

## CHAPTER 3

NONLINEAR MODELS AND THEIR STRUCTURAL PARAMETERS  
AS DESCRIPTORS OF GROWTH IN A MOUSE POPULATION

## 3.1 INTRODUCTION

The growth curve of an animal fed *ad libitum* is commonly characterised by a sigmoid curve, the rate of growth being initially low but increasing until it reaches a maximum and then slowly declining to zero at the animal's mature size or weight. This type of growth, although not ubiquitous, is nonetheless sufficiently common as to have warranted considerable investigation into the development of equations to describe this type of curve.

Two approaches to the historical development of growth equations have been made. One school is devoted to the mathematical description of growth in purely empirical terms, and the other is more concerned with the aetiology of growth, that is, with the 'why' of growth (Parks, 1972b). More recently, attempts have been made to reconcile the two approaches and combine them (Blaxter, 1968; Parks, 1972a, 1972b, 1975, 1982; Monteiro, 1975; Roux, 1974, 1976).

### 3.1.1 Growth Models as Output Descriptors

#### I. The Polynomial Function.

Considering  $m$  repeated observations, as in the growth curve of an individual, a simplistic view is the construction of a polynomial of degree  $n < m$  in terms of time,  $t$ . Such a method has been used to create a large number of tables of smooth growth data (Brody, 1945). The basic problem is well known and documented; extrapolation of polynomials produces nonsense. Functions of the polynomial type can be used safely only within the range of the experimental data. Although polynomials are formidable mathematically and often provide very good fits to the data, 'goodness of fit' is not necessarily sufficient justification for using a function (Grossman, 1969).

#### II. Brody's Exponential Function.

Brody (1945) divided the growth curve into two segments, the division being the point of inflection in the weight/age curve. His analysis of growth data from a number of different species appeared to show that the slope of the curve just prior to  $t'$  (Fig. 3.1) was different to the slope just past  $t'$ . This he associated with age at puberty and as a discontinuity in the growth rate curve. Growth prior to  $t'$  was designated as being the 'self-accelerating' phase and after  $t'$  the region of 'self-inhibiting' growth. Thus, Brody (1945) suggested two independent growth curves.

The first describes growth prior to puberty or the point of

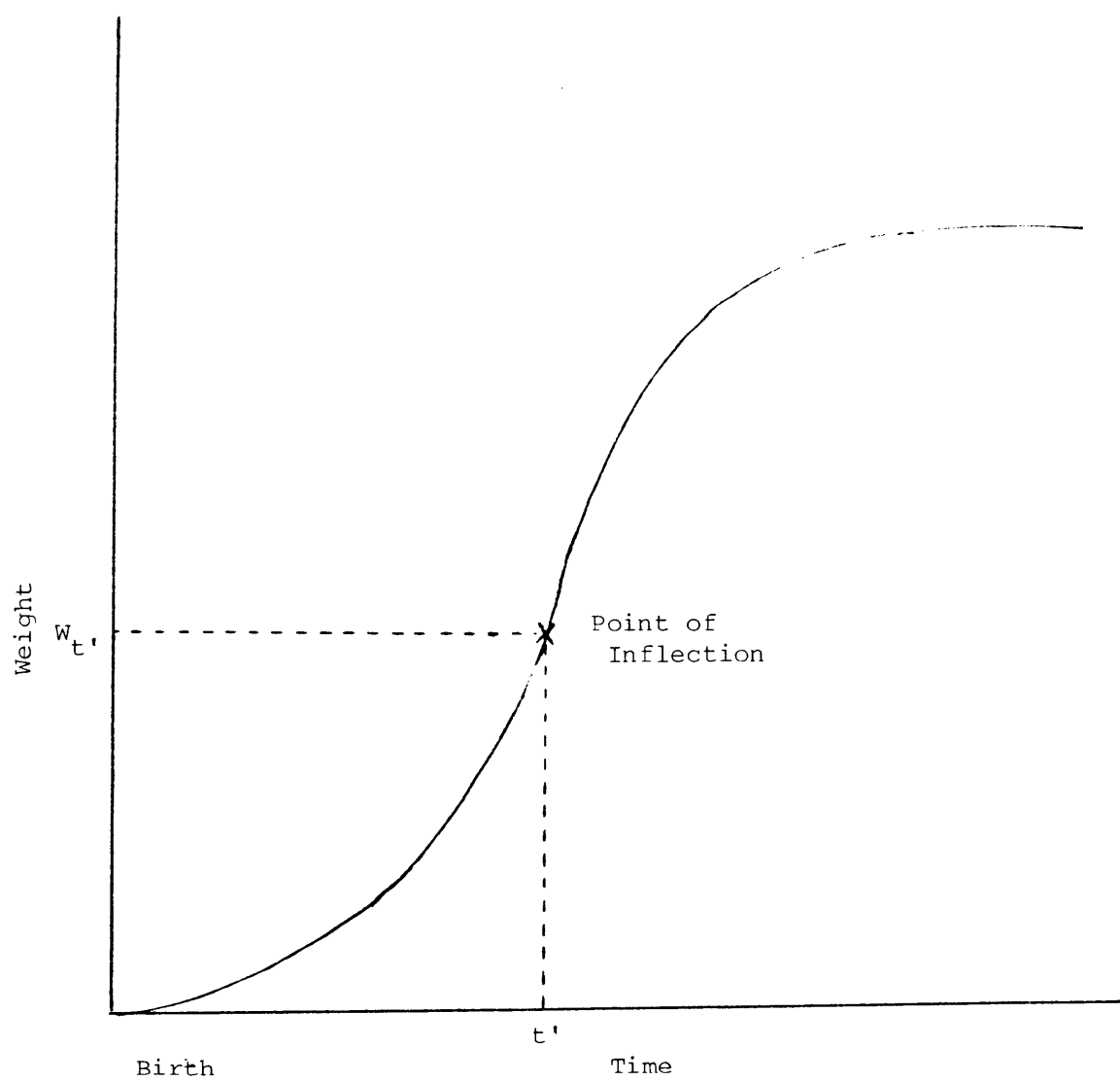


Figure 3.1: Sigmoidal growth pattern.

inflection, where the instantaneous rate of gain  $\frac{dW_t}{dt}$  is proportional to the growth already made.

The function describing the instantaneous growth rate was

$$\frac{dW_t}{dt} = kW_t \quad (3.1)$$

where,  $k$  is the growth rate constant or, as will be shown, the exponential growth constant, and  $W_t$ , is the weight of the animal at time  $t$ .

Re-arranging 3.1 and integrating with respect to time, from  $t'$  to  $t$ , Brody obtained

$$\begin{aligned} \frac{dW_t}{W_t} &= k dt \\ \int_{t'}^t \frac{dW_t}{W_t} &= k \int_{t'}^t dt \\ \ln W_t - \ln W_{t'} &= k (t-t') \\ W_t &= W_{t'} e^{k(t-t')} \end{aligned} \quad (3.2)$$

where,  $\ln$  is the natural logarithm, and  $W_{t'}$  = initial weight when  $t' = 0$ .

The second curve describes growth in the 'self-inhibiting' phase. The premise is that the tendency for growth is limited and

the rate of gain is proportional to the amount of growth to be made in order to reach the mature weight, A.

Instantaneous growth rate was described as

$$\frac{dW_t}{dt} = -k'(A - W_{t'}) \quad (3.3)$$

where,  $k'$  is the growth rate constant.

Re-arranging equation 3.3 and integrating with respect to time from  $t'$  to  $t$

$$\begin{aligned} \frac{dW_t}{(A-W_{t'})} &= -k' dt \\ \int_{t'}^t \frac{dW_t}{(A-W_{t'})} &= -k' \int_{t'}^t dt \\ W_t &= A - (A - W_{t'}) e^{-k'(t-t')} \end{aligned} \quad (3.4)$$

where,  $W_{t'}$  is the initial weight of the animal.

Criticisms of Brody's model stem from his reasons for splitting the growth curve into two segments at the point of inflection. The argument for the discontinuity being related to age at puberty is dubious, for example, in chickens the point of inflection occurs at about 12 - 14 weeks of age, where age at sexual maturity is about 20 weeks (Grossman, 1969). Brody, however, argues that many such discontinuities may occur in the growth curve. The true basis for

criticism is more aligned to the subjectiveness with which the partitioning may be done.

A further criticism of Brody's approach is that  $k$  (equation 3.2) is not necessarily equal to  $k'$  (equation 3.4). Although not a serious criticism, since growth rate may change over the total growth curve, the estimated values of  $k$  and  $k'$  will depend upon the partitioning. Finally, it is well documented that correlations exist between pre- and post-pubertal weights, a fact not recognised by partitioning the growth curve.

### III. The Bertalanffy Function

Bertalanffy (1938, 1957, 1960) suggests that the rate of growth of an animal is the result of the processes of anabolism and catabolism. In the equation

$$\frac{dW_t}{dt} = \alpha W_t^M - \beta W_t \quad (3.5)$$

$\alpha$  and  $\beta$  are the constants of anabolism and catabolism. Based on Bertalanffy's exposition of the 'surface rule',  $M$  was used as a metabolic index. Three metabolic types were suggested

- 1) Metabolic rate is proportional to a surface or the 2/3 power of weight ( $M = 2/3$ ), e.g., fish and mammals.
- 2) Metabolic rate is proportional to weight itself ( $M = 1$ ).
- 3) Metabolic rate is intermediate, i.e. neither proportional to

the surface area or to liveweight ( $2/3 < M < 1$ ).

Re-arranging and integrating 3.5 with respect to time

$$\int_{t'}^t \frac{dW_t}{W_t (1 - \frac{\alpha}{\beta} W_t)^{M-1}} = -\beta \int_{t'}^t dt = -\beta (t-t')$$

$$W_t = \left[ \frac{\alpha}{\beta} - \left( \frac{\alpha}{\beta} - W_{t'} \right)^{(1-M)} \exp(-\beta (1-M) (t-t')) \right]^{\frac{1}{1-M}}$$

this is commonly reduced to

$$W_t = [A^{1/3} - (A^{1/3} - W_0^{1/3}) e^{-k't/3}]^3 \quad (3.6)$$

where  $W_0 = W_{t'}$ , the initial weight at  $t = 0$

$A$  = mature weight

$M$  is inserted, based on the metabolic type of animal. In mammals, the value  $2/3$  is commonly used.

From equation 3.6 the weight at maximum rate of gain or point of inflection (POI) is given by

$$W_{POI} = \frac{8A}{27}$$

Substituting this result in 3.6 and solving for  $t$ , age at the point of inflection is given by

$$t_{POI} = \frac{1}{k} (3.296 + 3 \log_n \left( \frac{A}{3} - (A^{1/3} - W_0^{1/3}) \right)).$$

Richards (1959) objected to some assumptions contained in the derivation of Bertalanffy's growth equation. For example, Richards suggested that values of  $M > 1$  are rejected, not because they do not occur biologically, but with such values the constants for catabolism ( $\beta$ ) and anabolism ( $\alpha$ ) would be negative, invalidating their interpretation as such.

Possibly the most severe criticism of a Bertalanffy function is the 'pretence' of biological foundation. The conclusion that anabolic factors act in proportion to surface area and catabolic factors in proportion to volume is based on rationalisation rather than evidence and thus is yet to be proved.

#### IV. The Gompertz Function

The Gompertz function was originally developed to describe death rates in a population. The Gompertz presents rate of gain as a function of the weight of the individual and the gain to be made.

$$\frac{dW_t}{dt} = kW_t (\ln A - \ln W_t) \quad (3.7)$$

Integrating 3.7 with respect to time,

$$\int_{t'}^t \frac{dW_t}{W_t (\ln A - \ln W_t)} = k \int_{t'}^t dt$$

$$W_t = Ae^{-(\ln A - \ln W_{t'})e^{-k(t-t')}} \quad (3.8)$$



where A = mature weight

$W_{t'}$  = initial weight at  $t'$

k = growth rate constant

t = time.

From 3.8, the weight at maximum gain or the point of inflection is given by

$$W_{POI} = \frac{A}{e} = \frac{A}{2.7183}$$

Substituting this result in 3.8 and solving for t, age at point of inflection (POI) is

$$t_{POI} = \frac{1}{k} (\ln A - \ln W_0) + t'$$

if  $W_0$  is birth weight at  $t' = 0$ .

Although the Gompertz equation has no biological meaning, it has been used widely and in various forms (Brody, 1945; Laird *et al.*, 1965; Laird and Howard 1967; Parks, 1970; Roux, 1974). In situations where extensive growth data are available, this equation often fails to fit the last 'linear' part of the growth curve, as it tends to overpredict the growth response (Laird *et al.*, 1965; Meissner, 1977).

Roux (1976) and Meissner (1977) suggest that the criticisms relating to the lack of biological meaning do not apply when the Gompertz is written on the logarithmic scale, because then it is equivalent to the law of diminishing returns. Roux (1974, 1976)

attests to the biological significance of the 'law of diminishing returns' by illustrating how the parameter describing the proportional growth rate with time can be partitioned. The logarithmic form is given as

$$X_i = \alpha_i - \beta_i \exp(-\gamma t) \quad (3.9)$$

where,  $X_i = \ln W_t$ ,  $\alpha_i = A$  at  $t = \infty$ ,  $\beta_i = \text{constant}$  and  $\gamma = \text{proportional growth rate}$  which can be expressed in terms of its components:

$$\gamma = C (1 + b_2^2 + b_3^2 + b_4^2) \quad (3.10)$$

where  $C$  is a constant and  $b_2, b_3, b_4$  are distribution coefficients of heat production, protein and fat.

The Roux model is discussed in greater detail later.

#### V. The Logistic Function.

The logistic function developed in 1838 by Verhulst (cited by Grossman, 1969) has been used extensively to describe weight by time data. It has the following properties: firstly, there is a point of inflection (when rate of gain is maximum); secondly, there is an upper asymptote, where rate of gain tends toward zero; and thirdly, zero is the lower asymptote or limiting point.

Equation 3.11 is the rate of gain equation from which the logistic can be derived and indicates that the instantaneous rate of gain is a function of both growth already made and the potential for

growth to be made.

$$\frac{dW_t}{dt} = kW_t \left( \frac{A-W_t}{A} \right) \quad (3.11)$$

Re-arranging and integrating 3.11 with respect to time from  $t'$  to  $t$ , we obtain

$$\frac{dW_t}{W_{t'} \left( \frac{A-W_{t'}}{A} \right)} = k dt$$

$$\int_{t'}^t dW_t \left( \frac{1}{W_{t'}} + \frac{1}{A-W_{t'}} \right) = k \int_{t'}^t dt$$

$$W_t = A \left[ 1 + \left( \frac{A-W_{t'}}{W_{t'}} \right) e^{-k(t-t')} \right]^{-1} \quad (3.12)$$

where  $A$  = mature weight

$W$  = initial weight; at  $t' = 0$ ,  $W_{t'} = W_0$

$t'$  = initial age;

$k$  = growth rate constant

Solving 3.12 for weight at the inflection point

$$W_{POI} = A/2.$$

Thus, weight at the point of maximum gain is exactly one half of the mature weight. Similarly, if we substitute  $W_{POI}$  in 3.12, age at point of inflection is found as

$$t_{POI} = 1/k [\ln(A-W_{t'}) - W_{t'}] + t'$$

when,  $W_{t'} = W_0$  and  $t' = 0$ .

$$t_{POI} = 1/k [ \ln (A - W_0) - W_0 ]$$

The first problem with the logistic is already apparent, namely, the curve is symmetrical about the point of inflection. Empirically, the growth curves for a number of species of animals have been shown to be asymmetrical (Grossman, 1969). Criticisms of the logistic generally follow the same arguments as those against the Gompertz, Brody and Bertalanffy and will not be considered further at the moment.

#### VI. The Generalised Logistic

Nelder (1961) described a four parameter function defined by the differential equation

$$\frac{dW_t}{dt} = kW_t \left[ 1 - \left( \frac{W_t}{A} \right)^{1/\theta} \right] \quad (3.13)$$

This function is a generalization of the logistic equation. When  $\theta = 1.0$ , equation 3.13 is equivalent to 3.11. To overcome the initial restrictions on 3.13, namely that  $\theta$  be greater than zero, Nelder (1962) reparameterised 3.13 to

$$\frac{dW_t}{dt} = kW_t \left( 1 - \left( \frac{W_t}{A} \right)^z \right) \quad (3.14)$$

by letting  $z = \frac{1}{\theta}$ . Integrating 3.14 with respect to time, from  $t'$  to  $t$ ,

$$W_t = \frac{A}{\left( 1 + \left[ \left( \frac{A}{W_{t'}} \right)^z - 1 \right] e^{-zk(t-t')} \right)^{1/z}} \quad (3.15)$$

The interpretation of  $z$  must be similar to  $\theta$ ; however, both are difficult to specify in relation to the biology of the animal.

The most important consequences of equation 3.15 are the resulting point of inflection co-ordinates.

$$W_{POI} = A/(z + 1)^{1/z}$$

and

$$t_{POI} = \frac{\ln(A_z - W_t^z) - \ln(W_t^z) - \ln(z)}{zk} + t'$$

The point of inflection is not fixed as a proportion of the final weight ( $A$ ), so that this function is much more flexible than any of the previous equations.

#### VII. The Richards' Function

Richards (1959) proposed that the Brody, Bertalanffy, Logistic and Gompertz were all special cases of the general indeterminate form;

$$W_t = A(1 + be^{-kt})^M \quad (3.16)$$

$M > 1$  upper sign (-)

$M < 0$  lower sign (+)

$M = (1-m)^{-1}$  used by Richards

$A$  = asymptotic weight as  $t \rightarrow \infty$

$b$  = 'a constant of integration'

$k$  = commonly referred to as the maturing index, also sometimes referred to as the 'intrinsic growth rate constant' (Grossman, 1969).

Fitzhugh (1976) has explained, in detail, parameter derivation and characteristics of equation 3.16. A summary of some of the relationships to the other functions are shown in Table 3.1, which is adapted directly from Fitzhugh (1976).

#### VIII. Derived Characters

A number of characters with plausible biological meaning can be derived from the various growth functions.

##### a) Point of Inflection (P.O.I.)

Inflection in the growth data marks the approximate weight of the animal at which the rate of increase begins to decrease. The rates prior to the P.O.I. and after the P.O.I. determine the shape of the weight-age curve.

Although inflection has often been associated with sexual maturity, this association is purely empirical and as such, any conclusions or inferences regarding the point of inflection must be treated with caution.

Any interpretation concerning the inflection should involve the relationship that exists between the P.O.I. and asymptotic limits. If an individual's asymptotic weight is under genetic control, then the P.O.I. is also under genetic control. Nevertheless, it is difficult to conceive the inflection point as being anything other than the age and weight at which the complexities of an energy dependent system have reached a maximum.

TABLE 3.1

EQUATIONS AND CHARACTERISTICS FOR SPECIAL CASES OF THE RICHARDS' GROWTH FUNCTION<sup>a</sup>

Model	Equation for $w_t$	M	$\mu_{POI}$	Asymptote	$\frac{dw_t}{dt}$ [1]	$A^{-1} \frac{dw_t}{dt}$ [2]	$w_t^{-1} \frac{dw_t}{dt}$ [3]
Brody	$A(1 - be^{-kt})$	1	-	A	$kA(1-\mu)$	$k(1-\mu)$	$k(\mu^{-1}-1)$
Bertalanffy	$A(1 - be^{-kt})^3$	3	8/27	A	$3kw_t(\mu^{-1/3}-1)$	$3k\mu(\mu^{-1/3}-1)$	$3k(\mu^{-1/3}-1)$
Logistic	$A(1 + be^{-kt})^{-1}$	-1	0.5	A	$kW_t(1-\mu)$	$k\mu(1-\mu)$	$k(1-\mu)$
Gompertz	$A \exp(-be^{-kt})$	$M \rightarrow \infty$	$e^{-1}$	A	$kW_t \ln(\mu^{-1})$	$k\mu \ln(\mu^{-1})$	$k \ln(\mu^{-1})$
Richards	$A(1 \mp be^{-kt})^M$	Variable	$[(M-1)/M]^M$	A	$MkW_t(\mu^{-1/M}-1)$	$Mk\mu(\mu^{-1/M}-1)$	$Mk(\mu^{-1/M}-1)$

<sup>a</sup>Adapted from Fitzhugh (1976).

