinct non-normal distributions in parameter estimates. Comparisons between the two forms of the Logistic, models I and VII, and the Gompertz, models II and VIII, suggest that the distributions for all parameters were similar, with exception of the asymptote parameter, A, for models I and VII (a skewness value of 0.12 for both models). For these four models, the distribution of the parameter A was positively skewed, when different from zero, and negatively skewed for the k parameter. However, for the Parks weight/age model, Model VIa, both A and k had positively skewed distributions, whilst estimates of the para-

TABLE 5.2
 MEANS, VARIANCES AND MEASURES OF NORMALITY FOR
 NONLINEAR MODELS

	Parameter	Mean	Variance	Skewness ¹	Kurtosis ¹	
LOGISTIC	A	31.97	13.52	0.12	-0.38	
Model I	b	15.58	6.48	0.68**	1.47**	
	k	0.123	0.002	-0.36*	-0.06	
	POI age	22.80	7.50	1.16**	2.81**	
	POI weight	15.98	3.37	0.10	-0.36	
Model VII	A	31.26	12.75	0.12	-0.38	
	k	0.137	0.002	-0.21*	0.72	
	POI age	18.77	5.36	0.84**	1.62**	
	POI weight	15.62	3.18	0.12	-0.38	
GOMPERTZ	A	35.00	21.17	0.43*	0.42	
	Model II	b	3.27	0.63	2.63**	22.32**
		k	0.060	0.0001	-0.48**	0.40
		POI age	19.75	0.62	1.65**	7.62**
		POI weight	12.88	2.87	0.42*	0.32
Model VIII	A	34.68	19.93	0.30**	-0.11	
	k	0.061	0.0001	-0.44**	0.45	
	POI age	18.69	8.08	1.35**	4.00**	
	POI weight	12.76	2.70	0.30	-0.11	
PARKS	A	37.06	48.57	0.89**	3.60**	
	Model VIa	k	0.036	0.0001	0.84**	0.77
		t*	4.99	1.08	-0.21*	0.28
Model VIb and XI	A	33.65	20.36	0.65**	3.91**	
	(AB)	0.400	0.055	2.11**	5.56**	
	C	6.79	0.70	0.54**	0.55	
	t*	4.99	16.77	2.21**	7.62**	
	T ₀	5.09	17.52	0.65**	0.59	

¹ * P < .05, ** P < 0.01.

meter t^* exhibited a negatively skewed distribution (-0.21). The parameter b , for Models I and II, had a positively skewed distribution, quite markedly so for the Gompertz model (2.63). The degree of skew obtained for the parameters of the Parks' models VIb and XI indicates distinctly non-normal behaviour in their respective distributions. All parameters exhibited positive skewness for their distribution of estimates for this sample of the total population.

The results from the measures of kurtosis were less pronounced. For Models I, II, VII and VIII the values obtained for parameters A and k are not significantly different from 0 and therefore could be representative of normal distributions. The values for parameter b , 1.47 for Model I and 22.32 for Model II, illustrates a peaked or leptokurtic distribution in actual parameter values. The large deviations from normality for parameter b are also reflected in the distributions for age at the point of inflection for these two models. Both showed positively skewed and leptokurtic distributions (1.16 and 2.81, for Model I, and 1.65 and 7.62 for Model II). A similar result is evident for Models VII and VIII, although the parameter b is not involved in the calculation of the age at the point of inflection.

The results for the measure of normality for the Parks' models, VIa, VIb and XI shows that these model types, when fitted to individual information, gave parameter estimates in the population that were markedly non-normal. This was particularly evident for the combined models VIb and XI, where all parameters had distribu-

tions that were positively skewed and only the parameter C , representing estimated mature feed intake, and the parameter T_0 , which is directly related to C ($T_0 = A/C$), were not leptokurtic.

5.3.2 Reduced Number and Altered Structure of the Data Points

Results from altering the number of data points and structure of the data are shown in Table 5.3. The data presented are for the 379 male and female mice in Group 1 (see Chapter 2, Section 2.2.1).

Paired t - test comparisons between the mean values for the full data set, Type I, and values for the reduced models show that reducing the number of data points by up to 4 measurements from the endpoint, that is 12 days, had little effect on the estimated parameter values. However, by reducing the period of measurement from 0 - 84 days (Type I and II sets) to 21 - 84 days (Type VII and VIII data sets) significantly altered the parameter estimates. Note, because the variances for the parameters increased considerably for reduced data sets VI, VII and VIII caution should be taken when interpreting levels of significance below $\alpha = 0.05$, and also in light of the apparent skewness in some parameter distributions (Table 5.2).

Reducing the number of data points whilst maintaining the same endpoints in the data structure, for example comparisons between Type I and Type II data sets or Type III and Type IV data sets, had no apparent effects on the parameter means or errors for the Gompertz

TABLE 5.3
 MEANS AND STANDARD ERRORS FOR THE PARAMETERS OF THE LOGISTIC AND GOMPERTZ MODELS
 WITH REDUCED DATA SETS

DATA SET		MODEL							
Type	No. of Points	Logistic Parameters			Gompertz Parameters				
		A	b	k x 10 ⁻¹	A	b	k x 10 ⁻²		
I	29	32.4+0.11	16.2+0.07	1.23+0.04	35.4+0.13	3.13+0.03	6.09+0.54		
II	15	32.1+0.11	16.1+0.07	1.23+0.05	35.2+0.13	3.14+0.03	6.17+0.53		
III	27	32.6+0.13	16.2+0.09	1.24+0.04	35.4+0.14	3.13+0.03	6.09+0.55		
IV	14	31.8+0.14	17.2+0.10**	1.29+0.05	35.2+0.13	3.14+0.03	6.18+0.55		
V	25	32.0+0.12	16.1+0.10	1.24+0.05	35.4+0.14	3.13+0.03	6.10+0.58		
VI	13	32.2+0.14	17.3+0.32**	6.14+0.15**	34.1+0.13**	5.30+0.35**	7.98+2.02		
VII	22	43.2+0.15**	8.3+0.25**	3.27+0.10**	34.1+0.12**	4.51+0.28**	7.34+1.78		
VIII	11	38.8+0.14**	8.1+0.26**	6.13+0.13**	34.6+0.13**	4.99+0.33**	7.72+1.87		

* P < 0.05; ** P < 0.01 for comparisons between means of Data Set I and reduced data sets (II - VIII).

model for periods up to and including 78 days of age. With the exception of the b parameter, estimated by using data set Type IV (0 - 78 day in 6 day intervals) the same result was found for the Logistic model. Parameter estimates based on data sets for the age interval from 0 - 72 days, with measurements every 3 days, did not significantly alter the mean parameter estimates. Over the same age interval, but with measurements every 6 days, mean and variances for the parameters changed considerably. No t- test comparisons were made for the Gompertz parameter k for data sets VI, VII, and VIII because of the large differences in the variances.

5.3.3 Correlation Structure Between Parameters of the Same Model

The means for the correlations between parameters, estimated during the actual nonlinear regression analysis, and the range of values obtained for all individuals are presented in Table 5.4.

The mean correlations between A and b for both the Logistic, model I and Gompertz, model II, were very similar, 0.2564 and 0.2550, although the range was greater for the Gompertz model. The correlations between A and k for the two Gompertz models were higher than those between A and k for the two Logistic models. However, the correlations between b and k were lower for the Gompertz model, 0.2039, when compared with the Logistic model, 0.5418, though the range of correlations obtained was much greater for the Gompertz, -0.438 to 0.380 compared to 0.216 to 0.640. The correlation between A and k for the Parks weight/age model, model VIa, was -0.8963, with

TABLE 5.4

CORRELATION STRUCTURE BETWEEN PARAMETERS OF THE SAME MODEL

Model Type	Parameter	Correlations (Range of Values)		
		b	k	k
Logistic, Model I	A	0.2564 (0.162 to 0.420)	-0.4447 (-0.694 to -0.312)	
	b		0.5418 (0.216 to 0.640)	
Model VII	A			k
			-0.4193 (-0.612 to -0.237)	
Gompertz, Model II	A	b	-0.7433 (-0.958 to -0.568)	k
	b	0.2550 (0.137 to 0.674)	0.2039 (-0.438 to 0.380)	
Model VIII	A		-0.7487 (-0.943 to -0.398)	k
Parks,	A	t*		k
Model VIa	t*	-0.4024(-0.667 to 0.0)	-0.8963 (-0.999 to -0.634)	
		(AB)	0.6145 (0.00 to 0.866)	
Models VIb and XI	A	0.8191 (0.0 to 1.0)	0.0513 (-1.0 to 1.0)	t*
	(AB)		0.0702 (-1.0 to 1.0)	
	C		-0.3363 (-1.0 to 1.0)	

values ranging between -0.999 to -0.634.

The range of values for the correlations between parameter estimates for Parks' models, Model VIa and VIb and XI, were mostly from both ends of the scale, i.e. -1.0 to 1.0. Although the mean correlations between parameters were quite low in some instances, 0.0513 between parameters A and C, and 0.0702 between parameters (AB) and C, the large ranges of values makes single point interpretations based on the means difficult.

5.3.4 Measures of Nonlinearity for Nonlinear Models and Model Parameters

Table 5.5 gives the results obtained for four alternative appraisals of nonlinearity for the seven models considered throughout this study. Both the intrinsic and parameter-effects curvature may be assessed by comparing them with the critical $1/\sqrt{F}$. The value for $\alpha < 0.05$ for models I, II and VIa is 0.5793, for models VII and VIII the value is 0.4856, and for Parks' models VIb and XI the critical value is 0.6226. It can be seen that all models have acceptable intrinsic curvatures, that is, the solution locus may be acceptably approximated by a plane. In contrast, all models have unacceptable parameter-effects curvatures. The worst behaved models being the two forms of the Parks' models.

Assessment of the biases inherent in the estimation procedure was examined by two methods, estimation by simulation and utilizing equation 5.1 (page 201). The bias calculated by equation 5.1 shows general agreement with the bias estimated by simulation.

TABLE 5.5

MEASURES OF NONLINEARITY FOR NONLINEAR MODELS AND MODEL PARAMETERS

Model	Bias % From Simulation	Bias % Calculated (Box, 1971)	Parameter Effects Curvature ¹	Intrinsic Curvature ¹
Logistic, A	-0.0265	0.0582		
Model I b	0.2891	0.1595	0.6435**	0.0733
k	0.0243	0.0100		
Logistic, A	-0.0406	0.0221	1.0212**	0.159
Model VII k	0.7610	0.7001		
Gompertz, A	-0.9280	-0.6829		
Model II b	0.5877	0.3042	1.8132**	0.0819
k	0.2623	0.1161		
Gompertz, A	-0.6663	-0.3118	2.7852**	0.2787
Model VIII k	0.5921	0.4365		
Parks, A	0.3263	0.2211		
Model VIa k	5.6521	2.3573	15.5641**	0.2733
t*	10.1859	8.5995		
Parks, A	-	0.427		
Models (AB)	-	16.368	35.6623**	0.2992
VIb and C	-	3.792		
XI t*	-	15.621		

* $P < 0.05$; ** $P < 0.01$

¹ Critical Value $1/\sqrt{F}$, where $F = (p, v; \alpha)$; where P = number of parameters, v = residual degrees of freedom.

For convenience and ease of comparison both are presented as percentages. Reparameterisations of Models VII and VIII to their model general forms, Models I and II improved the measures of non-linearity with parameter biases in the estimates decreasing, for example -0.0406% to -0.0265% for parameter A of the Logistic models.

All parameters of the Parks' model, with exception of parameter A, the estimated mature weight, show unacceptably high percentage bias when compared with alternative model descriptors. The Parks' input/output models, VIb and XI, were not included in the simulation exercise and therefore percentage biases based on simulation were not available for the parameters of these models.

5.4 DISCUSSION

The results presented for skewness and kurtosis on the parameters of each model suggest that careful consideration should be given to techniques of analysing and utilising the different model parameters. Transformations of the parameter estimates may overcome some problems of non-normality for parameters, however, it is doubtful that this would be possible for all parameters of the Gompertz and Parks' models, whilst still maintaining meaningful interpretations of the parameters. The correlated error structure associated with data of weight/age or weight/feed intake form can cause considerable problems. Using ordinary least-squares procedures correlated errors result in an under-estimation of the covariance matrix of the parameter estimates. This problem was

first encountered when initiating the simulation exercise and although simulation using a correlated error structure was considered, as the assumptions would be vague and the exact nature of the covariance matrix difficult to define, an independent error structure was assumed. This may account for the discrepancies between the estimates of bias by simulation when compared with those obtained by equation 5.1. Although, this situation may affect decisions on which model to ultimately use, any selection programme using parameters of a model as selection criteria should be unaffected. In using truncation selection based on the criteria of a parameter or parameter set the under-estimation of the covariances, due to correlated errors, will apply to each animal and therefore affect all to the same extent.

In terms of the two measures of normality, skewness and kurtosis, some parameters estimated for this population of mice, show considerable deviations from normality. The distribution of the parameters for the Logistic models (Model I and VII) were close to normal, while those of the Parks' models (Models VIa, VIb and XI) were markedly non-normal.

Correlations between parameters estimates (Table 5.4) concur with one of the most quoted problems associated with using nonlinear models, that the parameters are not independent and therefore biases would occur in utilising them as selection criteria. Certainly, the results suggest that there is problems with the high degree of association between some parameters. This problem is further exaggerated by the correlated errors associated with measurements taken on the same individual. However, the large range of correlations

obtained for individuals in this population would suggest, that there may be instances where the correlations between parameters estimated for an individual would be low.