[1] Instantaneous absolute growth rate.

[2] Absolute maturing rate.

[3] Instantaneous growth rate.

Models which have fixed inflection points are obviously of less value in terms of their biological applicability when compared with those having variable inflection points.

b) Asymptotic Weight

Genetically, the asymptotic weight represents the size potential of the animal. It is interpreted as being the average size at maturity independent of short-term fluctuations due to environmental variations in nutrition and climate.

All functions described, except the polynomial, enable estimation of the asymptotic weight directly from the equation (Table 3.1).

c) Grossman (1969), Brown (1970), Brown *et al.* (1976) and Fitzhugh (1976) describe a number of characters that can be derived from growth equations relating weight to age. Brown *et al.*, and Fitzhugh were concerned with the Richards' function and its special cases. They proposed a number of characters based on the Richards' function (equation 3.16) which are summarised below and in Table 3.1.

1. The instantaneous absolute growth rate: The instantaneous absolute growth rate is the ratio of differentials of the derivative,

$$\begin{aligned} \frac{dW_t}{dt} &= \pm \frac{Mk}{W_t} be^{-kt} (1 \mp be^{-kt})^{-1} \\ &= \pm \frac{MAk}{W_t} be^{-kt} (1 \mp be^{-kt})^{-1} \end{aligned}$$



if  $\mu_t = W_t/A$ , then

$$\frac{dW_t}{dt} = MkW_t (\mu^{-1/M-1})$$

2. Instantaneous growth rate and absolute maturing rate:

Formulae for the instantaneous growth rate ( $W_t^{-1}dW/dt$ ), and absolute maturing rates ( $A^{-1}dW/dt$ ) are presented in Table 3.1.

3. Weighted average lifetime rates:

$$\text{Absolute Growth Rate} = \frac{0.5 MAk}{2M-1}$$

$$\begin{aligned} \text{Absolute Maturing} \\ \text{Rate} \end{aligned} = \frac{0.5 Mk}{2M-1}$$

$$\text{Relative Growth Rate} = \frac{Mk}{M-1}$$

4. Instantaneous rates at the P.O.I. ( $W_{POI}, t_{POI}$ )

$$\text{Absolute Growth Rate} = \left(\frac{Mk}{M-1}\right) W_{POI}$$

$$\begin{aligned} \text{Absolute Maturing} \\ \text{Rate} \end{aligned} = k \left(\frac{M-1}{M}\right)^{M-1}$$

$$\text{Relative Growth Rate} = \frac{Mk}{M-1}$$

In addition to the above characters, Fitzhugh and Taylor

(1971) have suggested an 'equation-free' model,  $W_t = \mu_t A$ . The primary concern is the attainment of an adequate measure of the mature weight. They suggest a number of growth traits that may be derived from their model,

$$\text{Average absolute growth rate (A.G.R.)} = \frac{W_{t_2} - W_{t_1}}{(t_2 - t_1)}$$

$$\text{Average absolute maturing rate (A.M.R.)} = \frac{(\mu_2 - \mu_1)}{(t_2 - t_1)}$$

$$\text{Average relative growth rate (R.G.R.)} = \frac{\ln W_{t_2} - \ln W_{t_1}}{(t_2 - t_1)}$$

They also suggest the use of 'age at a given degree of maturity' ( $t_\mu$ ) as a measure of time taken to mature.  $t_\mu$  is similar to the 'k' parameter of the nonlinear models (Fitzhugh, 1976), both attempt to characterise individuals as either early or late maturing. Fitzhugh (1976) suggests  $t_\mu$  or  $\ln t_\mu$  allows more flexibility than k, since k is a constant of the whole growth period. The use of  $t_\mu$  is less likely to obscure interesting sources of variation in maturing patterns.

In addition to characters derived from the various growth functions, interest in the directly measurable characteristics of growth are of considerable importance. Knowledge of the associations between various growth function characters and such traits as weight gains over specific growth periods, specific weights, feed conversion efficiency, feed conversion ratio and feed intake is of considerable importance in determining selection criteria and responses.

### 3.1.2 Growth Models as Input/Output Descriptors

#### I. Blaxter and Monteiro's model of energy intake and retention.

Blaxter (1968) derived the following equation to describe the increase in body mass with time,

$$W - W_0 = k_m (M - M_0) \frac{k_m}{k_f} \frac{W_0^{1-n}}{A_n} \left[ 1 - \exp \left( - \frac{k_f}{k_m} \frac{A_n W_0^{n-k_f}}{B} \right) \right] \quad (3.17)$$

Equation 3.17 is the approximate solution of the differential equation relating rate of energy intake and rate of energy retention, expressed as

$$\frac{dW_t}{dt} = \frac{Mk_f}{B} - \frac{AW^n k_f}{Bk_m}$$

or  $M = \frac{BdW_t}{k_f dt} + \frac{AW^n}{k_m} \quad (3.18)$

3.18 redefines 3.17 as the relationship between rate of energy retention and feed intake above maintenance, where for both 3.17 and 3.18

$\frac{BdW_t}{dt}$  = rate of energy retention (B = caloric value of grains)

$k_f$  = efficiency of utilisation of metabolisable energy (M.E.) for growth and fattening

$AW^n$  = fasting metabolism expressed in terms of body mass

$k_m$  = efficiency of utilisation of metabolisable energy  
for maintenance

$M$  = rate of intake of metabolisable energy.

Equation 3.17 illustrates the asymptotic approach of body mass to a new value of  $M$  when the animal's diet is changed from a maintenance value,  $M_0$  to a new value  $M$ , and then kept constant. It is also notable that as  $B$  decreases, that is, the less fat and higher the contents of protein and associated water, the more rapid the approach to the new equilibrium.

Monteiro (1975) adopted a similar approach, but under the simplifying assumptions,

- i) animal growth is composed primarily of two components, fat and fat-free tissue plus an increase in the contents of the digestive tract,
- ii) nutritive requirements for the deposition of these tissues are independent of the age and stage of growth.

Equation 3.19 attempts to partition feed intake between maintenance requirement and feed utilised for growth of fat and non-fat components.

$$F_t = \beta \sum_{i=1}^t \mu_i M^{0.73} (1 - 0.54 \ln \mu_i) + \phi (W_t - W_0) + \gamma W_t^b + k \quad (3.19)$$

where,  $F_t$  = cumulative food intake up to time  $t$

$\beta$  = a coefficient representing the expected mature maintenance requirement per unit of mature metabolic body mass

$\mu_i$  = the degree of maturity in body mass at time  $i = 1, 2, 3 \dots t$

$M$  = estimated mature body mass

$\phi$  = 'fat' parameter, which includes a conversion coefficient of fat

$W$  = body mass

$\gamma$  = 'fat-free' parameter, which includes a conversion coefficient of fat-free tissue.

$b$  = parameter estimating the relative changes in body composition occurring during growth

$k$  = constant, which represents fat-free body mass in feed units at time  $t = 0$ .

Both equations 3.17 and 3.19 imply an additivity of the growth processes in the ordinary scale, which is not necessarily so for the total growth period from birth to senescence. A problem with this approach arises from the very high correlation between maintenance requirement and energy retention (Roux pers. comm). In essence this would make estimation of the conversion coefficients,  $\phi$  and  $\gamma$ , incalculable by conventional least squares procedures.

## II. Parks' Input/Output Models

Parks (1970) extended the work of Brody (1945) and Hendricks, Jull and Titus (1931) by observing that 'the law of diminishing returns' describes the relationship between *at libitum* feed intake

and age - thus describing the animal as an input-output device. Parks has since elaborated on this approach (Parks, 1972a, b; 1973; 1975; and 1982). The mathematical basis for the model formulation is by the differential equation

$$\frac{dW}{dt} = \left(\frac{dW}{dF}\right) \left(\frac{dF}{dt}\right) \quad (3.20)$$

Simply stated, growth rate,  $\frac{dW}{dt}$ , is a product of the 'true' growth efficiency,  $\frac{dW}{dF}$ , and feed intake,  $\frac{dF}{dt}$ . The term 'true' growth efficiency is used because it is the ratio of the differential change in output,  $dW$ , to the differential change in input,  $dF$ .

Parks' theory suggests that a combination of three continuous functions, related directly by equation 3.20, could describe weight in the time and food domains. The three equations are

$$\frac{dF}{dt} = (C - D) (1 - \exp(-t/t^*)) + D \quad (3.21)$$

where,  $\frac{dF}{dt}$  = feed intake at time  $t$

$D$  = initial feed intake at  $t = 0$

$C$  = mature feed intake

$t^*$  = time taken to reach approximately 63% of the mature feed intake.

Integrating 3.21 over time

$$F_t = C(t-t^* (1-D/C) (1-\exp(-t/t^*))) \quad (3.22)$$

where,  $F_t$  = cumulative food consumed to time  $t$   
 Parameters  $C$ ,  $D$  and  $t^*$  are as above.

The Liveweight-Cumulative Food Consumed function is given  
 as

$$W_t = (A - W_0) \left( 1 - \exp \left( - (AB) \frac{F_t}{A} \right) \right) + W_0 \quad (3.23)$$

where,  $F_t$  is given by equation 3.22

$A$  = estimated mature weight  
 $(AB)$  = 'efficiency' factor  
 $W_0$  = initial liveweight.

Substituting 3.22 into 3.23

$$W_t = (A - W_0) \left( 1 - \exp \left( \left[ - (AB) C / A \right] \left( t - t^* (1 - D / C) (1 - \exp (-t / t^*)) \right) \right) \right) + W_0 \quad (3.24)$$

Equations 3.21, 3.22 and 3.23 form the basis of Parks' theory of growth in the food-time domains. Equation 3.24 relates feed intake and weight in the time domain.

When information is not available on feed intake, a common situation for animal data,  $C$  and  $(AB)$  cannot be estimated. The relation  $(AB)C/A$  is replaced by  $k$  so that equation 3.24 becomes

$$W_t = (A - W_0) \left( 1 - \exp \left( -k \left( t - t^* (1 - \exp (-t / t^*)) \right) \right) \right) + W_0 \quad (3.25)$$

where,  $W_t$  is weight at time  $t$ ,

parameters  $A$ ,  $W_0$  and  $t^*$  are synonymous to the above

$k$  = Brody's maturing rate constant.

Parks (1982) suggests that by plotting the input and output relations in a 3-dimensional plane we arrive at a more useful approach to growth. After standardisation of the three variables so that

a) Fraction of maturity at age  $t$ ;  $\mu_t = \frac{W_t}{A}$

b) Standardised age;  $T = t/t^*$

c) Normalised Food Equivalents;  $Z = C(AB)F_{t/A}$

Figure 3.2 shows a plot of the animal's growth against these variates. Parks named this curve the 'biotrace' of the animal.

A further geometric representation of growth in the 3-dimensional euclidean space promoted the concept of the *ad libitum* growth phase curve. Time ( $t$ ), feed intake ( $q^*$ ) and weight ( $W$ ) are plotted together (Fig. 3.3). The weight versus  $q^*$  plane, with height  $A$  and width  $C$ , is called the Growth Phase Plane (Fig. 3.4).

The diagonal from the origin  $(0, 0)$  to  $(C, A)$  has slope  $A/C$  equal to  $T_0$ , the 'Taylor Time Constant', which can replace the relation  $A/C$  in equation 3.24. From equation 3.20, Parks reformulates the input/output relations in the following way for the *ad*



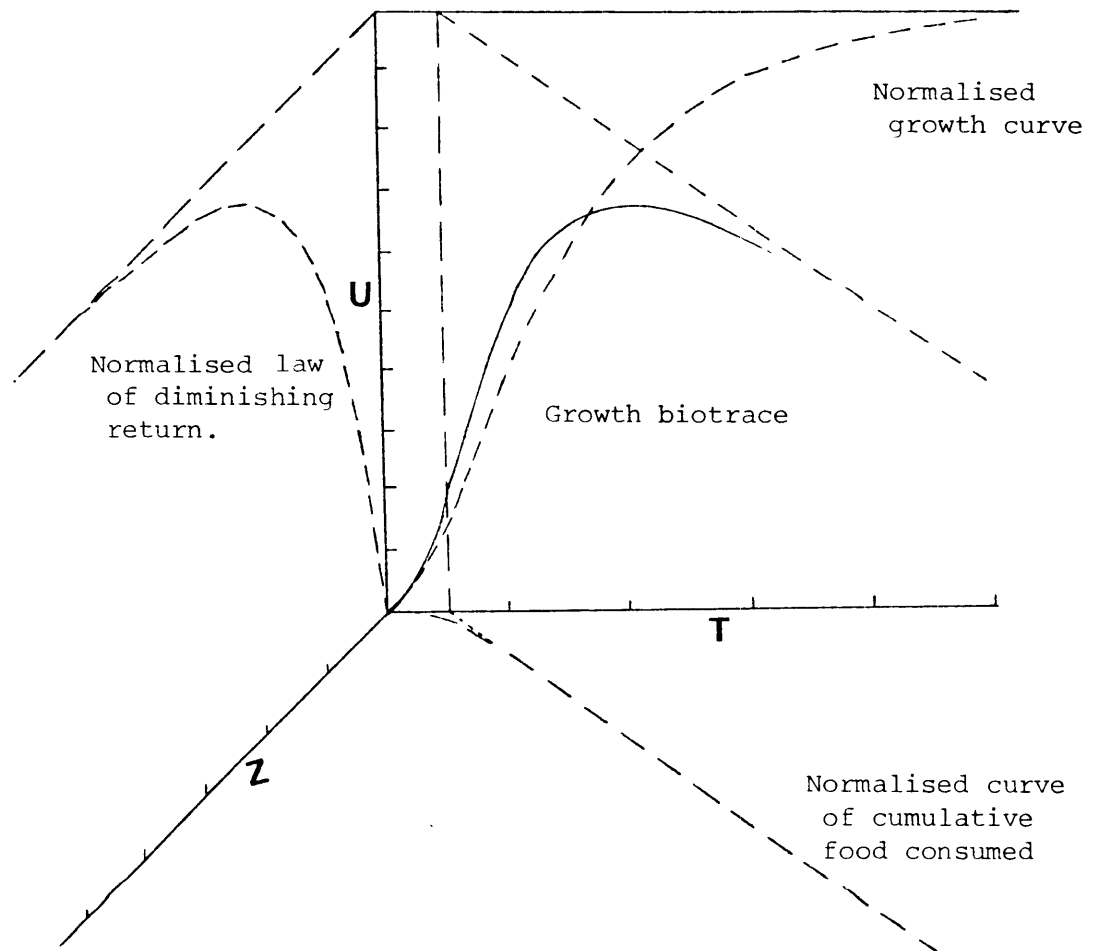


Figure 3.2: Normalised growth curves (Source: Parks (1982)).

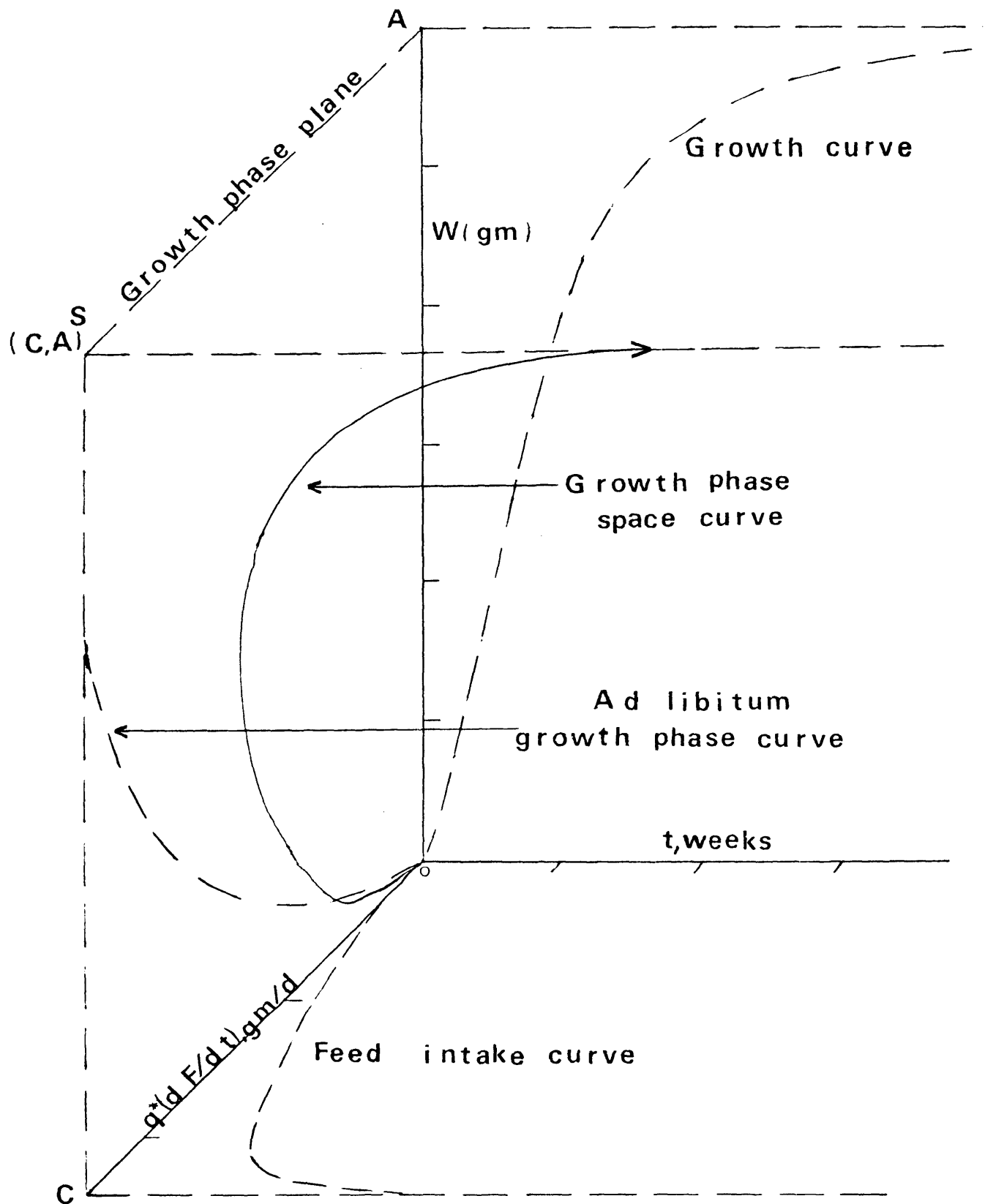


Figure 3.3: Growth in a 3-dimensional plane (Source: Parks (1982)).