The fundamental theme throughout this chapter is that in choosing a nonlinear model, the user should be seeking one whose behaviour closely approaches that of linear models, that is, given the assumption that the stochastic error is independently and identically distributed, the least squares estimators of the model parameters should be close to being unbiased, normally distributed and having the minimum possible variance. Given these conditions and good initial estimates of the parameters, the Gauss-Newton iterative selection should converge quickly to the least squares solutions. This will provide an asymptotic covariance matrix which should closely approximate an unbiased estimate of the true covariance matrix. Ratkowsky (1979) suggested percentage biases less than 1% should provide parameters whose behaviour is guaranteed to be normal. From the results presented here it would appear that the two forms of the Logistic and Gompertz models would satisfy this criteria. All parameters of these models had biases less than 1% when computed either by simulation or equation 5.1. In direct contrast to this result, the parameters of the Parks' models, except parameter A, had bias estimates greater than 1%. The extremely high biases associated with the parameter t^* is probably due to the fact that this parameter occurs more than once in both models VIa and XI. Ratkowsky (pers. comm) has suggested reparameterisation of the models would possibly alleviate the problem. However, reparameterisation of the models could remove any biological inter-

pretation that could be placed on the model parameters. High degrees of parameter effects curvature, as found for all models, suggest that one or more of the parameters of a model are biased. This was particularly evident for the Parks' equations. Models with both significant parameter effects curvature and highly biased parameter estimates have a variance well in excess of the minimum variance bound (Bates and Watts, 1980).

Utilising parameters of nonlinear models as possible selection criteria has some major drawbacks, possibly the most significant of these is the early estimation of mature weight, usually estimated by the parameter A. This problem was examined by altering the structure of the data set and changing the number of data points available. It was shown that for the two models considered, reducing the final endpoint of measurements by 12 days did not significantly affect the parameter estimates, as long as the time interval between measurements was not increased (that is, from 3 to 6 days). However, by changing the initial age of first measurement, from birth to 21 days of age, parameter estimates for both models changed significantly. It should be remembered that this data structure, with measurements beginning at 21 days of age and finishing at 84 days, is the same as was used for the Parks' models VIb and XI. The failure of both the Gompertz and Logistic models to give similar means and variances for the parameter estimates with this particular data structure was undoubtedly due to a lack of a true inflection point in the actual data.

From the results presented and the discussion above it is

apparent that, on the criteria examined and within the overall aim of this chapter, the generalised form of the Logistic model (Model I) provided the best fit of the data. The parameters of this model most closely approximated a normal distribution, had the least biased parameters estimates, the smallest intrinsic curvature and parameter-effects curvature and exhibited the most stable correlations estimates between parameters during the estimation process.

GENERAL CONCLUSIONS

From evaluations of farm animals there appears to be certain growth patterns that are considered more desirable than others, for mostly economic reasons. It is natural then that consideration be given to exploring different shaped growth curves in animal species, whether they are the result of natural or artificial selection pressures.

It is important to note that in attempting to alter the shape of the growth curve, specifically the weight/age growth curve, that consideration should be given to the genetic and phenotypic relationships among body weights and weight gains over the total growth curve. In Chapter 2 of this thesis these relationships along with feed intakes and efficiencies at various ages were considered. The results obtained suggested that the more conventional selection procedures, that is selection for weights or weight gains over specified time periods, would, in this population, produce changes in the total growth curve consistent with results from selection experiments with mice. As body weights at different ages have a part-whole relationship and are generally positively correlated, selection to increase early weights will increase weights at later ages. The magnitude of the correlated responses in later weights will be determined by the chronological difference in age between the age at selection and the later weights. Although, selection on this basis produces changes in the weight/age growth curve and the feed intake/age curve, these changes, unfortunately, do not give growth patterns that could be considered economically desirable. Mature animal maintenance

costs are increased and animals have tended to become over-fat at later ages. Within this framework then, there is a need to develop alternative selection strategies to produce individuals economically and biologically viable. The work reported in Chapters 3, 4 and 5 of this thesis was an attempt to consider one such alternative.

Results reported in Chapter 3 suggested that the models considered provided a good fit to the data and that there was significant genetic and phenotypic variation for all parameters of each model. This indicates direct selection on any single parameter or parameter set would produce changes in the growth patterns of this population of mice. The results presented showed general agreement with similar studies, whether in cattle, mice or poultry. However, it was shown that the results do indicate that the correlations, at times strongly positive or negative, would make changes in one parameter independent of any other parameter difficult to achieve.

In terms of the biological interpretations that can be placed on individual parameters, the Parks' models offers the most comprehensive information, particularly his input/output models. Simulated expected direct and correlated responses to selection using the parameters of the Parks' models suggest that results to selection would not, unfortunately, be that different from those of selection for combinations of weights, weight gains and feed intakes. This has strong negative implications for any practical application of selection criteria based on the parameters of nonlinear models. Examination of the changes possible under direct selection for model parameters would appear to fit the biological model presented in Chapter 1. Selection would act at different pathways in the model in a manner similar to those described for direct selection.

on body weights or weight gains.

Just as body weights, and weight gains are affected by maternal effects so are the parameter estimates for different models. This was shown to be particularly true for the rate parameters, k , of the Logistic and Gompertz models. The results suggested that, as with selection programmes, for example involving weaning weight, there is the possibility of negative genetic correlations existing between direct maternal and additive genetic components for the parameters of nonlinear models fitted to animal data. Because of the direct relationship between the parameter estimates and the data used to obtain the estimates this result should not be unexpected.

As mentioned previously each model gave good apparent fits to the data, whether expressed as a visual fit or based on low residual variances. However, the examination of the distributional and statistical properties of the models and their parameter estimates illustrated considerable problems in the application of nonlinear models to data for any particular individual. All models presented exhibited some degree of non-normal behaviour. The Parks' input/output model provided the worst fit for the data based on the criteria suggested in Chapter 5. However this could be associated with the more restricted age range for the data points used to obtain parameter estimates for this model. If compared to results presented on the Logistic and Gompertz models, when fitted to the same range of points (Table 5.3), the Parks' models may provide better fits to the data.

Although not considered in this study, Taylor's (1980, 1982) and

Park's suggestions of utilising standardised growth curves for comparisons between and within breeds may provide additional information on possibilities for changing the structures of growth curves. However, as both procedures are still dependent on estimating mature weight, and mature feed intake, either by fitting a model to the data or by obtaining actual measurements, both methods could suffer the problems alluded to above. Utilising Taylor's model, Webster *et al.* (1982) presented results that would suggest a very poor fit to their data for Charolais, Hereford and Aberdeen Angus. It should, however, be noted that the nonlinear model Webster *et al.* used to estimate mature weight, the Brody function, over-estimated 2000 - day weight for each breed. This may account for the poor results obtained using these estimated mature weights. Both Taylors' and Parks' approaches to standardising the input/output growth curves could provide useful information for between and within breeds or species for assessing physiological and nutritional differences.

The results presented and discussed in this thesis suggest that the model, most appropriate to describe the weight/age growth curve of this mouse population, would be the generalised Logistic model. The ability to utilise the parameters of this or any alternative models as selection criteria to alter the structure of the growth curves would be possible. However, if these results can be repeated for livestock species, and there is no reason to believe they cannot be if given sufficient data input, the possibilities of attaining changes in growth patterns that would provide economically and biologically viable alternatives to present selection strategies appear limited. There is a need, still to be fulfilled, in the ability to accurately determine an animals' mature weight and feed intake at early ages. This would allow information on corre-

lated changes in the total growth patterns after selection at early ages, to be assessed and if undesirable remedied.

REFERENCES

- BAKER, R.L. (1980). The role of maternal effects on the efficiency of selection in beef cattle - a review. *Proc. N.Z. Soc. Anim. Prod.* 40: 285-303.
- BAKKER, H. (1974). Effects of selection for relative growth rate and body weight of mice on rate, composition and efficiency of growth. *Meded. Lanbouwhogeschool Wageningen* 8: 1-94.
- BATEMAN, N. (1957). Some physiological aspects of lactation in mice. *J. Agr. Sci., Camb.* 49: 60-77.
- BATES, D.M. and WATTS, D.G. (1980). Relative curvature measures of nonlinearity. *J.R. Statist. Soc. B.* 42: 1-25.
- BERG, R.T. and BUTTERFIELD, R.M. (1966). Muscle: bone ratio and fat percentage as measures of beef carcass composition. *Anim. Prod.* 8: 1-11.
- BERTALANFFY, von L. (1938). A quantitative theory of organic growth. *Human Biology* 10: 181-243.
- BERTALANFFY, von L. (1957). Quantitative laws on metabolism and growth. *Quart. Rev. of Biol.* 32: 217-231.
- BERTALANFFY, von L. (1960). Principles and theory of growth, pp. 137-259. In: *Fundamental aspects of normal and malignant growth.* (ed. W.W. Nowinski.) Elsevier, Amsterdam.
- BLAXTER, K.L. (1968). The effect of dietary energy supply of growth. In: *Growth and development of mammals.* (ed. G.A. Lodge and G.E. Lamming.) Butterworths, London.
- BOER, de H. and MARTIN, J. eds. (1978). *Patterns of growth and development in cattle.* Martinus Nijhoff, London.
- BOX, M.J. (1971). Bias in nonlinear estimation. *J.R. Statist. Soc. B.* 33: 171-201.
- BRODY, S. (1945). *Bioenergetics and growth.* Reinhold, N.Y.
- BROWN, J.E. (1970). A comparison of five stochastic models on their ability to describe the weight/age relationship in cattle. *Ph.D. Dissertation, Univ. Texas.*
- BROWN, J.E.; BROWN, C.J. and BUTTS, W.T. (1972). A discussion of the genetic aspects of weight, mature weight and rate of maturing in Hereford and Angus cattle. *J. Anim. Sci.* 34: 525-537.

- BROWN, J.E.; FITZHUGH, H.A. and CARTWRIGHT, T.C. (1976). A comparison of nonlinear models for describing weight-age relationships in cattle. *J. Anim. Sci.* 42: 810-818.
- CARTER, A.H. (1982). Efficiency of production in the pasture-animal grazing complex. *Proc. 2nd World Congress on Genetics Applied to Livestock Production*, Madrid.
- DICKERSON, G.E. (1947). Composition of hog carcasses as influenced by heritable differences in rate and economy of gain. *Iowa Agr. Exp. Stat. Bull.* 354.
- DIXON, W.J. and BROWN, M.B. (1979). *Biomedical Computer Programmes: P. Series.* Uni. of California, Los Angeles.
- EISEN, E.J. (1967). Mating designs for estimating direct and maternal genetic variances and direct maternal genetic covariances. *Can. J. Genet. Cytol.* 9: 13-22.
- EISEN, E.J. (1974). The laboratory mouse as a mammalian model for the genetics of growth. *Proc. 1st Wld. Genet. Appl. Livest. Prod. Madrid*, 1: 467-491.
- EISEN, E.J. (1976). Results of growth curve analysis in mice and rats. *J. Anim. Sci.* 42: 1002-1023.
- EISEN, E.J. (1977). Restricted selection index: an approach to selecting for feed efficiency. *J. Anim. Sci.* 44: 958-972.
- EISEN, E.J.; LANG, B.G. and LEGATES, J.E. (1969). Comparison of growth functions within and between lines of mice selected for large and small body weight. *Theor. Appl. Genet.* 39: 251-260.
- FITZHUGH, H.A. (1976). Analysis of growth curves and strategies for altering their shape. *J. Anim. Sci.* 42(4): 1036-1051.
- FITZHUGH, H.A. and TAYLOR, St. C.S. (1971). Genetic analysis of degree of maturity. *J. Anim. Sci.* 33: 717-725.
- FOULLEY, J.L. and LEFORT, G. (1978). Methods of estimating direct and maternal effects in animal breeding. *Annales de Genetique et de Selection Animale* 10: 457-495.
- FRAHM, R.R. and BROWN, M.A. (1975). Selection for increased preweaning and postweaning weight gain in mice. *J. Anim. Sci.* 41: 33-42.
- GILLIS, R.R. and RATKOWSKY, D.A. (1978). The behaviour of estimators of the parameters of various yield density relationships. *Biometrics* 34: 191-198.
- GROSSMAN, M. (1969). A genetic and biometric study of growth in chickens. *Ph.D. Thesis, Univ. Purdue.*

- GROSSMAN, M. and GALL, G.A.E. (1968). Covariance analysis with unequal subclass numbers: component-estimation in quantitative genetics. *Biometrics* 24: 49-59.
- GUILBERT, H.R. and GREGORY, P.W. (1944). Feed utilisation tests with cattle. *J. Anim. Sci.* 3: 143-153.
- GUILBERT, H.R. and GREGORY, P.W. (1952). Some measures of growth and development of Hereford cattle. *J. Anim. Sci.* 11: 3-16.
- HANRAHAN, J.P. (1976). Maternal effects and selection response with an application to sheep data. *Anim. Prod.* 22: 359-369.
- HANRAHAN, J.P. and EISEN, E.J. (1973). Sexual dimorphism and direct and maternal genetic effects on body weight in mice. *Theor. Appl. Genet.* 43: 39-45.
- HARVEY, W.R. (1977). Mixed model least-squares and maximum likelihood computer program. Users Guide for LSML76 Monogr. Ohio. Univ., p.76.
- HAYES, J.F. and McCARTHY, J.C. (1976). The effects of selection at different ages for high and low body weight on the pattern of fat deposition in mice. *Genet. Res., Camb.* 27: 384-433.
- HENDRICKS, W.A.; JULL, M.A. and TITUS, H.W. (1931). A possible physiological interpretation of the law of diminishing increment. *Science, N.Y.* 73: 427-429.
- HETZEL, D.J.S. (1978). Genetic studies of growth and body composition in mice. *Ph.D. Thesis, Univ. Sydney.*
- HUXLEY, J.S. (1932). *Problems of relative growth.* Methuen and Co., London.
- JARA-ALMONTE, M. and WHITE, J.M. (1973). Genetic relationships among milk yield, growth, feed intake and efficiency in laboratory mice. *J. Anim. Sci.* 37: 410-416.
- KLEIBER, M. (1961). *The fire of life. An introduction to animal energetics.* John Wiley, N.Y.
- KOCH, R.M. (1972). The role of maternal effects in animal breeding. VI. Maternal effects in beef cattle. *J. Anim. Sci.* 35: 1316-1323.
- KOCH, R.M. and CLARK, R.T. (1955). Genetic and environmental relationships among economic characters in beef cattle. III. Evaluation maternal environment. *J. Anim. Sci.* 14: 979-996.
- KOCH, R.M.; DIKEMAN, M.E.; ALLEN, D.M.; MAY, M.; GROUSE, J.D. and CAMPION, D.R. (1976). Characterisation of biological types of cattle. III. Carcass composition, quality and palatability of steers. *J. Anim. Sci.* 43: 48-62.