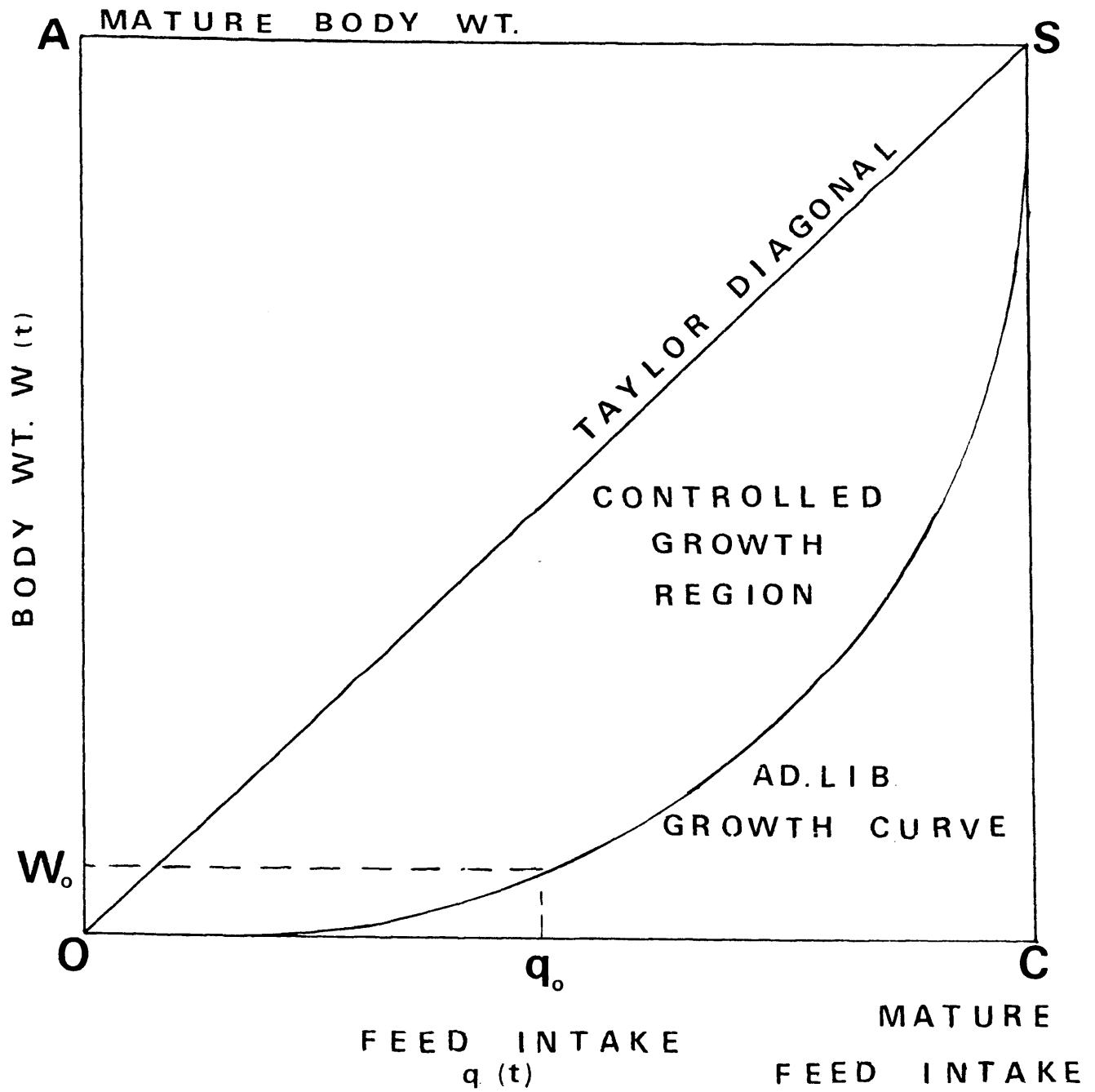


Figure 3.4: The growth phase plane and Taylor diagonal  
(Source: Parks (1982)).

*libitum* feeding situations,

$$\frac{dq^*}{dt} + \left(\frac{1}{t^*}\right) q_t^* = (A/T_0) t^* \quad (3.26)$$

$$\text{and} \quad \frac{dW}{dt} + \left(\frac{(AB)q_t^*}{A}\right) W_t = (AB)q_t^*$$

where,  $q_t^*$  is  $dF/dt$ , the feed intake function (eq. 3.21).

$(AB)q_t^*$  is the liveweight equivalent of feed intake which is partitioned between growth,  $\frac{dW}{dt}$ , and 'no-growth',  $\left(\frac{(AB)q_t^*}{A}\right)W_t$ . The 'no-growth' component includes maintenance requirements, purely in an energetic sense, and also unknown factors contributing to a portion of the feed intake being directed to other than to weight gain.

Park's equations 3.20 - 3.24 appear to satisfy the requirements for characterising both the output and input relationships of growth, namely, that growth is continuous and possesses continuous rates of change of all orders, the first order of change being  $\frac{dW}{dt}$ .

Parks utilised concepts of the above equations for growth in both time and food domains to formulate the biological interpretations for the nonlinear parameters. In addition to the descriptions given above, Parks (1982) presents the following:

$t^*$	The internal resistance to build up of appetite.
$C/t^*$ or $A/T_0 t^*$	Internal drive of the animal to increase

	its appetite toward the maximum $C$ .
$q^*(t)$	Rate of change of the cumulative food consumed, Appetite.
$T_0$	'efficiency of maintenance' of equilibrium weight. Changes in $T_0$ relate to changes in the liveweight equivalent of feed intake being directed toward growth in body mass.
$Z(t)$	$Z(t) = (AB)F(t)/A$ ; the body weight equivalent of cumulative food consumed in units of the mature weight, $A$ .

There are few examples of the application of equations 3.21, 3.22, 3.23 and 3.24. Parks (1982) has subjected his modelling techniques to a vast array of weight and feed intake data and attests strongly to their appropriateness in a number of situations.

### III. Roux's Input/Output Model

Roux (1974, 1976) attempted to link two fields of growth curve analysis, combining the empirical descriptions of the Gompertz equation and multivariate allometry, with biological principles of growth.

Several authors have recognised the concept of allometry in growth (Huxley, 1932; Brody, 1945; Bertalanffy, 1960). The principle of allometric growth simply states that the relative growth of a body component is in constant ratio to the relative growth of the body as a whole. Roux (1974, 1976) and Meissner *et al.* (1975) have attempted to relate body mass, the components of the body (e.g. fat, protein) and heat production to cumulative food intake by an

allometric equation describing an input-output system of growth.

By assuming that the two variables of equation 3.27 follow a Gompertz relationship in time, Roux suggested that an allometric relationship would be evident between the variables. Thus, if the two variables are allometrically related they can be linearly related on a logarithmic scale.

$$w(t) = a v^b \quad (3.27)$$

$$\log w(t) = \ln a + b \ln v(t)$$

where,  $w(t)$  is weight at time  $t$

$v(t)$  is cumulative total digestible nutrients at time  $t$ .

If  $x_1(t) = \ln v(t)$  and  $x_2(t) = \ln w(t)$ , then from Roux (1976) and Meissner (1977)

$$x_1(t) = \alpha_1 - \beta_1 \exp(-\gamma t) \quad (3.28)$$

$$x_2(t) = \alpha_2 - \beta_2 \exp(-\gamma t) \quad (3.29)$$

Note, the allometric relationship between the two variables can only hold when  $\gamma$  from equations 3.28 and 3.29 are equal. It follows from 3.28 and 3.29 that

$$x_2(t) = \left(\alpha_2 - \frac{\beta_2}{\beta_1} \alpha_1\right) + \frac{\beta_2}{\beta_1} x_1(t)$$

or  $x_2 = a + bx_1$

$$\text{where, } b = \frac{\beta_2}{\beta_1} \text{ and } a = (\alpha_2 - \frac{\beta_2}{\beta_1} \alpha_1) \quad (3.30)$$

Equation 3.30 is an allometric equation in linear form.

Roux (1976) suggested that by multivariate allometry,  $\gamma$  in 3.28 and 3.29 could be partitioned into biological components, i.e.

$$\gamma = c(1 + b_2^2 + b_3^2 + b_4^2)$$

where,  $c = \text{constant}$ ,

$b_2, b_3, b_4 = \text{distribution coefficients of heat production, protein and fat respectively.}$

Meissner (1977) suggested that as protein and fat contents of the body are also related to cumulative food intake they can be substituted in equation to 3.27 for  $W(t)$ . The parameters  $\alpha$  and  $\beta$  for protein can be obtained from equation 3.28.

The approach of Roux to input/output modelling has obvious appeal in the ability to differentiate between individuals in relative growth rates of fat, protein, body heat and mass. However, detailed information is necessary from slaughter analyses to provide accurate predictions. Roux (pers. comm.) recognises that the model tends to suffer from disjunctures at various points on the log-log scale, and can only be expected to hold for the period of active growth; the model does not hold for animals at maturity.

### 3.1.3 Experimental Objectives

Within the framework of the projects' goals, set out in

Chapter 1, a series of objectives were formulated for the studies undertaken in this chapter.

1. to examine the accuracy and predictive ability of each model.
2. to determine the magnitude of the genetic variation for any particular parameter of a given model.
3. to investigate the phenotypic and genetic relationships between the parameters of a particular model and body weights, measures of growth rate, feed intake and feed efficiency.
4. to determine the extent to which parameters of a particular model may be used as selection criteria to change the structure of the weight/age growth curve.

### 3.2 MATERIALS AND METHODS

A detailed description of the mice and management practices used in this study was given in Chapter 2. Individual weights were recorded from birth to 84 days old, at three-day intervals. Feed intake measurements were recorded at three-day intervals post-weaning (21 days of age) until the mice were 84 days old. Mice cross-fostered in group 2 were excluded from analyses to estimate heritabilities, genetic and phenotypic correlations.



### 3.2.1 Models Describing the Weight/Age Relationship

A total of eleven algebraic models, all nonlinear, were fitted to weight/age data from birth to 84 days old for each individual. Estimates for the parameters for each model were obtained using a modified Gauss-Newton iterative procedure. The models considered and relevant properties are described in Table 3.2. Models I to IV are specialised cases of the generalised Richards' equation (Model V). Models VIa to IX were fitted by the same nonlinear regression procedure but with the proviso of constraining the y intercept to  $W_0$  (the initial weight, weight at birth). Parks (1982) suggests that using the parameter b, a 'scaling' factor, in equations I to V can bias estimates obtained for the other characteristic parameters of the models. For example, if we consider the Gompertz equation (Model II) at time or age zero, then

$$W_0 = Ae^{-b}$$

$$\text{and } b = \ln(A/W_0)$$

b is confounded with the parameter A, (an estimate of the mature weight) and the initial condition  $W_0$ .

Similar relations can be found in Models I, III, IV and V. However, as these five models are common in the literature on nonlinear model applications to animal weight versus age data, it was considered essential that they be investigated in this study.

In addition to the parameters of the models described in

TABLE 3.2

## GROWTH MODELS AND FITTED PARAMETERS

Model	Equation for $W_t$	Asymptote	Parameters Rate Parameter and initial conditions (i.c.)	Source
I Logistic	$A(1 + be^{-kt})^{-1}$	A	k	Brown (1970)
II Gompertz	$Ae^{-be^{-kt}}$	A	k	Brown (1970)
III Bertalanffy	$A(1 - be^{-kt})^3$	A	k	Brown (1970)
IV Brody	$A(1 - be^{-kt})$	A	k	Brown (1970)
V Richards	$A(1 + be^{-kt})^{1/(1-m)}$	A	k, m	Richards (1959)
VI Parks	a) $(A-W_0)(1 - e^{-kt-t^*(1 - e^{-t/t^*})}) + W_0$ b) $(A-W_0)(1 - e^{-(AB)F/A}) + W_0$	A	k, t* i.c. $W_0$  (AB), t* i.c. $W_0$	Parks (1982)  Parks (1982)
VII Logistic	$A(1 + (\frac{A}{W_0} - 1)e^{-kt})^{-1}$	A	k	Grossman (1969)

Table 3.2 (cont.)

Model	Equation for $W_t$	Asymptote	Parameters Rate Parameter and initial conditions (i.c.)	Source
VIII Gompertz	$Ae^{-k(A-W_0)}e^{-kt}$	A	k i.c. $W_0$	
IX Bertalanffy	$\frac{1}{3} \frac{1}{3} \frac{1}{(A-W_0)^3} e^{-kt/3}$	A	k i.c. $W_0$	
X Brody	$A-(A-W_0)e^{-kt}$	A	k i.c. $W_0$	
XI Parks	Equation for Cumulative Food Intake $\frac{(F)}{C(t-t^*(1-D/C)(1 - e^{-t/t^*}))}$	C	$t^*$ i.c. D	Parks (1982)

<sup>1</sup> F = the function for Cumulative Food Intake (Model XI)

Table 3.2, the points of inflection were investigated (Table 3.3). The points of inflection were considered important for several reasons. Firstly, they are directly related to parameters of the growth functions and can aid in the interpretation of specific models, both mathematically and biologically. Secondly, as the overall aim of this research was to investigate alternative methods for altering the structure of growth curves, these additional characters and their relationship to the structural parameters of the models could provide valuable additional information in developing selection criteria. Finally, they provide information on the predictive ability of the models.

### 3.2.2 Models Describing the Weight/Feed Intake Relationship

Roux's (1974, 1976) and Blaxter's (1968) models were not considered applicable to the data sets available as no information was available on the partitioned body components. To obtain an accurate assessment of their models considerable body composition analysis is required at different ages and body weights on a large number of individuals. This work was beyond the scope of this study.

### Parks' Model of Weight, Feed Intake and Time

Utilising both weight and feed intake information from measurements taken at three-day intervals, postweaning to 84 days old, individual estimates of the parameters of Parks' growth and

TABLE 3.3

## CHARACTERISTIC PARAMETERS AND BIOLOGICAL INTERPRETATIONS

Model	Characteristic Parameters	Points of Inflection Age <sup>(1)</sup>	Weight
I	A, k, b	$\ln b/k$	A/2
II	A, k, b	$\ln b/k$	A/e
III	A, k, b	$\ln 3b/k$	0.296 A
IV	A, k, b	None	None
V	A, k, b, m	$\ln(b/(1-m)/k)$	$A \left(\frac{m-1}{m}\right)^m$
VIa	A, k, t <sup>*</sup> (1)	-	-
b	A, (AB), t <sup>*</sup> (2)	-	-
VII	A, k		A/2
VIII	A, k		A/e
IX	A, k		0.296 A
X	A, k	None	None
XI	C or A/T <sub>0</sub> , t <sup>*</sup> (2)	None	None

where k = maturing rate parameter

b = integration parameter or scaling factor

A = estimated mature weight

m = 'shape' parameter

(AB) = 'efficiency' factor

T<sub>0</sub> = 'Taylor Time Constant'

C = estimated mature feed intake

t<sup>\*</sup>(1) = 'Brody's' t

t<sup>\*</sup>(2) = Parks designated this parameter as being the animal's internal resistance to increases in appetite.

(1) See Introduction (pages 85, 87 and 89) for formulae for age at point of inflection for Models VII, VIII and IX.

*ad libitum* feeding functions were obtained. The models and relevant properties are described in Table 3.2. Additional characters and their interpretation are summarised in Table 3.3.

Parks (pers. comm. 1980) suggested that weights prior to weaning should not be included in the model fitting procedure as they are obtained prior to the animal being offered a diet of constant composition. Therefore, in all analyses involving this model  $W_0$ , the initial weight, was the weight of the mouse measured at 21 days old.

### 3.2.3 Statistical Procedures

a) Nonlinear Estimation: The exact statistical model for each set of parameters consisted of the specified model (Table 3.2), plus a residual error term which was assumed to be normally and independently distributed (NID  $(0, \sigma^2)$ ). The same procedure was used to estimate individual parameters for all models considered. Only multiplicative error assumptions were considered in these analyses. Assumptions on the error structure of residuals are discussed and analysed in Chapter 5. An example of the models as fitted is, for Model I:

$$\text{Loge } (W_t) = \text{Loge } [A(1 + be^{-kt})^{-1} + e_1(t)]$$

where  $e_1(t)$  is the residual error term.

b) Criteria of Fit: Although a number of objective criteria are now available for determining 'best' fit when comparing

several nonlinear models, none can be considered as satisfying both biological and statistical criteria (Bates and Watts, 1980; Gillis and Ratkowsky, 1978; Ratkowsky, pers. comm.; Parks, pers. comm.). For the purposes of the present analyses, three criteria were considered:

i) Pooled Residual Variances were obtained by averaging over the groups, the error mean squares obtained from fitting each model to the growth data of individual mice.

The coefficient of determination ( $R^2$ ) was obtained by subtracting the residual sums of squares (RSS) obtained by fitting the model from the total sums of squares (TSS). These were averaged over groups for all individuals.

$$\bar{R}^2 = \frac{n}{\sum_{i=1}^n} \frac{(TSS-RSS)}{TSS} / n$$

where  $n$  = number of individuals.

ii) To obtain an indication of the predictive ability of the various models, each was evaluated at a number of weights corresponding to a time of recording. Product moment correlations between predicted weights obtained for each model and observed weights were calculated. Models that provide a good 'fit' of the data should produce means and variances equal to those observed and a correlation close to 1.00 between predicted and observed weights for the same age.

iii) The ability to assess the parameters of a particular model in terms of a 'biological meaning'. Although, of necessity, a subjective measure of fit this assessment of a model is important to understanding the aetiology of growth.

The 'tests' are by no means exhaustive, but can only act as a guide to a researcher. Chapter 5 deals in much greater detail with problems of choosing the 'best' model statistically, examining both the biases inherent in the estimation procedure and the structure of the residual associated with the various models.

c) Estimation of Genetic Parameters: Genetic variances and covariances were estimated from paternal and maternal half-sib and full-sib correlations using a mixed model least-squares procedure (Harvey, 1977). The assumed statistical model was identical to that presented in Chapter 2.

#### 3.2.4 Predicted Direct and Correlated Responses

Utilising information obtained by the genetic analyses of the characteristic parameters, and associated traits, expected direct and correlated responses to selection were examined. Responses were calculated by assuming a single generation of selection with a standardised selection differential of 1.0.

### 3.3 RESULTS

#### 3.3.1 Weight/Age Models

Considerable problems were encountered in fitting the generalised Richards' function (Model V) to individual data sets. As



more than 25% of the individual analyses failed to satisfy the convergence criterion after 50 iterations, this model was excluded from the study. Similar problems with this model have occurred in other studies (Brown, 1970; Eisen *et al.*, 1969).

a) Comparisons of Different Functions: Residual sums of squares, variances and coefficients of determination ( $R^2$ ) of the nine weight-time models are presented in Table 3.4. The results are pooled estimates from fitting each model to the growth data of individual mice and averaged over individuals, groups and sexes. Models I to IV are forms of the generalised Richards' function (Model V) and as such incorporate the parameter  $\underline{b}$  in the model, whereas models VIa to X (excluding VIb) are solved for the initial conditions and involve the value of  $W_0$ , weight at birth. In each case, models I to IV provided lower residual variances and higher  $R^2$  values than their counterparts, models VII to X. Of the models examined, the two forms of the Gompertz and Logistic and the Parks' model gave the lowest residual sum of squares and error mean squares.

Plots of each of the models for a randomly selected male and female are shown in Figures 3.5 to 3.13. For each plot, the estimates of the structural parameters and the correlations between the parameters obtained during the fitting process are provided with each figure.

All models varied in their ability to adequately fit the data over various periods of growth. The two forms of the Logistic equation (Figs. 3.5 and 3.6) tended to underestimate both earlier

TABLE 3.4

RESIDUALS AND COEFFICIENTS OF DETERMINATION ( $R^2$ )  
 OF EACH OF THE FUNCTIONS FITTED TO THE GROWTH DATA  
 OF INDIVIDUAL MICE AND AVERAGED OVER INDIVIDUALS,  
 GROUPS AND SEXES

	Model	Residual Sum Squares <sup>a</sup>	$R^2$	Residual Variances (Error M.S.)
I	Logistic	0.0513	0.9870	0.00197
II	Gompertz	0.0420	0.9893	0.00162
III	Bertalanffy	0.1138	0.9019	0.00438
IV	Brody	0.0979	0.9324	0.00377
VIa	Parks	0.0513	0.9850	0.00197
VII	Logistic	0.0773	0.9800	0.00286
VIII	Gompertz	0.0452	0.9884	0.00167
IX	Bertalanffy	0.1813	0.8493	0.00672
X	Brody	0.1166	0.8973	0.00432

<sup>a</sup>All individuals had an equal number of data points per fit, 29.