- LAIRD, A.K.; TYLER, S.A. and BARTON, A.D. (1965). Dynamics of normal growth. *Growth*, 29: 233-248.
- LAIRD, A.K. and HOWARD, A. (1967). Growth curves in inbred mice. *Nature, Lond.* 25: 786-788.
- LAWRENCE, T.L.J. (ed.). (1980). *Studies in agricultural and food sciences: growth in animals.* Butterworths, Boston.
- LISTER, D.; RHODES, D.N.; FOWLER, V.R. and FULLER, M.F. (eds.). (1976). *Meat Animals Growth and Productivity.* Plenum Press, N.Y.
- LOHMAN, T.G. (1971). Biological variation in body composition. *J. Anim. Sci.* 32: 647-653.
- LUSH, J.L. (1945). *Animal Breeding Plants.* Iowa State Univ. Press, Iowa.
- MCCARTHY, J.C. (1977). Quantitative aspects of the genetics of growth. *In: Growth and poultry meat production.* (Eds. Boorman and Wilson). British Poultry Science.
- MCCARTHY, J.C. (1980). Morphological and physiological effects of selection for growth rate in mice. *Proc. Selection Experiments in Laboratory and Domestic Animals.* (ed. A. Robertson). pp.100-109. Comm. Agric. Bureaux, Slough, U.K.
- MCCARTHY, J.C. and BAKKER, H. (1979). The effects of selection for different combinations of weights at two ages on the growth curve of mice. *Theor. Appl. Genet.* 55: 57-64.
- MCCLELLAND, T.H.; BONAITI, B. and TAYLOR, St. C.S. (1976). Breed differences in body composition of equally mature sheep. *Anim. Prod.* 23: 281-293.
- MCCLELLAND, T.H. and RUSSEL, A.J.F. (1972). The distribution of body fat in Scottish Blackface and Finnish Landrace sheep. *Anim. Prod.* 15: 301-306.
- MEISSNER, H.H. (1977). An evaluation of the Roux mathematical model for the functional description of growth. *Ph.D. Thesis, Univ. P.E., South Africa.*
- MEISSNER, H.H.; ROUX, C.Z. and HOFMEYR, H.S. (1975). Voluntary feed intake, growth, body composition and efficiency in the sheep: breed and sex differences. *Agroanimalia* 7: 105-114.
- MONTEIRO, L.S. (1975). Food efficiency in relation to estimated growth of body components in cattle. *Anim. Prod.* 20: 315-335.
- MONTEIRO, L.S. and FALCONER, D.S. (1966). Compensatory growth and sexual maturity in mice. *Anim. Prod.* 8: 179-192.

- NELDER, J.A. (1961). A fitting of a generalisation of the logistics curve. *Biometrics* 17: 89-110.
- NELDER, J.A. (1962). An alternative form of a generalised logistic function. *Biometrics* 18: 614-616.
- PARKS, J.R. (1970). Growth curves and the physiology of growth. I. Animals. *Am. J. Physiol.* 219: 833-836.
- PARKS, J.R. (1972a). Cybernetics in animal nutrition. *Proc. Int. Summer School Computer and Research in Nutrit. and Vet. Medicine.* pp 37-51. Elsinore, Denmark.
- PARKS, J.R. (1972b). Physiology of growth: animals as input-output devices. *Proc. Int. Summer School Computer and Research in Nutrit. and Vet. Medicine.* pp 388-403. Elsinore, Denmark.
- PARKS, J.R. (1973). A stochastic model of animal growth. *J. Theor. Biol.* 42: 505-518.
- PARKS, J.R. (1975). A theory of animal weight response to controlled feeding. *J. Theor. Biol.* 55: 371-380.
- PARKS, J.R. (1982). *A theory of feeding and growth of animals.* Springer-Verlag, Heidelberg.
- PARRATT, A.C.; ROBERTS, R.C. and BARKER, J.S.F. Growth curve analysis of mice selected for large and small body size. *Proc. 3rd Conference Australian Assoc. Animal Breeding and Genetics 1982:* 265-266.
- RATKOWSKY, D.A. (1979). Choosing nonlinear regression models. *In: Regression Analysis, A symposium of the N.S.W. Branch of Stat. Soc. of Aus.*
- RICARD, F.H. (1975). Essai de selection sur la forme de la courbe de croissance chez le poulet. *Ann. Genet. Select. Anim.* 7: 427-443.
- RICHARDS, F.J. (1959). A flexible growth function for empirical use. *J. Expt. Bot.* 10: 290-300.
- ROBERTS, R.C. (1979). Side effects of selection for growth in laboratory animals. *Livest. Prod. Sci.* 6: 93-104.
- ROBERTS, R.C. (1981). Growth of mice selected for large and small size in relation to food intake and the efficiency of conversion. *Genet. Res.* 38: 9-24.
- ROUX, C.Z. (1974). The relationship between growth and feed intake. *Agroanimalia* 6: 49-52.
- ROUX, C.Z. (1976). A model for the description and regulation of growth and production. *Agroanimalia* 8: 83-94.

- RUTLEDGE, J.J.; ROBISON, O.W.; EISEN, E.J. and LEGATES, J.E. (1972). Dynamics of genetic and maternal effects. *J. Anim. Sci.* 35: 911-918.
- SPRAY, C.M. and WIDDOWSON, E.M. (1950). The effect of growth and development on the composition of mammals. *Brit. J. Nutr.* 4: 332-353.
- STAINER, M.W. and MOUNT, L.E. (1972). Growth rate, food intake and body composition before and after weaning in strains of mice selected for mature body weight. *Brit. J. Nutr.* 28: 307-325.
- SUTHERLAND, T.M.; BIONDINI, P.E.; HAVERLAND, L.H.; PETTUS, D. and OWEN, W.B. (1970). Selection for rate of gain, appetite and efficiency of feed utilization in mice. *J. Anim. Sci.* 31: 1049-1057.
- TAYLOR, St. C.S. (1965). A relation between mature weight and time taken to mature in mammals. *Anim. Prod.* 7: 203-220.
- TAYLOR, St. C.S. (1968). Time taken to mature in relation to mature weight for sexes, strains and species of domesticated mammals and birds. *Anim. Prod.* 10: 157-169.
- TAYLOR, St. C.S. (1980). Genetic size-scaling rules in animal growth. *Anim. Prod.* 30: 161-165.
- TAYLOR, St. C.S. (1982). Theory of growth and feed efficiency in relation to maturity in body weight. *Proc. 2nd World Congress on Genetics Applied to Livestock Production, Madrid.* V:218-230.
- TIMON, V.M. and EISEN, E.J. (1969). Comparison of growth curves of mice selected and unselected for postweaning gain. *Theoret. Appl. Genet.* 39: 345-351.
- TIMON, V.M. and EISEN, E.J. (1970). Comparisons of *ad libitum* and restricted feeding of mice selected and unselected for postweaning gain. I. Growth, feed consumption and feed efficiency. *Genetics* 64: 41-57.
- VAN VLECK, L.D. (1976). Index selection for direct and maternal genetic components of economic traits. *Biometrics* 32: 173-181.
- WEBSTER, A.J.F. (1977). Selection for leanness and energetic efficiency of growth in meat animals. *Proc. Nutr. Soc.* 36: 53-59.
- WEBSTER, A.J.F.; AHMED, A.A.M. and FRAPPELL, J.P. (1982). A note on growth rates and maturation rates in beef bulls. *Anim. Prod.* 35: 281-284.
- WILLHAM, R.L. (1963). The covariance between relatives for characters composed of components contributed by related individuals. *Biometrics* 19: 18-27.

- WILLHAM, R.L. (1972). Role of maternal effects in animal breeding. *J. Anim. Sci.* 35: 1288-1293.
- WILLHAM, R.L. (1980). Problems in estimating maternal effects. *Livest. Prod. Sci.* 7: 405-418.
- YOUNG, C.W. and LEGATES, J.E. (1965). Genetic, phenotypic and maternal inter-relationships of growth in mice. *Genetics* 52: 563-576.
- YÜSKEL, E. (1978). Selection for efficiency of feed utilization in mice. *Ph.D. Thesis, Univ. of Edinburgh.*

APPENDIX 1

LISTS OF THE PARTIAL FIRST AND SECOND DERIVATIVES OF WEIGHT
WITH RESPECT TO EACH VARIABLE FOR WHICH THEY ARE FUNCTIONS

Function

1. a) Logistic $W_t = A(1 + be^{-kt})^{-1}$

Partial Derivative

Its Evaluation

$$\frac{\partial W_t}{\partial A} \quad (1 + be^{-kt})^{-1}$$

$$\frac{\partial W_t}{\partial b} \quad -A(1 + be^{-kt})^{-2} e^{-kt}$$

$$\frac{\partial W_t}{\partial k} \quad A(1 + be^{-kt})^{-2} bte^{-kt}$$

$$\frac{\partial^2 W_t}{\partial A \partial b} \quad (1 + be^{-kt})^{-2} -e^{-kt}$$

$$\frac{\partial^2 W_t}{\partial A \partial k} \quad (1 + be^{-kt})^{-2} bte^{-kt}$$

$$\frac{\partial^2 W_t}{\partial b \partial k} \quad A(1 + be^{-kt})^{-3} te^{-kt}$$

$$\frac{\partial^2 W_t}{\partial A^2} \quad 0$$

$$\frac{\partial^2 W_t}{\partial b^2} \quad 2A(1 + be^{-kt})^{-3} e^{-2kt}$$

$$\frac{\partial^2 W_t}{\partial k^2} \quad Abt^2 e^{-kt} (1 + be^{-kt}) [2be^{-kt} (1 + be^{-kt})^{-1} - 1]$$

$$\frac{dW_t}{dt} \quad A(1 + be^{-kt})^{-2} bke^{-kt}$$

1. b) Logistic $W_t = A(1 + (\frac{A}{W_0} - 1)e^{-kt})^{-1}$

Partial Derivative

Its Evaluation

$$\frac{\partial W_t}{\partial A} \quad [1 + (\frac{A}{W_0} - 1)e^{-kt}]^{-1} [1 - \frac{A}{W_0}(1 + (\frac{A}{W_0} - 1)e^{-kt})^{-1}e^{-kt}]$$

$$\frac{\partial W_t}{\partial k} \quad (\frac{A^2}{W_0} - A)[1 + (\frac{A}{W_0} - 1)e^{-kt}]^{-2}(te^{-kt})$$

$$\frac{\partial^2 W_t}{\partial A^2} \quad [1 + (\frac{A}{W_0} - 1)e^{-kt}]^{-2} (1 + (\frac{2A}{W_0}(1 + (\frac{A}{W_0} - 1)e^{-kt})^{-1}))(-e^{-kt})$$

$$\frac{\partial^2 W_t}{\partial k^2} \quad At^2e^{-kt}(\frac{A}{W_0} - 1) ([2(1 + (\frac{A}{W_0} - 1)e^{-kt})^{-3}(\frac{A}{W_0} - 1)e^{-kt}] - [1 + (\frac{A}{W_0} - 1)e^{-kt}]^{-2})$$

$$\frac{\partial^2 W_t}{\partial A \partial k} \quad te^{-kt}(1 + (\frac{A}{W_0} - 1)e^{-kt})^{-2} ((\frac{A}{W_0} - 1) + \frac{A}{W_0}) - [2A(\frac{1}{W_0}e^{-kt})(1 + (\frac{A}{W_0} - 1)e^{-kt})^{-1}]$$

$$\frac{\partial W_t}{\partial t} \quad (\frac{A^2}{W_0} - A)[1 + (\frac{A}{W_0} - 1)e^{-kt}]^{-2}(ke^{-kt})$$

2. a) Gompertz $W_t = Ae^{-be^{-kt}}$

Partial Derivative

Its Evaluation

$$\frac{\partial W_t}{\partial A} = e^{-be^{-kt}}$$

$$\frac{\partial W_t}{\partial b} = -Ae^{-kt}e^{-be^{-kt}}$$

$$\frac{\partial W_t}{\partial k} = Abte^{-kt}e^{-be^{-kt}}$$

$$\frac{\partial^2 W_t}{\partial A^2} = 0$$

$$\frac{\partial^2 W_t}{\partial b^2} = Ae^{-2kt}e^{-be^{-kt}}$$

$$\frac{\partial^2 W_t}{\partial k^2} = Abt^2e^{-kt}[(be^{-kt}e^{-be^{-kt}}) - (e^{-be^{-kt}})]$$

$$\frac{\partial^2 W_t}{\partial A \partial k} = bte^{-kt}e^{-be^{-kt}}$$

$$\frac{\partial^2 W_t}{\partial A \partial b} = -e^{-kt}e^{-be^{-kt}}$$

$$\frac{\partial^2 W_t}{\partial b \partial k} = Ate^{-kt}[(e^{-be^{-kt}}) - (be^{-kt}e^{-be^{-kt}})]$$

$$\frac{\partial W_t}{\partial t} = Abke^{-kt}e^{-be^{-kt}}$$

2. b) Gompertz $W_t = A \left(\frac{A}{W_0}\right)e^{-kt}$ or $A^{1+e^{-kt}} \left(\frac{1}{W_0}\right)e^{-kt}$