Figure 3.5: Logistic equation, Model I, fitted to individual growth data of a male and a female.

$$\text{Model } W_t = A(1 + be^{-kt})^{-1}$$

	<u>Parameter Estimates</u>		<u>Correlations</u>			
	Male	Female	Male		Female	
	A	b	A	b	A	b
A	32.18	28.19				
b	16.968	16.968	b	0.209	0.199	
k	0.1450	0.1468	k	-0.407	0.600	-0.376
Error MS	0.0020	0.0034				
R <sup>2</sup>	0.9861	0.9765				

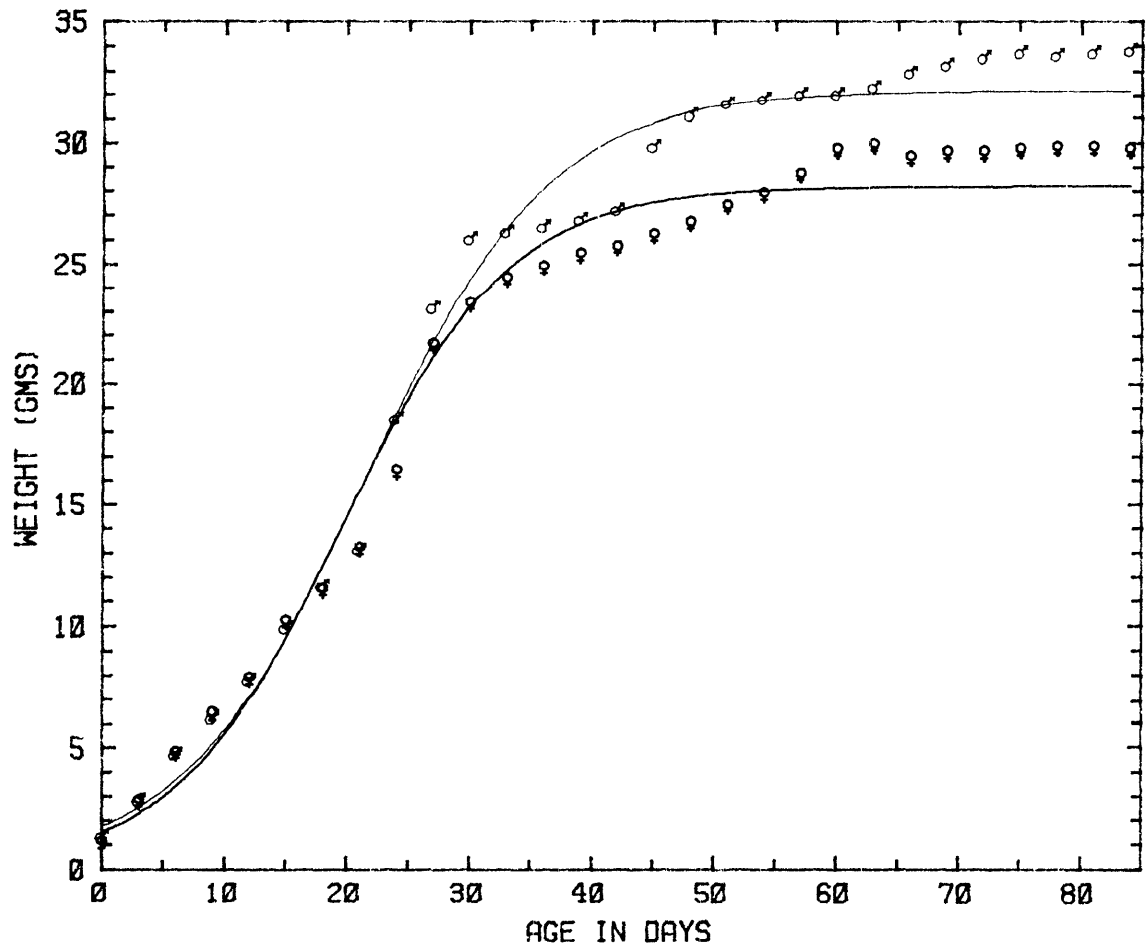


Figure 3.6: Logistic equation, Model VII, fitted to individual growth data of a male and a female.

$$\text{Model } W_t = A \left( 1 + \left( \frac{A}{W_0} - 1 \right) e^{-kt} \right)^{-1}$$

	<u>Parameter Estimates</u>		<u>Correlations</u>	
	Male	Female	Male	Female
A	31.31	27.18	k	-0.339
k	0.1584	0.1880	A	-0.315
Error MS	0.0036	0.0061		
R <sup>2</sup>	0.9750	0.9560		

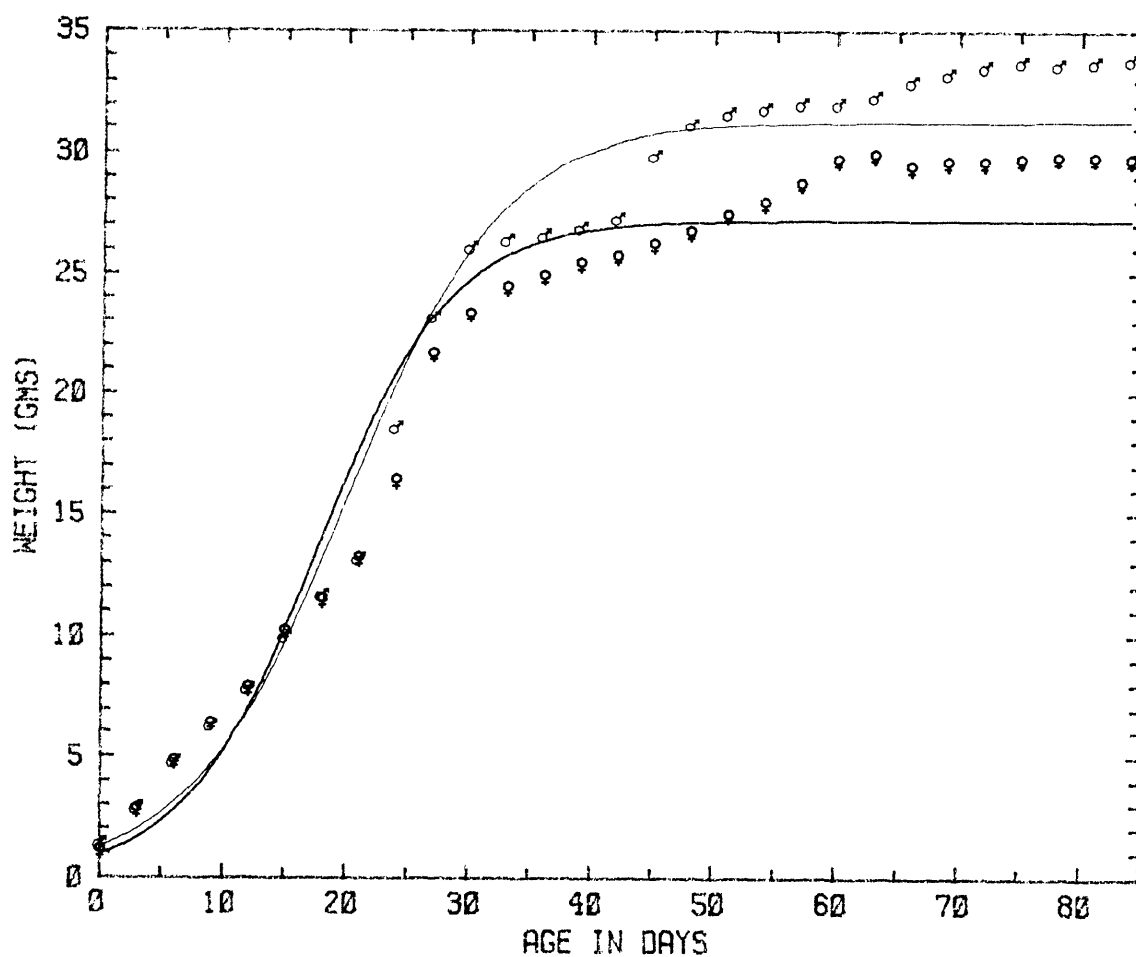


Figure 3.7: Gompertz equation, Model II, fitted to individual growth data of a male and a female.

$$\text{Model } W_t = Ae^{-be^{-kt}}$$

	<u>Parameter Estimates</u>		<u>Correlations</u>			
	Male	Female	Male		Female	
			A	b	A	b
A	34.55	29.78	b	0.162	0.146	
k	3.182	3.206	k	-0.699	0.344	-0.649
k	0.0666	0.0766				0.374
Error MS	0.0011	0.0013				
R <sup>2</sup>	0.9927	0.9908				

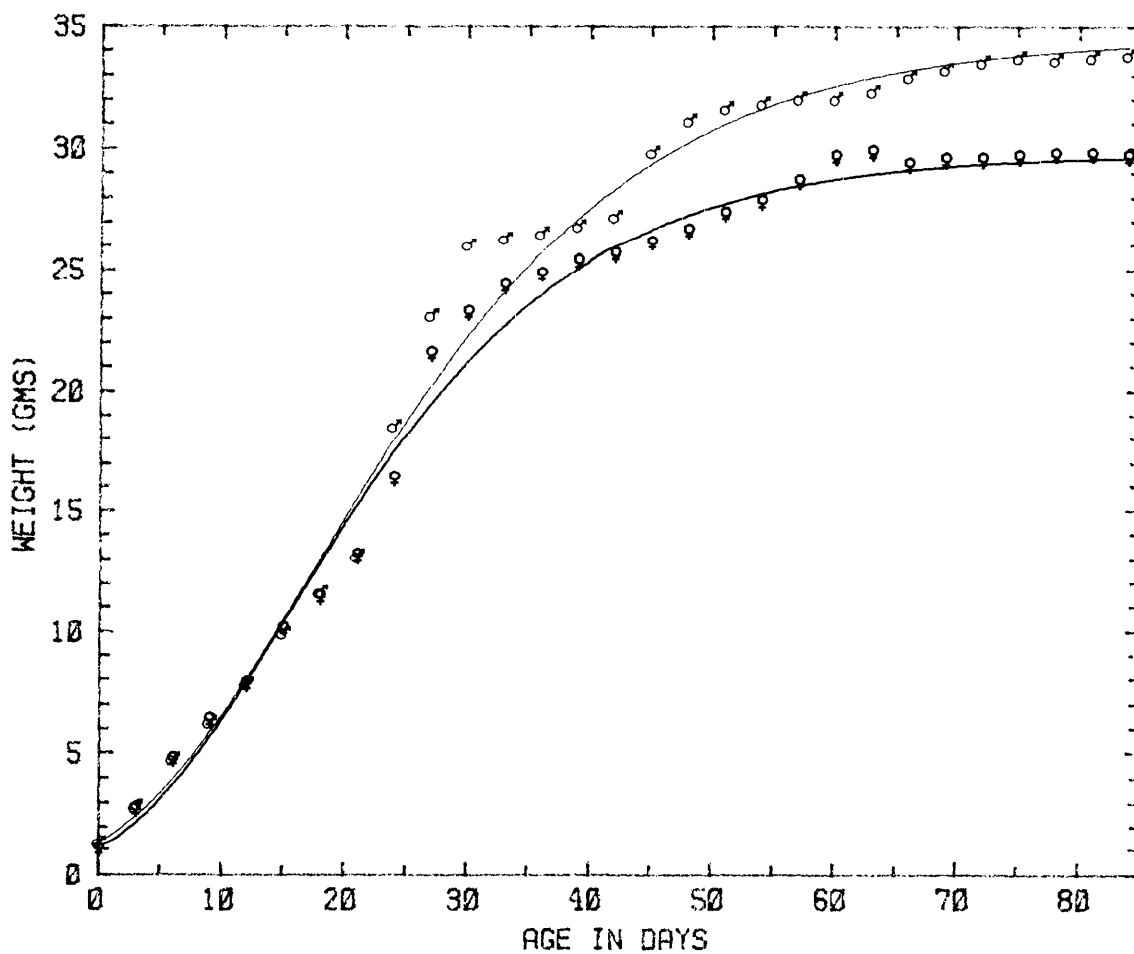


Figure 3.8: Gompertz equation, Model VIII, fitted to individual growth data of a male and a female.

$$\text{Model } W_t = Ae^{-(\ln A - \ln W_0)e^{-kt}}$$

	<u>Parameter Estimates</u>		<u>Correlations</u>	
	Male	Female	Male	Female
A	34.98	28.59	A	A
k	0.0630	0.0684	-0.763	-0.736
Error MS	0.0032	0.0088		
R <sup>2</sup>	0.9820	0.9260		

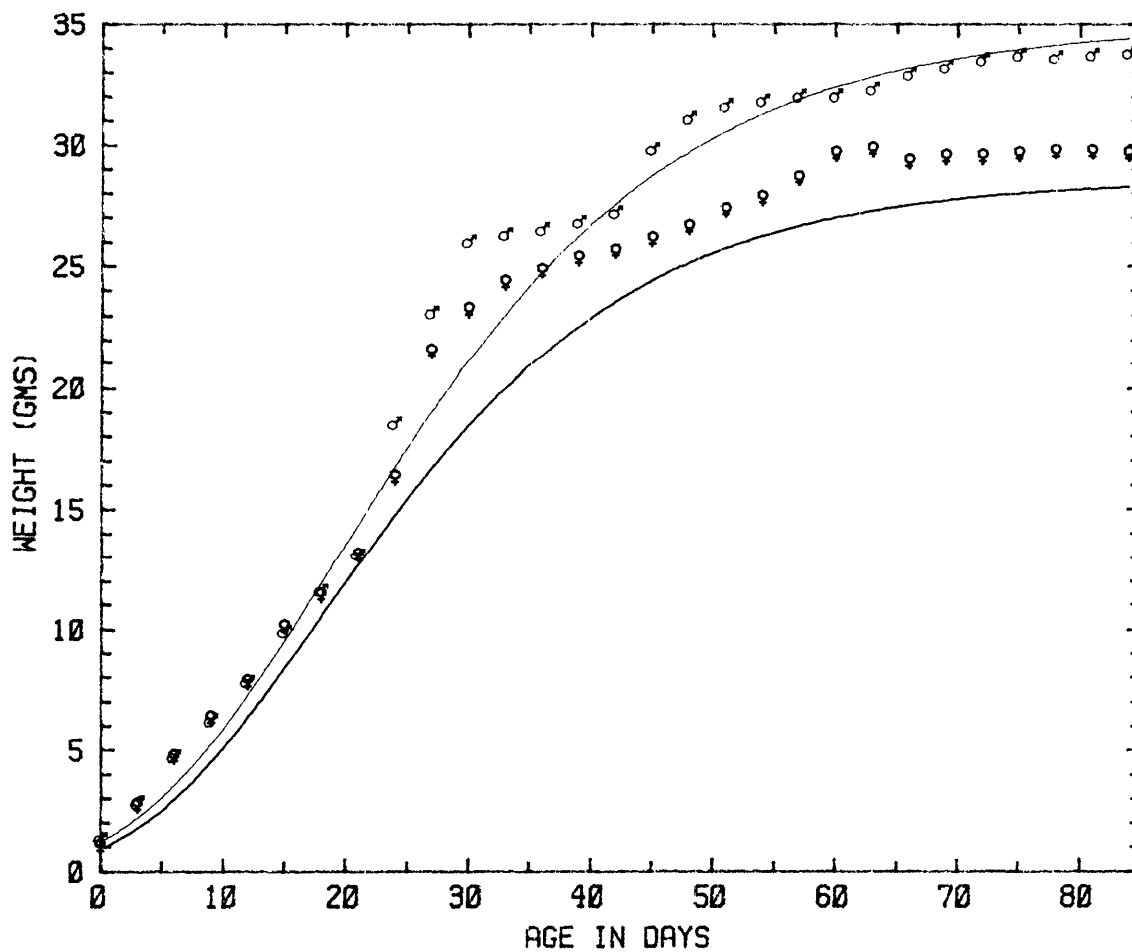


Figure 3.9: Bertalanffy equation, Model III, fitted to individual growth data of a male and a female.

$$\text{Model } W_t = A(1 - be^{-kt})^3$$

		<u>Parameter Estimates</u>		<u>Correlations</u>			
		Male	Female	Male		Female	
				A	b	A	b
A		30.15	27.43				
b		0.7281	0.7313	b	-0.483	-0.482	
k		0.0788	0.0797	k	-0.501	0.909	-0.497
Error MS		0.0084	0.0082				
R <sup>2</sup>		0.9407	0.9337				

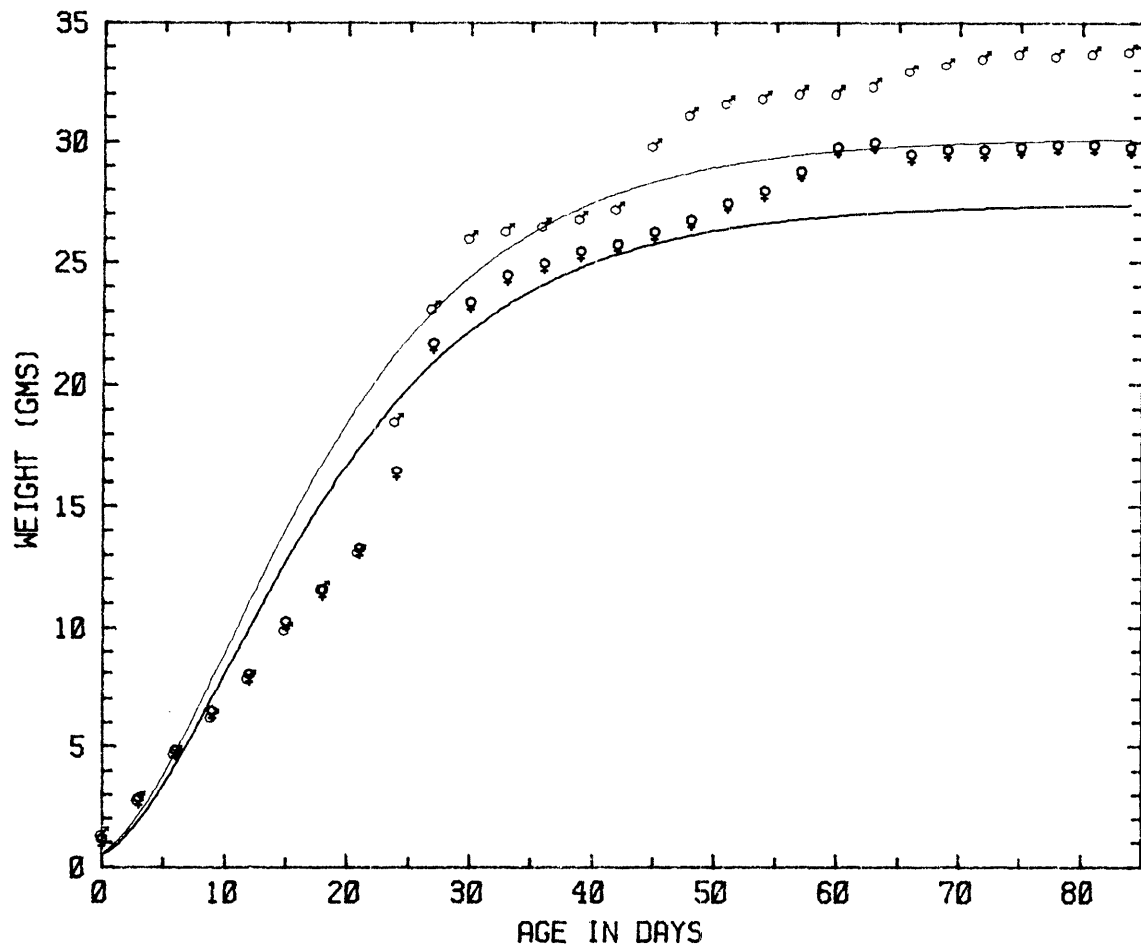


Figure 3.10: Bertalanffy equation, Model IX, fitted to individual growth data of a male and a female.

$$\text{Model } W_t = (A^{1/3} - (A^{1/3} - W_0^{1/3})e^{-kt/3})^3$$

		Parameter Estimates		Correlations	
		Male	Female	Male	Female
				A	A
A		33.60	28.27		
k		0.1134	0.1246	k	-0.533
Error MS		0.0097	0.0096		
R2		0.9030	0.8890		