Partial Derivative Its Evaluation

$$\frac{\partial W_t}{\partial A} \quad (1 + e^{-kt}) \left(\frac{A}{W_0}\right) e^{-kt}$$

$$\frac{\partial W_t}{\partial k} \quad kt^2 A \left(\frac{A}{W_0}\right) e^{-kt}$$

$$\frac{\partial^2 W_t}{\partial A^2} \quad (1 + e^{-kt}) e^{-kt} A (e^{-kt} - 1) \left(\frac{1}{W_0}\right) e^{-kt}$$

$$\frac{\partial^2 W_t}{\partial k^2} \quad At^2 \left(\frac{A}{W_0}\right) e^{-kt} (k^2 t^2 + 1)$$

$$\frac{\partial^2 W_t}{\partial A \partial k} \quad kt^2 (1 + e^{-kt}) \left(\frac{A}{W_0}\right) e^{-kt}$$

$$\frac{\partial W_t}{\partial t} \quad Ak^2 t \left(\frac{A}{W_0}\right) e^{-kt}$$

3. a) Bertalanffy $W_t = A(1 - be^{-kt})^3$

Partial Derivative

Its Evaluation

$$\frac{\partial W_t}{\partial A} \quad (1 - be^{-kt})^3$$

$$\frac{\partial W_t}{\partial b} \quad -3Ae^{-kt}(1 - be^{-kt})^2$$

$$\frac{\partial W_t}{\partial k} \quad 3Abte^{-kt}(1 - be^{-kt})^2$$

$$\frac{\partial^2 W_t}{\partial A^2} \quad 0$$

$$\frac{\partial^2 W_t}{\partial b^2} \quad 6Ae^{-2kt}(1 - be^{-kt})$$

$$\frac{\partial^2 W_t}{\partial k^2} \quad 3At^2be^{-kt}[2e^{-kt}(1 - be^{-kt}) - (1 - be^{-kt})^2]$$

$$\frac{\partial^2 W_t}{\partial A \partial b} \quad -3e^{-kt}(1 - be^{-kt})^2$$

$$\frac{\partial^2 W_t}{\partial A \partial k} \quad 3bte^{-kt}(1 - be^{-kt})^2$$

$$\frac{\partial^2 W_t}{\partial b \partial k} \quad 3Ate^{-kt}(1 - be^{-kt})[(1 + be^{-kt}) - 2be^{-kt}]$$

$$\frac{\partial W_t}{\partial t} \quad 3Abke^{-kt}(1 - be^{-kt})^2$$

4. a) Brody $W_t = A(1 - be^{-kt})$

Partial Derivative

Its Evaluation

$$\frac{\partial W_t}{\partial A}$$

$$1 - be^{-kt}$$

$$\frac{\partial W_t}{\partial b}$$

$$-Ae^{-kt}$$

$$\frac{\partial W_t}{\partial k}$$

$$Abte^{-kt}$$

$$\frac{\partial^2 W_t}{\partial A^2}$$

$$0$$

$$\frac{\partial^2 W_t}{\partial b^2}$$

$$0$$

$$\frac{\partial^2 W_t}{\partial k^2}$$

$$-Abt^2e^{-kt}$$

$$\frac{\partial^2 W_t}{\partial A \partial b}$$

$$-e^{-kt}$$

$$\frac{\partial^2 W_t}{\partial A \partial k}$$

$$bte^{-kt}$$

$$\frac{\partial^2 W_t}{\partial b \partial k}$$

$$Ate^{-kt}$$

$$\frac{\partial W_t}{\partial t}$$

$$Abke^{-kt}$$

4. b) Brody $W_t = A - (A - W_0)e^{-kt}$

Partial Derivative

Its Evaluation

$$\frac{\partial W_t}{\partial A}$$

$$-e^{-kt}$$

$$\frac{\partial W_t}{\partial k}$$

$$(A - W_0)te^{-kt}$$

$$\frac{\partial^2 W_t}{\partial A^2}$$

$$0$$

$$\frac{\partial^2 W_t}{\partial k^2}$$

$$(A - W_0)-t^2e^{-kt}$$

$$\frac{\partial^2 W_t}{\partial A \partial k}$$

$$te^{-kt}$$

$$\frac{\partial W_t}{\partial t}$$

$$(A - W_0)ke^{-kt}$$

5. Parks' Function (weight versus time)

$$W_t = (A - W_0)(1 - e^{-kt-t^*(1 - e^{-t/t^*})}) + W_0$$

Partial Derivative

Its Evaluation

$$\frac{\partial W_t}{\partial A} = 1 - e^{-kt-t^*(1 - e^{-t/t^*})}$$

$$\frac{\partial W_t}{\partial t^*} = (A - W_0)(e^{-kt-t^*(1 - e^{-t/t^*})})(1 - e^{-t/t^*}) - (t/t^* e^{-t/t^*})$$

$$\frac{\partial W_t}{\partial k} = t e^{-kt-t^*(1 - e^{-t/t^*})}$$

$$\frac{\partial^2 W_t}{\partial A^2} = 0$$

$$\frac{\partial^2 W_t}{\partial t^{*2}} = \frac{t^2}{t^{*3}} e^{-t/t^*} (A - W_0) e^{-kt-t^*(1 - e^{-t/t^*})}$$

$$\frac{\partial^2 W_t}{\partial k^2} = -(A - W_0) t^2 e^{-kt-t^*(1 - e^{-t/t^*})}$$

$$\frac{\partial^2 W_t}{\partial A \partial t^*} = -e^{-kt-t^*(1 - e^{-t/t^*})} \left[1 - e^{-t/t^*} - \frac{te^{-t/t^*}}{t^*} \right]$$

$$\frac{\partial^2 W_t}{\partial A \partial k} = t e^{-kt-t^*(1 - e^{-t/t^*})}$$

$$\frac{\partial^2 W_t}{\partial k \partial t} = -t(A - W_0) e^{-kt-t^*(1 - e^{-t/t^*})} \left[1 - e^{-t/t^*} - \frac{te^{-t/t^*}}{t^*} \right]$$

6. Parks, Weight versus Feed Intake

$$W_t = (A - W_0)(1 - e^{-(AB)F/A}) + W_0 \quad \text{Weight versus feed intake}$$

$$\text{Let } (AB) = E$$

$$F = \left(\frac{A}{T_0} - D\right)(t - t^*(1 - DT_0/A))(1 - e^{-t/t^*}) + D \quad \text{feed intake versus time}$$