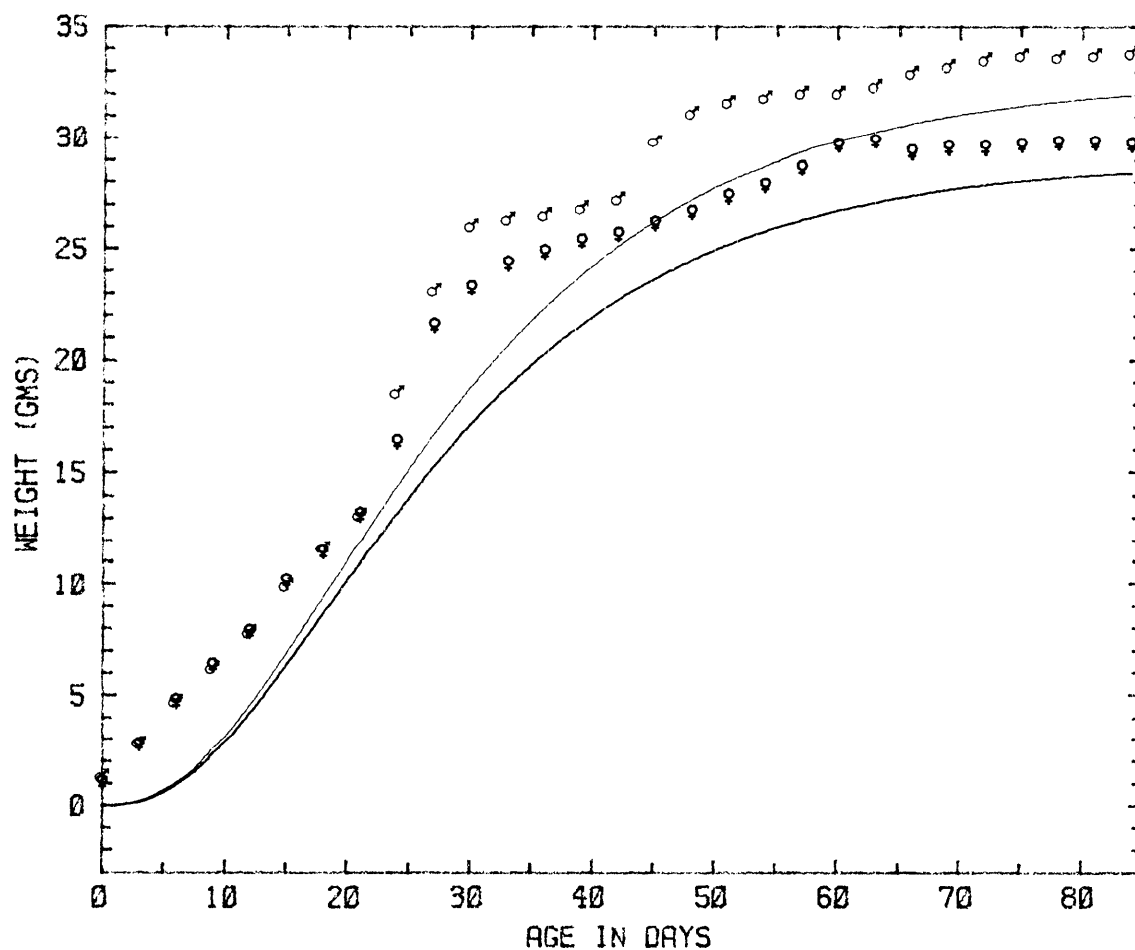




Figure 3.11: Brody equation, Model IV, fitted to individual growth data of a male and a female.

$$\text{Model } W_t = A(1 - be^{-kt})$$

	<u>Parameter Estimates</u>		<u>Correlations</u>			
	Male	Female	Male		Female	
			A	b	A	b
A	40.99	34.78				
b	1.028	1.027	b	-0.640	-0.568	
k	0.0257	0.0292	k	-0.940	0.694	-0.923
Error MS	0.0037	0.9832				
R <sup>2</sup>	0.9742	0.0024				

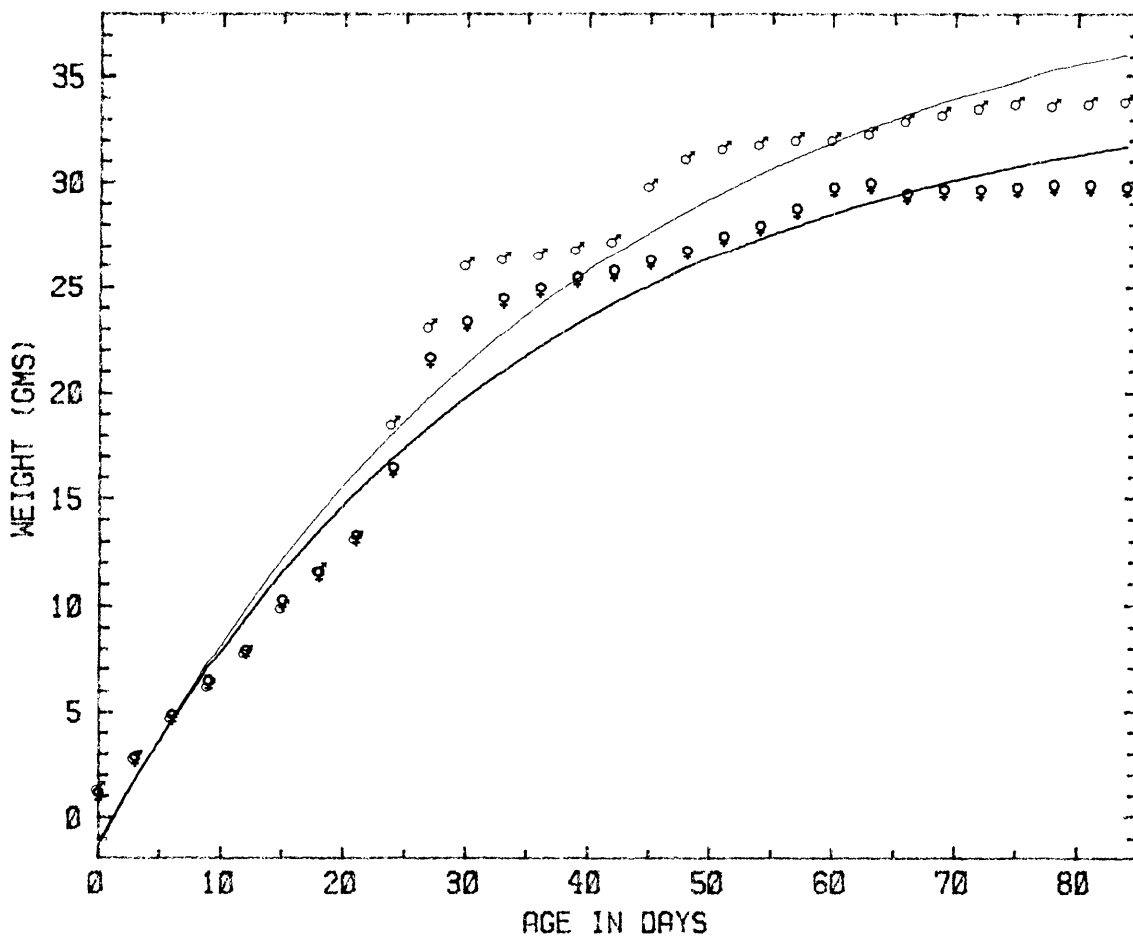


Figure 3.12: Brody equation, Model X, fitted to individual growth data of a single male and female.

$$\text{Model } W_t = A - (A - W_0)e^{-kt}$$

		<u>Parameter Estimates</u>		<u>Correlations</u>	
		Male	Female	Male	Female
				A	A
A		62.86	43.16		
k		0.0125	0.0179	k	-0.988
Error MS		0.0039	0.0026		
R <sup>2</sup>		0.9712	0.9803		

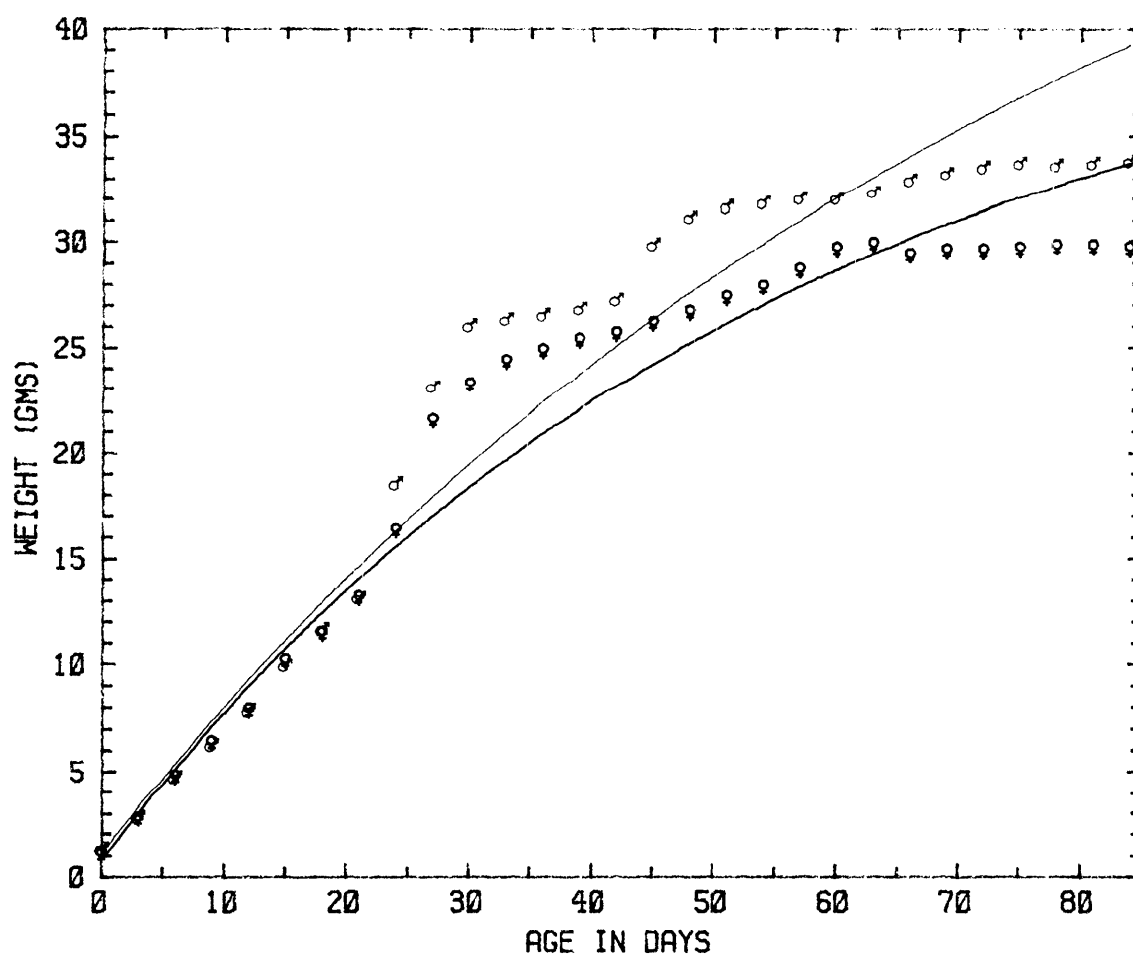
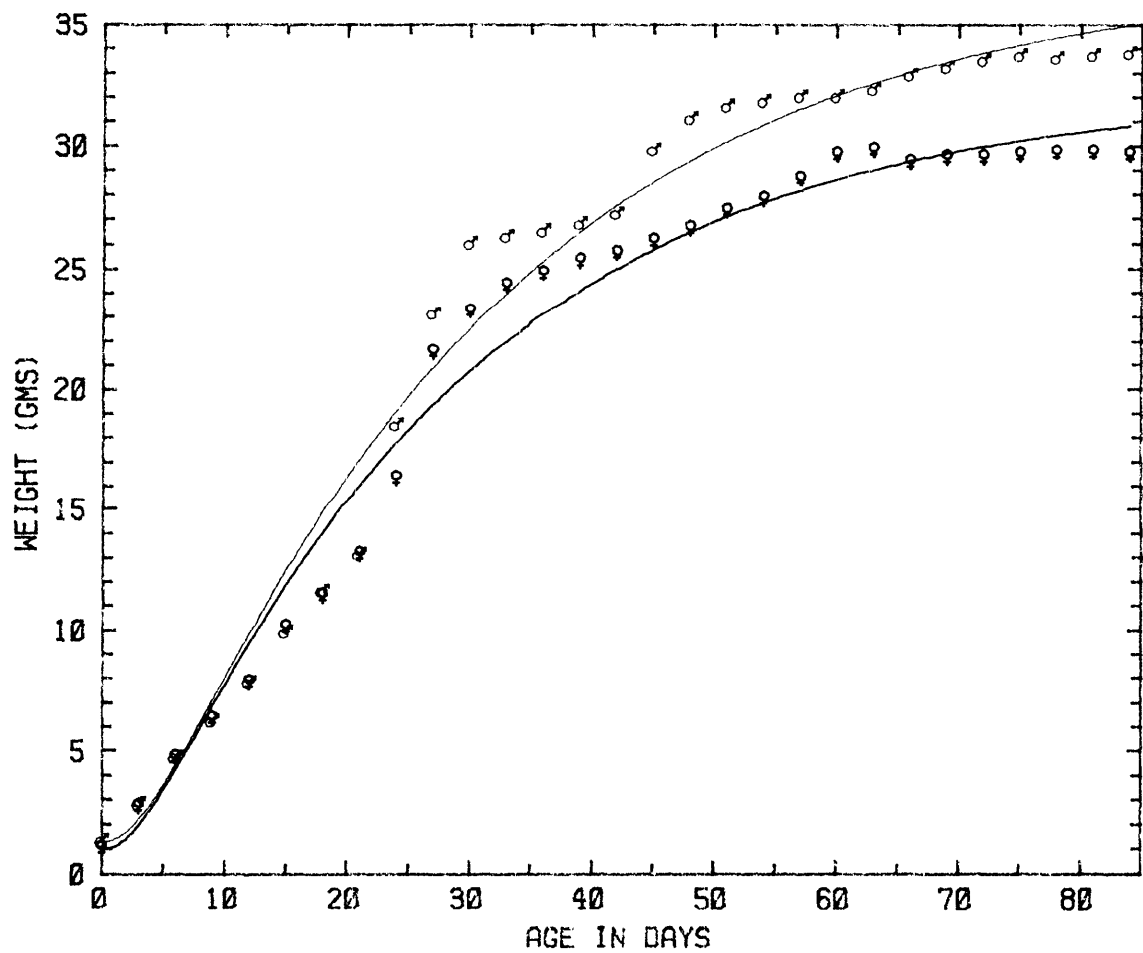


Figure 3.13: Parks' equation, Model VIa, fitted to individual growth data of a male and a female.

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

		<u>Parameter Estimates</u>		<u>Correlations</u>			
		Male	Female	Male		Female	
				A	k	A	k
A		37.156	32.263	k	-0.772	-0.787	
k		0.0352	0.0383	t*	0.276	0.247	-0.377
t*		4.2903	3.6584				
Error MS		0.0007	0.0011				
R <sup>2</sup>		0.9900	0.9880				



and late growth, Model VII more so than Model II. A similar pattern is evident for the Bertalanffy models (Figs. 3.9 and 3.10) particularly at later weights. The two forms of the Gompertz models shown in Figs. 3.7 and 3.8 illustrate the marked differences in possible fits when the extra parameter,  $b$ , is introduced. The  $b$  parameter enables Model II to follow the growth pattern much more precisely. Although the Brody's equation, Model IV (Fig. 3.11), describes the data set well, it illustrated one of the pitfalls associated with a failure to define the initial weight. This model consistently estimated negative birth weights, a situation not possible when  $W_0$  was set. However, when  $W_0$  was set for the Brody's equation (Model X, Fig. 3.12), there was a considerable overestimation of mature body weights. This reflects the inability of this particular parameterisation to plateau as individuals attain equilibrium weights. The lack of a point of inflection for these Brody models undoubtedly affects their ability to describe the data from birth to 84 days of age.

Parks' weight model (Fig. 3.13) provides an excellent fit to the data sets presented, giving both high  $R^2$  values and low error mean squares (Error, MS). However, as can be seen for this example, there was a tendency for the Parks' Model VIa to overestimate mature weight. This overestimation of  $A$  has been reported elsewhere (Brown, 1970) when using double exponential equations like Model VIa and the Gompertz forms.

The correlations between parameter estimates, which are obtained during the fitting process, indicate the degree of dependency among parameter estimates. For all models, there was a neg-

ative correlation between parameters A and k, values ranged from -0.988 (Model X) to -0.315 (Model VII). Similarly, for all models involving the parameter b, the correlation between b and k was positive, values ranged from 0.909 (Model III) to 0.344 (Model II). Correlations between A and b were positive for the Logistic (Model I) and the Gompertz (Model II) and negative for the Bertalanffy and Brody models (Model III and IV, respectively). Although these results are only for two individuals selected at random, the same patterns were repeated over all individuals studied.

As the two forms of the Brody and Bertalanffy models show poorer fits of individual data sets and had higher residual variances and lower  $R^2$  values, it was decided to exclude these two model types and concentrate further analyses on the Logistic, Gompertz and Parks models.

Means and standard errors for parameters and points of inflection of the remaining models are shown in Table 3.5. For the three types of models, the Logistic equations gave the lowest estimates of mature weight (A) and the Parks' equation the highest, with Gompertz values virtually at the midpoint between the two. The two more generalised parameterisations (Models I and II) gave higher estimates of A than their respective counterparts (Models VII and VIII).

The rate of maturing, estimated by the k parameter in each model, refers to the post-natal growth rate relative to the estimated mature weight (A). Simple paired t-tests were used to compare parameters of the different models. Though the errors were not independent the large t values suggest that there are differences

TABLE 3.5  
LEAST SQUARES MEANS AND STANDARD ERRORS OF ESTIMATES OF MODEL PARAMETERS

Males Parameter	Logistic			Gompertz			Parks VIa
	I	VII	II	VIII	VIII	VIII	
A (gms)	34.37 ± 0.185	33.55 ± 0.178	37.89 ± 0.222	37.51 ± 0.219	40.09 ± 0.401		
k	0.1193 ± 0.0008	0.1350 ± 0.0009	0.0582 ± 0.0005	0.0595 ± 0.0005	0.0350 ± 0.0008		
b	16.57 ± 0.152	-	3.27 ± 0.022	-	-		
t* (days)	-	-	-	-	5.207 ± 0.098		
P.O.I. weight (gms)	17.19 ± 0.093	16.78 ± 0.089	13.94 ± 0.082	13.80 ± 0.084			
P.O.I. age (days)	23.69 ± 0.158	19.47 ± 0.147	20.39 ± 0.157	19.67 ± 0.169			
Females							
A (gms)	29.62 ± 0.186	28.85 ± 0.223	32.31 ± 0.223	31.92 ± 0.220	34.77 ± 0.402		
k	0.1199 ± 0.0008	0.1373 ± 0.0009	0.0605 ± 0.0005	0.0624 ± 0.0005	0.0352 ± 0.0008		
b	14.37 ± 0.153	-	3.11 ± 0.027	-	-		
t* (days)	-	-	-	-	4.534 ± 0.098		
P.O.I. weight (gms)	14.81 ± 0.093	14.42 ± 0.189	11.88 ± 0.082	11.74 ± 0.081			
P.O.I. age (days)	22.43 ± 0.159	18.48 ± 0.148	18.75 ± 0.183	18.08 ± 0.170			

between  $k$  values for the three model types, although between sexes within model type differences are not as marked. Large  $k$  values indicate earlier maturing individuals and small  $k$  values late maturing animals. In each case, males appear as later maturing animals than females. No comparisons can be made between models of different forms.

The points of inflection (P.O.I.) are fixed by the model type and were calculated by the relations given in Table 3.1 in Section 3.1. The values for weight at the P.O.I. for the Logistic models are by definition higher than those obtained from the Gompertz models. In both cases, the rate of maximum growth rate occurred prior to or at weaning. Contrary to suggestions that the P.O.I. is closely aligned to sexual maturity (Brody, 1945), vaginal opening was not observed in any mice prior to 24 days of age.

The predictive ability of the five weight-time models was examined in two ways, firstly each individual parameter set for each model was used to generate predicted weights corresponding to ages when actual weights were recorded (Table 3.6). Secondly, predicted weights were included in the least squares analyses to obtain genetic and phenotypic correlations with actual weights (Table 3.7).