Partial Derivatives

$$\frac{\partial W_t}{\partial A} = (1 - e^{-E(F/A)}) - (A - W_0) \left(\frac{\partial e^{-E(F/A)}}{\partial A} \right)$$

$$\text{or } (1 - e^{-E(F/A)}) + E (A - W_0) \left(\frac{\partial (F/A)}{\partial A} \right) e^{-E(F/A)}$$

$$\text{where } \frac{\partial (F/A)}{\partial A} = -F/A^2 + 1/A \frac{\partial F}{\partial A}$$

$$\text{and } \frac{\partial F}{\partial A} = \frac{1}{T_0} [t - t^*(1 - D/A)(1 - e^{-t/t^*})]$$

$$\begin{aligned} \frac{\partial^2 W_t}{\partial A^2} &= E \frac{\partial (F/A)}{\partial A} e^{-E(F/A)} + E^2 [-F/A^2 + 1/A \frac{\partial F}{\partial A}] e^{-E(F/A)} \\ &+ e^{-E(F/A)} \left[\frac{2F}{A^3} - 1/A^2 \frac{\partial F}{\partial A} + 1/A \frac{\partial^2 F}{\partial A^2} \right] \\ &- E^2 (A - W_0) [-F/A^2 + 1/A \frac{\partial F}{\partial A}] \frac{\partial (F/A)}{\partial A} e^{-E(F/A)} \end{aligned}$$

$$\text{where } \frac{\partial^2 F}{\partial A^2} = -\frac{1}{T_0} \frac{t^* D}{A^2} (1 - e^{-t/t^*}) - \frac{t^* D}{T_0 A^2} (1 - e^{-t/t^*}) +$$

$$\frac{2}{A^3} t^* D \left(\frac{A}{T_0} - D \right) (1 - e^{-t/t^*})$$

$$\frac{\partial W_t}{\partial E} = F/A (A - W_0) e^{-E(F/A)}$$

$$\frac{\partial^2 W_t}{\partial E^2} = -F^2/A^2 (A - W_0) e^{-E(F/A)}$$

$$\frac{\partial W_t}{\partial E \partial A} = \frac{W_0}{A^2} e^{-E(F/A)} - E(F - \frac{W_0}{A}) \frac{\partial (F/A)}{\partial A} e^{-E(F/A)}$$

Parks cont.

$$\frac{\partial W_t}{\partial T_0} = E/A(A - W_0) \frac{\partial(F)}{\partial T_0} e^{-E(F/A)}$$

$$\text{or } (E - \frac{W_0}{A}) \frac{\partial(F)}{\partial T_0} e^{-E(F/A)}$$

$$\text{where } \frac{\partial(F)}{\partial T_0} = \frac{-A}{T_0^2} [t-t^*(1 - D/A)(1 - e^{-t/t^*})]$$

$$\begin{aligned} \frac{\partial^2 W_t}{\partial T_0^2} &= \frac{E^2}{A^2} (A - W_0) \left[\frac{\partial(F)^2}{\partial T_0} \right] e^{-E(F/A)} \\ &\quad + E/A (A - W_0) \frac{\partial^2 F}{\partial T_0^2} e^{-E(F/A)} \end{aligned}$$

$$\text{where } \frac{\partial^2 F}{\partial T_0^2} = \frac{2A}{T_0^3} [t-t^*(1 - D/A)(1 - e^{-t/t^*})]$$

$$\begin{aligned} \frac{\partial^2 W_t}{\partial A^2 \partial T_0} &= \frac{W_0}{A^2} \frac{\partial F}{\partial T_0} e^{-E(F/A)} + (E - \frac{W_0}{A}) \frac{\partial^2 F}{\partial T_0} e^{-E(F/A)} \\ &\quad - E(E - \frac{W_0}{A}) \frac{\partial(F/A)}{\partial A} e^{-E(F/A)} \end{aligned}$$

$$\text{where } \frac{\partial^2 F}{\partial T_0 \partial A} = \frac{-1}{T_0^2} [t-t^*(1 - e^{-t/t^*})]$$

$$\frac{\partial W_t}{\partial T_0 \partial E} = \frac{1}{A} (A - W_0) \frac{\partial(F)}{\partial T_0} e^{-E(F/A)} - \frac{EF}{A^2} (A - W_0) \frac{\partial(F)}{\partial T_0} e^{-E(F/A)}$$

$$\frac{\partial W_t}{\partial t^*} = E(A - W_0) \frac{\partial F}{\partial t^*} e^{-E(F/A)}$$

$$\text{where } \frac{\partial F}{\partial t^*} = -(\frac{A}{T_0} - D)(1 - D/A) [(1 - e^{-t/t^*}) - (t/t^* e^{-t/t^*})]$$

$$\frac{\partial^2 F}{\partial t^{*2}} = t^2/t^* e^{-t/t^*} [(\frac{A}{T_0} - D)(1 - D/A)]$$

$$\frac{\partial^2 W_t}{\partial t^{*2}} = E/A(A - W_0) \frac{\partial^2 F}{\partial t^{*2}} e^{-E(F/A)} - \frac{E^2}{A^2} (A - W_0) \left(\frac{\partial F}{\partial t^*} \right)^2 e^{-E(F/A)}$$

Parks cont.

$$\frac{\partial^2 W_t}{\partial t^* \partial T_0} = \frac{E}{A} (A - W_0) \frac{\partial^2 F}{\partial t^* \partial T_0} e^{-E(F/A)} - \frac{E^2}{A^2} \left[(A - W_0) \frac{\partial F}{\partial t^*} \right]^2 \frac{\partial F}{\partial T_0} e^{-E(F/A)}$$

$$\text{where } \frac{\partial^2 F}{\partial t^* \partial T_0} = \frac{A}{T_0^2} (1 - D/A) [(1 - e^{-t/t^*}) - t/t^* e^{-t/t^*}]$$

$$\frac{\partial^2 W_t}{\partial E \partial t^*} = \frac{1}{A} \frac{\partial F}{\partial t^*} (A - W_0) e^{-E(F/A)} + \frac{F^2}{A^2} (A - W_0) \frac{\partial F}{\partial t^*} e^{-E(F/A)}$$

$$\frac{\partial^2 W_t}{\partial t^* \partial A} = \frac{W_0}{A^2} \frac{F}{t^*} e^{-E(F/A)} + (E - \frac{W_0}{A}) \frac{\partial^2 F}{\partial t^* \partial A} e^{-E(F/A)} - E(E - \frac{W_0}{A}) \frac{\partial F}{\partial t^*} \frac{\partial(F/A)}{\partial A} e^{-E(F/A)}$$

$$\text{where } \frac{\partial^2 F}{\partial t^* \partial A} = - \left(\frac{1}{T_0} - \frac{D^2}{A^2} \right) [(1 - e^{-t/t^*}) - (t/t^* e^{-t/t^*})]$$