For males and females, both forms of the Logistic model followed a similar pattern, initially underestimating young weight, overestimating mid-period weights, and underestimating later weight. The two Gompertz models overestimated later weights for males and

TABLE 3.6  
 LEAST SQUARES MEANS AND STANDARD ERRORS FOR OBSERVED AND PREDICTED BODY WEIGHTS, IN  
 THE LOGISTIC (I, VII), GOMPertz (II, VIII) AND PARKS (VIa) MODELS. a) MALES

Trait	Observed <sup>1</sup>	Logistic			Gompertz			Parks	
		I	VII	II	VIII	VIa	VIIa	VIa	
Birth Weight	1.60 ± 0.01	1.95 ± 0.01	1.60 ± 0.02	1.44 ± 0.02	1.60 ± 0.02	1.60 ± 0.02	1.60 ± 0.02	1.60 ± 0.01	
12 day Weight	7.93 ± 0.07	7.15 ± 0.06	6.89 ± 0.07	7.44 ± 0.07	8.10 ± 0.18	8.10 ± 0.18	8.10 ± 0.18	10.30 ± 0.08	
21 day Weight	13.25 ± 0.15	15.18 ± 0.16	15.71 ± 0.16	14.44 ± 0.15	15.32 ± 0.13	15.32 ± 0.13	15.32 ± 0.13	18.02 ± 0.12	
24 day Weight	19.63 ± 0.20	18.28 ± 0.19	19.03 ± 0.18	19.02 ± 0.10	17.73 ± 0.15	17.73 ± 0.15	17.73 ± 0.15	20.19 ± 0.14	
30 day Weight	25.58 ± 0.19	24.02 ± 0.21	25.00 ± 0.18	29.62 ± 0.13	22.16 ± 0.16	22.16 ± 0.16	22.16 ± 0.16	23.94 ± 0.15	
42 day Weight	30.05 ± 0.16	31.00 ± 0.18	31.33 ± 0.20	33.34 ± 0.14	28.85 ± 0.17	28.85 ± 0.17	28.85 ± 0.17	29.47 ± 0.16	
54 day Weight	32.77 ± 0.19	33.37 ± 0.17	33.09 ± 0.17	35.37 ± 0.16	32.84 ± 0.17	32.84 ± 0.17	32.84 ± 0.17	33.11 ± 0.18	
60 day Weight	34.16 ± 0.20	34.04 ± 0.17	33.49 ± 0.16	36.43 ± 0.17	35.01 ± 0.18	35.01 ± 0.18	35.01 ± 0.18	35.51 ± 0.23	
72 day Weight	34.80 ± 0.19	34.15 ± 0.17	33.55 ± 0.16	36.75 ± 0.19	35.67 ± 0.18	35.67 ± 0.18	35.67 ± 0.18	36.38 ± 0.24	
84 day Weight	35.47 ± 0.22	34.25 ± 0.17	33.60 ± 0.16	37.73 ± 0.21	36.49 ± 0.19	36.49 ± 0.19	36.49 ± 0.19	37.65 ± 0.27	

<sup>1</sup> 538 males.



TABLE 3.6  
 LEAST SQUARES MEANS AND STANDARD ERRORS FOR OBSERVED AND PREDICTED BODY WEIGHTS, IN  
 THE LOGISTIC (I, VII), GOMPertz (II, VIII) AND PARKS (VIa) MODELS. b) FEMALES

Trait	Observed <sup>1</sup>	Logistic			Gompertz			Parks
		I	VII	II	VIII	VIa		
Birth Weight	1.56 ± 0.01	1.92 ± 0.01	1.56 ± 0.02	1.44 ± 0.02	1.56 ± 0.02	1.56 ± 0.02	1.56 ± 0.01	
12 day Weight	7.73 ± 0.07	6.90 ± 0.06	6.69 ± 0.07	7.18 ± 0.07	7.71 ± 0.08	7.71 ± 0.08	9.52 ± 0.08	
21 day Weight	12.68 ± 0.15	14.16 ± 0.16	14.75 ± 0.16	13.50 ± 0.14	14.21 ± 0.13	14.21 ± 0.13	15.09 ± 0.12	
24 day Weight	17.59 ± 0.20	16.83 ± 0.19	17.66 ± 0.18	17.01 ± 0.10	16.30 ± 0.15	16.30 ± 0.15	16.80 ± 0.13	
30 day Weight	22.32 ± 0.19	21.59 ± 0.21	22.51 ± 0.20	23.61 ± 0.13	20.06 ± 0.16	20.06 ± 0.16	19.97 ± 0.14	
42 day Weight	25.89 ± 0.16	27.08 ± 0.18	27.33 ± 0.17	25.90 ± 0.14	25.50 ± 0.17	25.50 ± 0.17	24.05 ± 0.16	
54 day Weight	28.26 ± 0.19	28.87 ± 0.17	28.56 ± 0.16	28.86 ± 0.16	28.58 ± 0.17	28.58 ± 0.17	26.88 ± 0.19	
60 day Weight	29.80 ± 0.20	29.36 ± 0.17	28.83 ± 0.16	30.41 ± 0.17	30.17 ± 0.18	30.17 ± 0.18	28.73 ± 0.23	
72 day Weight	30.43 ± 0.19	29.44 ± 0.17	28.87 ± 0.16	31.43 ± 0.19	30.65 ± 0.18	30.65 ± 0.18	29.48 ± 0.24	
84 day Weight	31.08 ± 0.22	29.51 ± 0.17	28.90 ± 0.16	31.71 ± 0.21	31.21 ± 0.19	31.21 ± 0.19	30.59 ± 0.27	

<sup>1</sup> 542 females.

TABLE 3.7  
GENETIC ( $r_g$ ) AND PHENOTYPIC ( $r_p$ ) CORRELATIONS BETWEEN OBSERVED AND PREDICTED WEIGHTS

Observed Trait: Weight at	I		Logistic		VII		II		Gompertz		VIII		Parks VIa	
	$r_g$	$r_p$	$r_g$	$r_p$	$r_g$	$r_p$	$r_g$	$r_p$	$r_g$	$r_p$	$r_g$	$r_p$	$r_g$	$r_p$
0 days	-0.50(.14) <sup>1</sup>	0.60	1.00 <sup>2</sup>	1.00	1.03(.03)	1.00	1.00 <sup>2</sup>	1.00	1.00 <sup>2</sup>	1.00	1.00 <sup>2</sup>	1.00	1.00 <sup>2</sup>	1.00
12 days	0.92(.03)	0.80	0.88(.04)	0.78	0.82(.05)	0.79	0.86(.04)	0.83	0.86(.04)	0.83	0.86(.04)	0.83	0.69(.10)	0.59
21 days	0.83(.04)	0.80	0.93(.02)	0.81	0.71(.06)	0.78	0.85(0.4)	0.80	0.85(0.4)	0.80	0.85(0.4)	0.80	0.55(.10)	0.61
24 days	0.88(.03)	0.83	0.67(.07)	0.71	0.81(.06)	0.72	0.83(.04)	0.79	0.83(.04)	0.79	0.83(.04)	0.79	0.89(.05)	0.81
30 days	0.88(.03)	0.84	0.68(.07)	0.74	0.84(.06)	0.68	0.86(.04)	0.78	0.86(.04)	0.78	0.86(.04)	0.78	0.83(.05)	0.88
42 days	0.66(.09)	0.85	0.62(.10)	0.85	0.74(.08)	0.86	0.69(.09)	0.82	0.69(.09)	0.82	0.69(.09)	0.82	0.88(.03)	0.90
54 days	0.99(.01)	0.94	0.95(.02)	0.93	0.98(.01)	0.94	0.98(.01)	0.93	0.98(.01)	0.93	0.98(.01)	0.93	0.89(.03)	0.86
60 days	0.92(.03)	0.94	0.78(.06)	0.91	0.94(.03)	0.95	0.96(.02)	0.95	0.96(.02)	0.95	0.96(.02)	0.95	0.95(.04)	0.86
72 days	0.88(.04)	0.93	0.74(.07)	0.90	0.84(.04)	0.92	0.89(.03)	0.93	0.89(.03)	0.93	0.89(.03)	0.93	0.93(.05)	0.86
84 days	0.82(.05)	0.84	0.69(.09)	0.80	0.82(.06)	0.83	0.83(.05)	0.84	0.83(.05)	0.84	0.83(.05)	0.84	0.89(.07)	0.83

<sup>1</sup>Standard errors for genetic correlations.

<sup>2</sup>No standard error as model contains weight at t=0 as an initial condition.

females. Eisen *et al.* (1969) reported similar problems with the Gompertz equation (Model II). The Parks' equation gave predicted weights higher than observed weights in both earlier and later phases of growth for males; however, for the females it underestimated observed weights from 24 to 84 days old. For all three model types, weaning weights were overestimated, reflecting each model's attempt to 'smooth-out' the large increases in growth rate from weaning to 24 days of age.

Genetic and phenotypic correlations between predicted and observed weights reflect the general pattern taken by the fitted functions (Table 3.7). Phenotypic correlations less than unity could be indicative of either deviations from the predicted value due to random environmental fluctuations, or a failure of the respective models to adequately describe the data, the most likely explanation being a combination of both. Noticeably, the genetic correlations between predicted and observed weights were high but, with the exception of the Parks' model, the correlation between observed and predicted weights at 42 days were poor in comparison to the correlations at 30 and 54 days. This gives a clear indication of the poorer fits for this region of the growth curve for each model. On an overall basis, there appears little to distinguish between the five models in their ability to act as predictors of weights on the genetic or phenotypic level.

#### b) Genetic Analyses - Weight/Age Models

Heritabilities, genetic and phenotypic correlations estimated from paternal half-sib components of variance are presented

for the five models in Tables 3.8, 3.9 and 3.10.

The heritabilities for the parameter estimates from each model show a general agreement when considering the same parameter. Heritabilities for estimated mature weight range from 0.34 for Models VII and VIII to 0.54 for Model VIa. There are few comparable estimates in the literature for laboratory species. Rutledge *et al.* (1972), after fitting the Logistic equation (Model I) to mouse data gave an estimate of 0.08 for A. McCarthy and Bakker (1979) gave a within-line estimate of 0.87. Heritabilities for the k parameter showed general agreement between Models I, II, VII and VIII, as values were within the range of 0.27 (Model VII) to 0.49 (Model II). The Parks' model gave a much higher value of 0.86 for the heritability of k. Models involving the parameter b gave higher estimates of k than their counterparts. As with estimates of A, there are few estimates available on the heritability of k. Grossman (1969) gave values ranging from 0.05 to 0.67 for k estimated by the Logistic equation on two populations of chickens. McCarthy and Bakker (1979) estimated the heritability of k as 0.46. No estimates for the parameter b were cited in the literature. Considerable differences are shown in the heritability of parameter b for Models I and II, 0.16 (0.08) and 0.44 (0.11) respectively. The heritability of Parks'  $t^*$  of 0.33 (0.09) is the only estimate presently available.

Tables 3.8 and 3.9 also show heritabilities for the coordinates of the points of inflection for each of the two forms of the Logistic and Gompertz. Estimates for weight at the inflection point ranged from 0.34 to 0.38 with estimates from the generalised

TABLE 3.8

HERITABILITIES, GENETIC AND PHENOTYPIC CORRELATIONS BETWEEN POINTS OF INFLECTION (POI)  
AND BETWEEN PARAMETERS OF THE LOGISTIC MODELS<sup>1</sup>

	Model I					Model VII				
	A	b	k	POI <sub>WT</sub>	POI <sub>AGE</sub>	A	k	POI <sub>WT</sub>	POI <sub>AGE</sub>	
A	0.38(0.10) <sup>2</sup>	0.49	-0.09	1.00	0.39	0.99	-0.10	0.99	0.31	
b	1.36(0.17)	0.16(0.08)	0.37	0.49	0.21	0.52	0.20	0.52	0.57	
k	-0.04(0.20)	-0.62(0.20)	0.33(0.10)	-0.09	-0.81	-0.04	0.87	-0.04	-0.48	
POI <sub>WT</sub>	1.00(0.00) <sup>3</sup>	1.37(0.17)	-0.04(0.20)	0.38(0.10)	0.39	0.99	-0.10	0.99	0.31	
POI <sub>AGE</sub>	0.42(0.15)	0.81(0.18)	-0.96(0.22)	0.42(0.15)	0.59(0.13)	0.35	-0.79	0.35	0.87	
A	0.99(0.00)	1.31(0.15)	0.01(0.21)	1.00(0.00)	0.37(0.16)	0.34(0.10)	-0.10	1.00	0.29	
k	0.32(0.21)	-0.07(0.28)	0.94(0.03)	0.32(0.21)	-0.76(0.24)	0.37(0.22)	0.27(0.09)	-0.10	-0.49	
POI <sub>WT</sub>	1.00(0.00)	1.31(0.15)	0.01(0.21)	1.00(0.00)	0.37(0.16)	1.00(0.00)	0.37(0.22)	0.34(0.10)	0.29	
POI <sub>AGE</sub>	0.58(0.13)	0.76(0.13)	-0.98(0.18)	0.58(0.13)	1.01(0.01)	0.51(0.15)	-0.67(0.21)	0.51(0.15)	0.62(0.13)	

<sup>1</sup>Heritabilities on the diagonal, genetic correlations below, phenotypic correlations above the diagonal.

<sup>2</sup>Standard errors in parentheses.

<sup>3</sup>Errors were less than 0.01.

TABLE 3.9

HERITABILITIES, GENETIC AND PHENOTYPIC CORRELATIONS BETWEEN POINTS OF INFLECTION (POI)  
AND BETWEEN PARAMETERS OF THE GOMPertz MODELS<sup>1</sup>

		Model II				Model VIII			
	A	b	k	POI <sub>WT</sub>	POI <sub>AGE</sub>	A	k	POI <sub>WT</sub>	POI <sub>AGE</sub>
A	0.36(0.10) <sup>2</sup>	0.40	-0.42	1.00	0.56	0.99	-0.44	0.99	0.59
b	1.17(0.08)	0.44(0.11)	-0.03	0.40	0.91	0.41	-0.08	0.41	0.31
k	-0.47(0.20)	-0.66(0.15)	0.49(0.14)	-0.42	-0.35	-0.39	0.95	-0.39	-0.88
POI <sub>WT</sub>	1.00(0.00) <sup>3</sup>	1.17(0.08)	-0.47(0.20)	0.36(0.10)	0.56	0.99	-0.44	0.99	0.59
POI <sub>AGE</sub>	1.00(0.05)	1.00(0.01)	-0.76(0.15)	1.00(0.05)	0.63(0.13)	0.55	-0.39	0.55	0.61
A	0.97(0.01)	1.06(0.08)	-0.41(0.20)	0.97(0.01)	0.91(0.07)	0.34(0.09)	-0.43	1.00	0.59
k	-0.35(0.21)	-0.45(0.18)	0.99(0.08)	-0.35(0.21)	-0.59(0.17)	-0.35(0.21)	0.41(0.11)	-0.43	-0.92
POI <sub>WT</sub>	0.97(0.01)	1.06(0.08)	-0.41(0.20)	0.97(0.01)	0.91(0.07)	1.00(0.00)	-0.35(0.21)	0.34(0.10)	0.59
POI <sub>AGE</sub>	0.59(0.12)	0.70(0.12)	-0.97(0.19)	0.59(0.12)	0.79(0.07)	0.59(0.12)	-0.95(0.22)	0.59(0.12)	0.53(0.18)

<sup>1</sup>Heritabilities on the diagonal, genetic correlations below, phenotypic correlations above the diagonal.

<sup>2</sup>Standard errors in parentheses.

<sup>3</sup>Errors were less than 0.01.

TABLE 3.10

HERITABILITIES, GENETIC AND PHENOTYPIC  
CORRELATIONS BETWEEN PARAMETERS OF THE  
PARKS' MODEL

	A	Model VIa <sup>1</sup> k	t*
A	0.54(0.11) <sup>2</sup>	-0.73	-0.06
k	-0.89(0.14)	0.86(0.15)	0.23
t*	0.04(0.19)	0.09(0.17)	0.33(0.09)

<sup>1</sup>Heritabilities on the diagonal, genetic correlations below, phenotypic correlations above the diagonal.

<sup>2</sup>Standard errors in parentheses.

Models I and II being slightly higher than those of their counterparts, VII and VIII. Heritabilities for age at the point of inflection for the four models ranged from 0.53 for Model VIII to 0.63 for Model II.

Genetic and phenotypic correlations between parameters of the five models give an indication of the potential for their utilisation as selection criteria to change the structure of the growth curves. The range of the genetic and phenotypic correlations between the parameters of each model and growth traits were examined to investigate possible repercussions of direct selection on a single or multiple of parameters derived from any particular model (Tables 3.11 to 3.13).

The pattern of the genetic relationships between similar parameters of the five different models appears consistent. Genetic correlations between the estimated mature weight, A, and birth weight for each model are highly negative. Values range from -1.11 (0.19) for the Gompertz function (Model II) to -0.83 (0.18) for the Parks' function (Model VIa). The genetic correlations between A and weights at various ages gradually rise to peak at high positive values for the correlations between 42 and 84 day weights. For the two Logistic models, the genetic correlations between A and 42 day weight (0.91 and 0.93 respectively) appear higher than those between A and 84 day weight (0.80 and 0.80 respectively). This decline in the genetic correlations is due to the larger sire component of variance for 84 day weight, although the additive genetic covariance between A and 84 day weight had nearly doubled. The genetic cor-



TABLE 3.11  
 GENETIC ( $r_g$ ) AND PHENOTYPIC ( $r_p$ ) CORRELATIONS BETWEEN PARAMETERS OF THE LOGISTIC MODELS (I AND VII) AND  
 WEIGHTS, WEIGHT GAINS AND FEED EFFICIENCIES

	Model I				Model VII						
	A	$r_p$	$r_g$	b	$r_p$	$r_g$	k	A	$r_p$	$r_g$	k
Birth Wt	-1.07(0.18) <sup>1</sup>	0.114	-0.84(0.4)	-0.610	0.65(0.24)	-0.364	-1.01(0.18)	0.139	0.13(0.27)	-0.483	
21 day Wt	-0.15(0.16)	0.211	-0.43(0.17)	0.022	0.87(0.07)	0.591	-0.11(0.16)	0.241	0.82(0.09)	0.535	
42 day Wt	0.91(0.06)	0.818	0.93(0.17)	0.451	0.43(0.21)	0.257	0.93(0.05)	0.838	0.76(0.19)	0.202	
84 day Wt	0.80(0.06)	0.842	1.03(0.13)	0.444	0.02(0.28)	-0.041	0.80(0.06)	0.833	0.29(0.18)	-0.021	
Gain - days											
0-21	-0.10(0.17)	0.202	-0.40(0.15)	0.084	0.85(0.06)	0.636	-0.10(0.13)	0.230	0.83(0.09)	0.593	
21-42	0.76(0.08)	0.684	1.00(0.14)	0.447	-0.49(0.18)	-0.179	0.74(0.09)	0.682	-0.21(0.17)	-0.194	
42-63	1.12(0.20)	0.367	2.11	0.131	-0.31(0.17)	-0.319	1.05(0.21)	0.327	0.04(0.11)	-0.215	
63-84	0.18(0.11)	-0.049	0.09(0.22)	0.004	-0.11(0.10)	-0.094	0.18(0.15)	-0.050	-0.05(0.18)	-0.091	
Efficiency											
21-42 days	0.38(0.12)	0.516	0.19(0.20)	0.344	-1.04(0.19)	-0.233	0.30(0.15)	0.507	-0.79(0.21)	-0.230	
42-63 days	0.88(0.17)	0.328	1.51	0.120	-0.15(0.14)	-0.298	0.82(0.19)	0.290	0.28(0.19)	-0.199	
63-84 days	0.12(0.16)	-0.072	0.08(0.21)	-0.004	-0.12(0.13)	-0.099	0.11(0.11)	-0.074	-0.05(0.18)	-0.091	

<sup>1</sup>Standard errors of genetic correlations in parentheses.

TABLE 3.12  
 GENETIC ( $r_g$ ) AND PHENOTYPIC ( $r_p$ ) CORRELATIONS BETWEEN PARAMETERS OF THE GOMPertz MODELS (II AND VIII) AND  
 WEIGHTS, WEIGHT GAINS AND FEED EFFICIENCIES

	Model II				Model VIII					
	A	b	k	A	A	k	k	k		
	$r_g$	$r_p$	$r_g$	$r_p$	$r_g$	$r_p$	$r_g$	$r_p$		
Birth Wt	-1.11(0.19) <sup>1</sup>	0.107	-1.01(0.27)	-0.464	0.59(0.23)	-0.216	-1.00(0.19)	0.119	0.35(0.14)	-0.256
21 day Wt	-0.32(0.16)	0.081	-0.44(0.14)	-0.046	0.81(0.07)	0.592	-0.27(0.10)	0.109	0.78(0.08)	0.554
42 day Wt	0.76(0.10)	0.714	0.71(0.15)	0.298	0.24(0.16)	0.134	0.76(0.10)	0.735	0.36(0.13)	0.089
84 day Wt	0.82(0.06)	0.828	0.80(0.09)	0.343	-0.15(0.11)	-0.207	0.78(0.07)	0.826	-0.05(0.11)	-0.202
Gain - days										
0-21	-0.27(0.11)	0.072	-0.39(0.15)	0.000	0.83(0.08)	0.622	-0.22(0.10)	0.098	0.78(0.08)	0.587
21-42	0.81(0.08)	0.673	0.88(0.09)	0.104	-0.56(0.17)	-0.307	0.76(0.09)	0.675	-0.45(0.16)	-0.324
42-63	1.02(0.21)	0.436	1.76	0.163	-0.63(0.25)	-0.396	1.06(0.20)	0.409	-0.61(0.23)	-0.341
63-84	0.20(0.12)	-0.016	0.00(0.17)	0.007	-0.15(0.10)	-0.134	0.16(0.18)	-0.022	-0.10(0.17)	-0.199
Efficiency										
21-42 days	0.52(0.15)	0.533	0.56(0.15)	0.289	-0.98(0.18)	-0.335	0.42(0.17)	0.527	-0.81(0.20)	-0.340
42-63 days	0.97(0.16)	0.398	1.47	0.157	-0.36(0.20)	-0.369	0.89(0.17)	0.370	-0.27(0.16)	-0.318
63-84 days	0.14(0.17)	-0.035	-0.03(0.17)	-0.002	-0.12(0.16)	-0.130	0.10(0.17)	-0.042	-0.06(0.17)	-0.114

<sup>1</sup>Standard errors of genetic correlations in parentheses.

TABLE 3.13  
 GENETIC ( $r_g$ ) AND PHENOTYPIC ( $r_p$ ) CORRELATIONS BETWEEN PARAMETERS OF PARKS<sup>1</sup>  
 MODEL (VIa) AND WEIGHTS, WEIGHT GAIN AND FEED EFFICIENCIES

	Model VIa					
	A		k		t*	
	$r_g$	$r_p$	$r_g$	$r_p$	$r_g$	$r_p$
Birth Wt	-0.83(0.18) <sup>1</sup>	0.006	0.42(0.18)	0.048	-0.18(0.20)	-0.040
21 day Wt	-0.25(0.13)	-0.063	0.36(0.13)	0.316	-0.65(0.16)	-0.265
42 day Wt	0.29(0.11)	0.320	0.18(0.16)	0.136	0.16(0.21)	0.346
84 day Wt	0.51(0.11)	0.649	-0.34(0.14)	0.108	0.01(0.12)	0.108
Gain 0-21 days	-0.21(0.11)	-0.064	0.34(0.10)	0.316	-0.65(0.17)	-0.265
Gain 21-42 days	0.42(0.14)	0.375	-0.19(0.15)	-0.098	0.68(0.11)	0.554
Gain 42-63 days	0.62(0.17)	0.503	-0.41(0.21)	-0.423	0.71(0.21)	-0.101
Gain 63-84 days	0.32(0.11)	0.153	-0.49(0.14)	-0.310	-0.40(0.13)	-0.188
Efficiency 21-42 days	-0.06(0.20)	0.048	0.23(0.11)	0.172	0.79(0.17)	0.117
Efficiency 46-63 days	0.35(0.16)	0.310	-0.42(0.15)	-0.121	0.50(0.16)	0.456
Efficiency 63-84 days	0.51(0.17)	0.482	-0.38(0.13)	-0.415	0.26(0.20)	-0.117

<sup>1</sup>Standard errors in parentheses.

relations between estimated mature weight for the five models and weight gain over the four 3 week periods are essentially the same. These were negative for pre-weaning growth rising to maximum for each model over the 6 - 9 week period and then declining for the period from 9 - 12 weeks. A similar pattern was evident for the genetic correlations between A and the three post-weaning feed efficiency measures. Values for these correlations were low (-0.06 to 0.52) for the 3 - 6 week measurements, medium to high (0.35 to 0.97) for the following three weeks, and then dropping (0.14 to 0.10) for all models, except the Parks' function (0.51), in the final period to 12 weeks.

For the two models involving the b parameter, Models I and II, genetic and phenotypic correlations show virtually the same trend. Parameter b is negatively correlated with birth and 21 day weight and positively correlated with later weights. The aberrant values for the correlations of b with gain and efficiency for the 42 - 63 day periods reflect extremely low sire components of variance for both b (0.001935) and feed efficiency (0.0000053). The low additive genetic variance for b casts doubts on its genetic correlations with other traits, but, these two are obvious extremes.

The phenotypic and genetic correlations between the maturing rate parameter, k, and all other measures of growth are similar for the five models, being positive with weight traits prior to 42 days of age and either close to zero or negative for traits after 42 days. For each model, excluding the Parks' and the Logistic (Model VII, 42 - 63 efficiency correlation is 0.28) functions, k is negatively correlated with feed efficiencies post-weaning. For

Parks' model, this negative association is not apparent until after the 21 - 42 day measurement period. The genetic correlations between  $k$  and weights at 21, 42 and 84 days are similar in direction, if not in magnitude, to those reported by McCarthy and Bakker (1979).

The parameter  $t^*$  from Parks' Model VIa appears to have properties similar to parameter  $b$  of Models I and II. It is negatively correlated to pre-weaning weights (including 21 day weight), as are the  $b$  parameters of Models I and II, but does not show the strong positive relationship with later weights. However, it does appear to be positively associated with feed efficiency over the three measurement periods, 0.79 (21 - 42 days), 0.50 (42 - 63 days) and 0.26 (63 - 84 days), but the error on the latter period is relatively high and the genetic and phenotypic correlation are of opposite sign.

### 3.3.2 Parks' Model of Weight, Feed Intake and Time

Means and standard errors for males and females, for the estimates of parameters of Parks' models, VIb and XI, are presented in Table 3.14. The functions are fitted simultaneously with both feed intake and weight information being used.

The lines of fit and observed data for a male and a female are shown in Figs. 3.14 and 3.15.

Predicted body weights and feed intake were calculated as an indication of the predictive ability of the models. These

TABLE 3.14

LEAST SQUARES MEANS AND STANDARD ERRORS FOR ESTIMATES OF PARAMETERS OF PARKS' MODELS, VIB AND XI

	Parameters		$T_0$	C (gms $d^{-1}$ )	Pooled	
	A (gms)	(AB)			RSS	$R^2$
		$t^*$ (days)				
Males	$34.88 \pm 0.22$	$0.39 \pm 0.016$	$4.708 \pm 0.248$	$5.241 \pm 0.063$	$6.755 \pm 0.064$	$0.0624$ $0.9997$
Females	$32.92 \pm 0.22$	$0.36 \pm 0.016$	$5.136 \pm 0.249$	$4.934 \pm 0.064$	$6.787 \pm 0.068$	$0.0673$ $0.9992$

A = estimated mature weight, gms

(AB) = growth efficiency factor

 $t^*$  = internal resistance of the animal to increase its appetite, days $T_0$  = 'Taylor Time Constant', days

C = mature feed intake.

Figure 3.14: Parks' equations, Models VIb and XI, fitted to individual growth data of a male and a female. Weights plotted against cumulative feed intake.

$$\text{Model } W_t = (A - W_0) (1 - e^{-(AB)F/A}) + W_0$$

	Parameter Estimates		Correlations						
	Male	Female	A	Male (AB)	C	A	Female (AB)	C	
A	39.86	29.709							
(AB)	0.254	0.227	(AB)	-0.891			-0.829		
C	5.796	6.389	C	-0.066	0.076		-0.048	0.065	
t*	2.398	4.935	t*	-0.074	0.098	0.882	-0.054	0.080	0.901
Error MS	0.0392	0.0583							
R <sup>2</sup>	0.9997	0.9996							

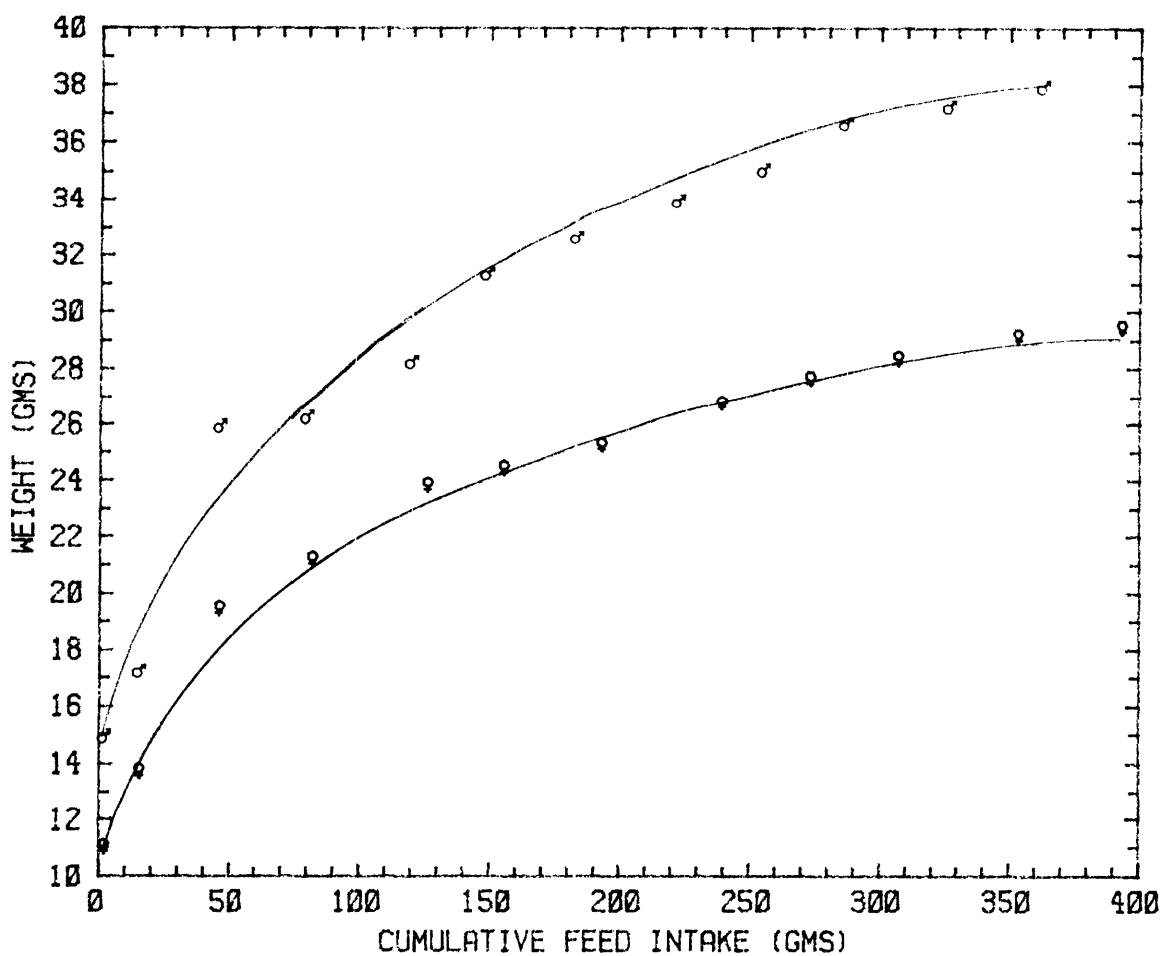
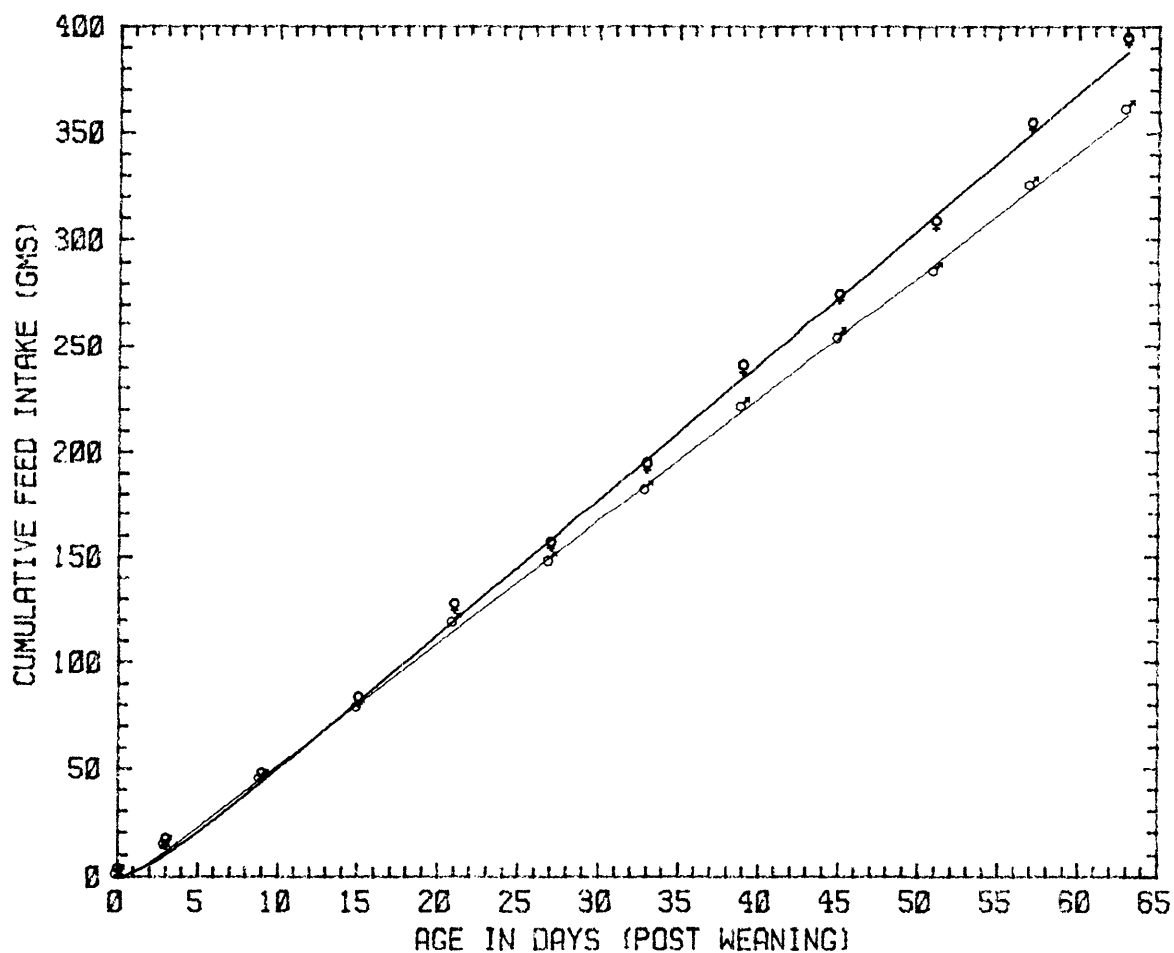


Figure 3.15: Parks' equation, Model XI, fitted to individual growth data of a male and a female. Cumulative feed intake plotted against time.

$$\text{Model } F_t = C(t-t^*(1-D/C))(1-e^{-t/t^*})$$

For parameter estimates and correlations see Figure 3.14.





results, along with genetic and phenotypic correlations, are shown in Table 3.15. Both female and male weights tend to be underestimated at early ages but, overestimated at later ages. The pattern is essentially the same for feed intakes, underprediction at early ages but with only slight overprediction for later ages.

The genetic and phenotypic correlations between the predicted and observed values re-inforce the apparently excellent fit of the models over all individuals. Phenotypic correlations never fall below 0.80 for either weight or feed intake. The one comparatively poor result was for the genetic correlation between 84 day weights (0.69).

The heritabilities and genetic correlations between the parameters of Models VIb and XI (Table 3.16) suggest there is considerable genetic variation for all parameters. The heritability of estimated mature weight, 0.14, is much lower than estimates obtained from other models in this study. As compared with Parks' Model VIa, both the sire component of variance and total variance for A were reduced for this model (VIb), resulting in a lower estimate of the heritability. As there are no other estimates available on the parameters (AB), C or  $T_0$ , it is difficult to make assessments on their accuracy. Parks (1982) suggested that a near constancy of the efficiency parameter, (AB), exists across species. However, the phenotypic coefficient of variation within this population was 11.19%, certainly suggesting this is, at least, not true on a within species basis.

Examination of the genetic and phenotypic correlations

TABLE 3.15  
 LEAST SQUARES MEANS AND STANDARD ERRORS FOR OBSERVED AND PREDICTED BODY WEIGHTS  
 AND FEED INTAKE - PARKS' MODELS, VIb AND XI

Trait Weight (gms)	Observed		Predicted		Correlations Between Observed and Predicted (Sexes Pooled)	
	Males	Females	Males	Females	Genetic	Phenotypic
24 days	19.63 + 0.20	17.59 + 0.20	19.15 + 0.13	16.95 + 0.13	0.89 (0.05) <sup>1</sup>	0.81
30	25.58 + 0.19	22.32 + 0.19	22.70 + 0.14	19.94 + 0.14	1.00 (0.02)	0.88
42	30.05 + 0.16	25.89 + 0.16	28.00 + 0.16	24.40 + 0.16	0.98 (0.03)	0.90
54	32.77 + 0.19	28.26 + 0.19	31.56 + 0.19	27.43 + 0.19	0.85 (0.05)	0.86
66	34.16 + 0.20	29.80 + 0.20	34.01 + 0.23	29.52 + 0.23	0.88 (0.06)	0.89
72	34.80 + 0.19	30.43 + 0.19	34.93 + 0.24	30.30 + 0.24	0.79 (0.07)	0.84
84	35.47 + 0.22	31.08 + 0.20	36.35 + 0.27	31.52 + 0.27	0.69 (0.08)	0.80
Feed Intake (gms)						
21-24 days	13.57 + 0.18	13.35 + 0.18	12.51 + 0.13	12.19 + 0.13	0.87 (0.06)	0.82
24-30	31.50 + 0.31	31.31 + 0.31	34.29 + 0.27	33.69 + 0.27	0.94 (0.04)	0.85
30-42	39.53 + 0.38	38.81 + 0.38	38.70 + 0.29	38.50 + 0.29	0.93 (0.05)	0.89
42-54	40.86 + 0.52	40.68 + 0.52	40.02 + 0.34	40.07 + 0.37	0.88 (0.06)	0.93
54-66	39.97 + 0.56	40.19 + 0.56	40.33 + 0.37	40.47 + 0.38	0.82 (0.07)	0.89
66-72	38.20 + 0.52	38.80 + 0.52	40.43 + 0.38	40.59 + 0.38	0.81 (0.08)	0.91
72-84	40.48 + 0.44	40.91 + 0.45	40.47 + 0.38	40.64 + 0.38	0.85 (0.07)	0.85

<sup>1</sup>Standard errors of genetic correlations in parentheses.

TABLE 3.16

HERITABILITIES, GENETIC AND PHENOTYPIC CORRELATIONS FOR ESTIMATES OF PARAMETERS OF  
PARKS' MODELS (VIB AND XI)<sup>1</sup>

	A	(AB)	C	t*	T <sub>o</sub>
A	0.14(0.07) <sup>2</sup>	-0.09	-0.08	-0.06	0.73
(AB)	-0.17(0.24)	0.80(0.14)	0.0	0.11	-0.05
C	-0.51(0.25)	0.39(0.14)	0.54(0.12)	0.51	-0.73
t*	0.00(0.33)	0.67(0.17)	0.66(0.14)	0.20(0.08)	-0.37
T <sub>o</sub>	0.74(0.13)	-0.31(0.15)	-0.96(0.18)	-0.51(0.24)	0.46(0.11)

<sup>1</sup>Heritabilities on the diagonal, genetic correlations below, phenotypic correlations above the diagonal.

<sup>2</sup>Standard errors in parentheses.

between the estimates of parameters of a model, in this case Models VIb and XI, give an indication of the 'biological' relevance of the parameters and their potential as selection criteria. In Table 3.17, the genetic and phenotypic correlations between A, (AB), C,  $t^*$  and  $T_0$  and weights, weight gains and feed efficiencies are presented. In all but a few instances, the phenotypic correlations between parameters and growth measures were extremely small. This was despite the fact that both genetic and phenotypic correlations between observed and predicted weights and feed intakes were very high.

Genetic correlations were variable and commonly associated with large errors. The genetic correlations between estimated mature weight, A, and the growth traits followed a similar pattern to those of other models. They were negative with early weights (-0.82 and -0.48 with birth weight and 21 day weight respectively) and tended to be positive with later weights (0.24 with 84 day weight), though the latter correlations were lower than those for models describing growth in the time domain only.

The positive genetic correlations between (AB), the efficiency parameter, and pre-weaning growth suggest it was primarily associated with pre-weaning efficiency. The strong negative correlations between gain and efficiency from 21 - 42 days of age and (AB) (-0.31 and -0.88 respectively) indicate that increases in (AB) would be detrimental to post-weaning growth.

The positive genetic associations between estimated mature feed intake, C, and early post-weaning growth and then a negative

TABLE 3.17  
 GENETIC ( $r_g$ ) AND PHENOTYPIC ( $r_p$ ) CORRELATIONS BETWEEN ESTIMATES OF PARAMETERS OF PARKS' MODELS  
 (VIB AND XI) AND WEIGHTS, WEIGHT GAINS AND FEED EFFICIENCIES

	A		(AB)		C		t*		T <sub>0</sub>	
	$r_g$	$r_p$	$r_g$	$r_p$	$r_g$	$r_p$	$r_g$	$r_p$	$r_g$	$r_p$
Birth Wt	-0.82(0.33) <sup>1</sup>	-0.004	0.28(0.20)	-0.023	-0.12(0.22)	0.047	0.25(0.28)	0.012	-0.15(0.22)	-0.030
21 day Wt	-0.48(0.23)	0.009	0.30(0.14)	-0.004	-0.09(0.17)	0.059	-0.28(0.20)	-0.003	-0.09(0.17)	-0.039
42 day Wt	-0.09(0.31)	0.071	-0.07(0.20)	-0.022	0.38(0.19)	0.151	-0.70(0.25)	-0.017	-0.38(0.21)	-0.064
84 day Wt	0.24(0.23)	0.216	0.13(0.15)	-0.072	0.28(0.15)	0.161	-0.21(0.20)	0.019	-0.16(0.16)	0.028
Gain - days										
0-21	-0.45(0.23)	0.009	0.29(0.13)	-0.002	-0.09(0.11)	0.055	-0.30(0.20)	-0.004	-0.09(0.16)	-0.036
21-42	0.34(0.27)	-0.003	-0.31(0.12)	-0.020	0.35(0.15)	0.110	-0.25(0.13)	-0.051	-0.17(0.15)	-0.018
42-63	0.44(0.25)	0.257	0.03(0.23)	-0.049	0.03(0.25)	0.092	0.09(0.18)	0.089	0.09(0.16)	0.099
63-84	0.25(0.17)	0.009	0.25(0.13)	-0.043	0.13(0.12)	-0.027	0.08(0.26)	-0.034	0.00(0.18)	0.035
Efficiency										
21-42	0.76(0.25)	0.008	-0.88(0.14)	-0.071	0.22(0.12)	0.028	0.19(0.18)	0.171	0.12(0.12)	-0.013
42-63	0.47(0.27)	0.053	-0.29(0.17)	0.051	0.11(0.10)	-0.102	0.08(0.24)	0.247	0.04(0.19)	0.114
63-84	0.65(0.26)	0.271	-0.13(0.21)	-0.034	-0.34(0.14)	-0.151	-0.04(0.29)	-0.005	0.44(0.18)	0.283

<sup>1</sup>Standard errors of genetic correlations in parentheses.

genetic correlation with later efficiency suggests that the parameter may be directly related to the animals partitioning of feed intake at all ages. The negative genetic correlations between  $t^*$  and weights post 21 days follow the pattern expected if  $t^*$  is a measure of appetite resistance, i.e., increases in  $t^*$  decrease intake and decreases in intake decrease weights. As  $T_0$  is directly related to A and C (i.e.  $T_0 = \frac{A}{C}$ ) the genetic correlations followed essentially the same trend as for A, but generally with lower estimates and lower standard errors.

### 3.3.4 Predicted Direct and Correlated Responses

As an extension of the genetic analyses described above, predicted direct and correlated responses to a single generation of selection were calculated for the Parks' functions, Models VIa, VIb and XI (Table 3.18). The two forms of Parks' models are directly related, but the data sets available for obtaining estimates of the parameters are different, in that feed intake is utilised for Model VIb and XI and the initial weight was taken as 21 day weight. Parameter values obtained by fitting the models need not necessarily be the same.

#### a) Parks' Weight/Age Equation, Model VIa

The contention (Section 3.1.1) that the k parameter is directly related to the rate of maturing is supported by results presented in Table 3.18. Animals with large k values mature rapidly and attain lower mature weights. Selection on k would place a heavy emphasis on pre-weaning growth. The reliance on

TABLE 3.18  
 EXPECTED DIRECT AND CORRELATED RESPONSES TO SELECTION FOR ESTIMATES OF PARAMETERS OF GROWTH MODELS<sup>a,b</sup>

Responses, % of Initial Mean	Model VIa			Models VIB and XI			Initial Mean		
	A	k	t*	A	(AB)	C		t*	T <sub>0</sub>
Model 1. A	7.30	-10.36	0.0	0.87	0.0	0.0	-6.66	0.0	37.430
k	-7.61	14.70	0.0	-1.05	-6.99	1.51	0.0	-2.35	0.035
t*	0.0	0.0	5.17	1.08	-8.55	2.57	5.17	-1.92	4.870
Model 2. A	0.38	-0.58	0.54	1.54	0.0	-1.42	0.0	2.92	33.900
(AB)	0.0	-2.54	-2.73	0.0	33.70	2.56	20.91	-2.95	0.375
C	0.0	1.88	2.91	-1.20	7.85	5.45	16.93	-7.11	6.771
t*	-0.52	0.0	0.46	0.0	5.05	0.98	15.61	-2.40	4.922
T <sub>0</sub>	0.0	-1.75	-1.31	1.48	-5.41	-3.12	-8.41	7.17	5.088
Birth Weight	-1.57	1.27	0.0	-1.56	4.60	0.0	0.0	0.0	1.559
21 Day Weight	-1.58	3.66	-3.85	-1.70	9.18	0.0	-7.94	0.0	12.547
42 Day Weight	0.63	0.0	0.0	0.0	0.0	1.32	-11.46	-1.86	27.835
84 Day Weight	3.14	-3.14	0.0	0.83	0.0	-1.64	-5.47	0.0	33.362
Gain 0-21 Days	-1.29	3.50	-3.79	-1.59	8.81	0.0	-8.44	0.0	10.988
Gain 21-42 Days	2.00	-1.45	2.93	1.09	-8.09	1.80	-6.04	-1.32	15.288
Gain 42-63 Days	0.80	-0.84	0.83	0.69	0.0	0.0	0.0	0.0	4.173
Efficiency 21-42 Days	1.11	-2.13	1.44	1.16	-6.18	0.0	0.0	0.0	0.123
Efficiency 42-63 Days	0.81	-0.96	0.37	1.14	0.0	-0.01	0.0	1.87	0.027

<sup>a</sup>Genetic correlations not significantly different from zero were set to zero.

<sup>b</sup>Responses from a single generation of selection with a standardised selection differential of one are expressed as percentage changes from the initial mean.

the maternal food supply could well be limiting to any actual changes achieved by selection on  $k$ , particularly as a reduction in mature size may limit the females biological ability for milk production. The importance of understanding relationships between  $k$  and  $A$  is discussed in detail later.

Selection to increase mature weight, as estimated by this model, suggest that there would be correlated decreases in early weights but increases in later weights. Important, in terms of altering the structure of the weight growth curve, is the expected increases in weight gain between 21 - 42 days and associated increases in efficiency in this and the following three week period. Increases in efficiency are also combined with increases in food consumption over the same time intervals.

Expected correlated responses to increases in  $t^*$  suggest beneficial increases in weight gain and efficiency between 21 and 63 days of age. Concomitant with these responses there would be no change in birth weight or 84 day weight. However, any selection on  $t^*$  would have to be reconciled with the decreases in pre-weaning growth.

b) Parks' Weight, Feed Intake/Time Equations, Models  
Vib and XI

As with the above, expected direct and correlated responses to selection on any particular parameter should be treated with some caution considering the size of the errors on some genetic relationships and differences between heritability estimates.



Expected correlated responses to selection on mature weight, as estimated by Model VIb, would be essentially the same as for A estimated by Model VIa. Correlated responses to selection on (AB), the efficiency parameter, would result in large increases in both birth weight and 21 day weight. The heavy emphasis on the pre-weaning environment could be expected to stress the role of positive maternal effects on growth.

Although mature feed intake, estimated by C, was highly correlated with (AB), selection to increase C would apparently result in little change in early weights, but would increase weight gain between 21 to 42 days. The correlated decrease in mature weight with selection to increase mature feed intake appears contradictory to normal expectations and should be treated with scepticism.

Though the values for  $t^*$  obtained from Models VIa and XI are similar, the genetic correlations between each of the two  $t^*$  parameters with weights, weight gains and feed efficiencies were quite different. Increases in  $t^*$ , estimated by Model XI, would be expected to decrease weights at all ages except birth, with no changes in feed efficiency. Thus, increasing  $t^*$  would also be associated with decreases in food consumption. As with  $t^*$ , increases in  $T_0$  would be expected to decrease weights, but only in the mid-period of growth.

### 3.4 DISCUSSION

During the initial phases of this study, three model types were excluded from further analyses; the Brody, Bertalanffy models and the generalised Richards' model. The basis for the exclusion

of these three model types was solely their inability to consistently provide adequate fits of the data. Of the remaining models, all provided adequate fits of the data in terms of the criteria described, i.e., small residual variances, consistent predictions of weights (and feed intakes, in the case of Model XI), and biologically interpretable parameters.

The genetic correlations and heritabilities of the parameters, for each model, suggest that selection on a single parameter or parameter set would produce changes in the growth curves of mice from this population. The ability to alter shape of the weight/age growth curve under selection by a parameter or parameter set, will depend upon the degree of independence among the parameters. For the two parameterisations of the Logistic model, Models I and VII, 80% and 40%, respectively, of the additive genetic variation for mature weight,  $A$ , was independent of the maturing rate parameter,  $k$ . Values for the two forms of the Gompertz models were lower, 31% for Model II and 23% for Model VIII. Reports in the literature show a considerable range of estimates for the degree to which parameters are genetically independent of one another. Estimates involving  $A$  and  $K$  in cattle vary between 10% for Hereford weight data (Brown, *et al.*, 1972) and 92% for Angus (Fitzhugh, 1976). For mice Eisen *et al.* (1969) suggested that 78% of the genetic variation in  $k$  was independent of  $A$ , whereas Timon and Eisen (1969) gave an estimate of 88%. The results presented in this study suggest that there are large differences between models and model parameterisations when fitted to the same data.

The negative genetic and phenotypic correlations between

estimated mature weight, A, and estimated maturing rate, k, for all the weight/age models considered in this study, are consistent with results from other studies. These correlations suggest that larger (smaller) mature weights are associated with smaller (larger) maturing rates and thus longer (shorter) maturing intervals ( $1.0/k$ ). This basic premise is supported by the trend in phenotypic and genetic correlations between the two parameters and the observed and predicted body weights.

The estimates obtained for A and k, for the Logistic and Gompertz type models, permit some interesting comparisons with estimates for other mouse populations reported in the literature. Eisen *et al.* (1969) obtained estimates of k from lines of mice selected for high and low six week weight. Fitting models identical to Models I and II (the Logistic and Gompertz) they obtained male k values of  $0.085 \pm 0.001$  and  $0.045 \pm 0.001$  respectively for the high line, and  $0.0704 \pm 0.001$  and  $0.035 \pm 0.001$  for the low line. The mean male k and A values obtained in this study ( $0.119 \pm 0.001$  and  $34.37 \pm 0.185$  for the Logistic and  $0.058 \pm 0.001$  and  $37.89 \pm 0.222$  for the Gompertz model) indicated these mice were both heavier at maturity and approached mature weights more rapidly than Eisen *et al.*'s mice. McCarthy and Bakker (1979) utilised the Gompertz equation, Model II, to examine the growth of a number of lines selected for between 14 and 22 generations on body weight. Comparison with their estimates for parameters A and k show that only their high five week and high ten week body weight lines had estimated mature weights greater than those reported for the population examined in this study. The apparently large mature size and high rate of maturing for this strain of mice may explain differ-

ences between results reported here and those reported in the literature. Whether there were sampling biases introduced at the initial establishment of the population at Armidale from the Sydney population, is unclear. Some consistency with Hetzel's (1978) results would tend to dismiss this idea. There was some suggestion, by Animal Technicians at Sydney University, that the strain may have been selected for bodyweight prior to being moved to the Animal Husbandry Department University of Sydney, though this could not be verified. It is, however, apparent that this population is unique in the form of its weight/age growth curve.

Because of the direct association between  $k$  and  $A$ , selection to alter the form of a weight/age growth curve, utilising either parameter, should not be undertaken without consideration of the structural and genetic dependencies between the two. The exact meaning of differences in  $k$  independent of  $A$  are difficult to quantify. Figure 3.16 indicates various representations of the combinations of  $A$  and  $k$ , as presented by Brown (1970). Diagram I represents differences in  $k$  as differences in persistency of growth but not in growth rate. Animals in this case would be gaining weight at the same rate but would attain different estimated mature weights. The second diagram represents two animals with very similar growth rates over most of the growth curve, but the lower curve would have a higher rate of maturing.

Distinct differences in growth rate are represented in the third diagram. Both animals are approaching the same mature weight but at different rates, particularly at early ages. In this case the upper curve would have the higher maturing rate parameter.

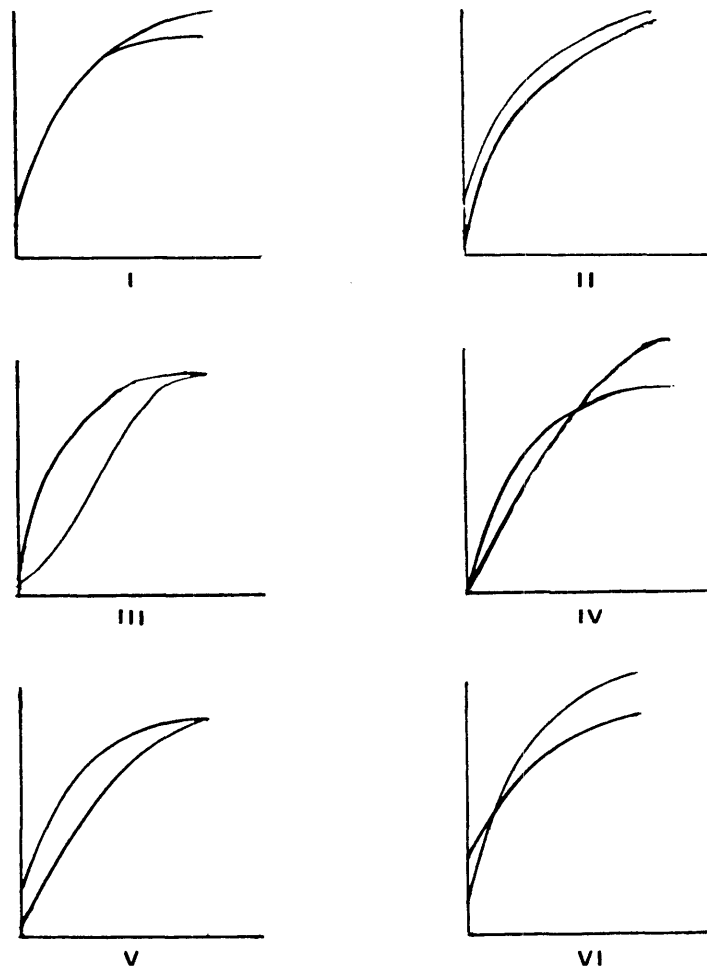


Figure 3.16: Diagrammatic representation of structural relations between A and k.

Because of the differences in mature weight, direct comparisons of  $k$  could be misleading for situations represented in diagram IV. In this case, it would be possible for both animals to have the same value of  $k$ .

Diagram V represents a composite of I, II and III. The differences in  $k$  may represent differences in growth rate, rate of approach to maturity and persistency of growth. In the final diagram, VI, the different growth curves could be represented by the same  $k$  value but different initial and final weights. The results of analysis of growth curves of mice selected for large and small size by Parratt *et al.* (1982) may be indicative of this pattern. They found positive correlated increases in  $k$  of the Gompertz and Logistic models for both large and small lines although the asymptote had significantly increased in the high line and decreased in the low line. This emphasises the need for careful consideration of the structural inter-relations between parameters if selection is to be undertaken on parameters of any of the models considered in this study.

Similar relational problems may be associated with the parameters of Parks' weight and cumulative food intake models (VIb and XI), particularly in relation to  $t^*$  and  $(AB)$ , and Parks' (1982) interpretation of the biological appropriateness of the parameters of models VIb and XI. In a re-analysis of the data of Timon and Eisen (1970), Parks suggested  $t^*$ , the parameter related to 'resistance' to increases in appetite, was decreased in females reflecting that the line selected for increased weight gain had reduced feed intake. However, the reduced feed intake was offset by an increase

in (AB) the efficiency parameter. In support of the change in efficiency,  $T_0$  had increased thus reducing the liveweight equivalent of feed intake being partitioned into the no growth component (see Section 3.1.2). Results from the study of expected correlated responses described here support Parks' interpretations. Increases in  $t^*$  would decrease feed intake resulting in decreases in weights at 21, 42 and 84 days, with little change in efficiency up to 63 days of age. If we at least accept the directional changes suggested by the genetic correlations, it is apparent that efficiency at early ages would be increased but there would be a decline in the efficiency of partitioning of feed intake between growth and no growth components. These latter points are based on the premise that the parameter (AB) was closely associated with pre-weaning efficiency and  $T_0$  was related to the partitioning of liveweight equivalents of feed intake. The role of  $T_0$  in partitioning of feed intake was further illustrated by examination of the possible correlated responses to selection on parameter C, estimated mature feed intake. Increases in C would extend the time taken for an individual to attain its mature feed intake. Animals would be slightly more efficient from birth to weaning but as they reach their estimated mature weight they become less efficient. They would consume food in excess of their weight requirements and the proportion of the liveweight equivalents of feed intake going to no-growth would be increased. It is important to again stress these conclusions are based on the results presented and caution is necessary in extrapolation because of the low values and the magnitude of the errors on the genetic estimates of some parameters.

In terms of the McCarthy/Roberts model presented in Chapter

1 (Fig. 1.1) it appears that selection on parameters of any of the seven models examined in detail in this study would elicit responses by intervention at one or more stages of the pathways in the model. However, there appears to be little to be gained, in terms of altering the structure of the growth curve to a more desirable form for livestock species, by selection on a single parameter. Emphasis on parameters related to pre-weaning growth, such as (AB), would be difficult in selection programmes because of biological limitations to the maternal environment.

It is difficult to make predictions on the likely outcome of selection on any parameter or parameter set in terms of the model presented in Chapter 1. If the results from studies by McCarthy and Bakker (1979), Eisen *et al.* (1969) and Parks (1982) are reliable indicators of correlated changes in parameters of certain models, then we could expect to achieve similar results under direct selection. Selection would act on a number of pathways, as indeed it does when selection is for weight or weight gain. The question remains as to whether selection based on parameters of nonlinear growth models would act on the pathways in the same or a different manner. Clearly there is the need to carry out selection studies based on the parameters of a nonlinear model. However, the results presented in this thesis would suggest that responses would not be different to those found when selection has been for weights or weight gain.

Utilising parameters of nonlinear models as alternative selection criteria to alter the structure of individual growth curves needs careful consideration. Although not discussed in detail here,



statistical problems associated with utilising nonlinear models have come under closer scrutiny in Chapter 5. In this study, the number of data points available on each individual allowed accurate predictions of parameter estimates; and this would not necessarily be so in domestic livestock species. Questions on the behaviour of nonlinear models, the distributional properties of parameters and their accuracy with more restricted data sets have not been considered when estimating genetic or phenotypic relationships.