Chapter 3: Models for Predicting Body Weight

3.1. Introduction

A principal objective of beef production is to grow animals to a desired endpoint (weight, fat content) with a high degree of efficiency and uniformity. The purpose of such a goal at all levels within the beef industry is to help meet the needs of components further down the supply chain. One possible means of achieving uniformity in beef production is to manipulate the growth pathways of animals, as discussed by Ball et al. (1997). However to prevent a compromise in overall efficiency any manipulation needs to be optimised. Optimisation relies upon the mathematical functions employed to describe the biological characteristics (eg. growth, development and energy requirements) and economic characteristics of beef production systems such that the results of alternative feeding treatments can be adequately predicted.

In most commercial production environments the main component of animal performance is live weight gain or growth. Prediction of all other animal performance attributes (feed intake efficiency, carcass weight, and carcass composition) relies upon the accurate prediction of live weight gain. Ideally, predictions of live weight gain would be based on information concerning age, feed intake, genetic information (both breed and family/EBV), prevailing environment (eg. temperature) and growth history. However, information from all these sources is generally not available with perhaps the exception of age. Having recognised that efficiency in beef producing enterprises can be defined as the ratio of outputs (typically live weight or weight of lean) to inputs (typically food input in kg or metabolisable energy, ME) (Thompson and Barlow 1986) it becomes apparent when feed intake is known the accuracy of prediction increases.

A large number of functions have been developed that could potentially be used for predicting the growth pathways of livestock. The approach used and the information required to make predictions of animal growth vary between functions. The well known Brody (1945) and Gompertz (1825) functions only use information concerning age to make growth predictions. On the other extreme is the more biological animal

model used in the GrazFeed (Freer et al. 1997) and GRAZPLAN (Donnelly et al. 1997) decision support tools, that predicts animal growth from current live weight using information concerning age and the prevailing environment (temperature, rainfall, wind) as well as feed intake and feed quality (digestibility, crude protein), that are estimated from pasture characteristics modelled by the GrassGro decision support system (Moore et al. 1997).

The model developed by Freer et al. (1997) forms part of a group of models referred to as animal growth simulation models. These also contain the Cornell Net Carbohydrate and Protein System (Fox et al. 2004) and the BABYBEEF model (Loewer et al. 1983a), which have been developed with the aim of improving the accuracy of growth prediction (Wellock et al. 2004a). The backbone of most growth simulation models is the mathematical function used to determine potential growth. An assortment of other functions, rules and logistical constraints used to predict growth (Bridges et al. 1992a; Wellock et al. 2003a) rely on this function to set limits on growth rate at any size, which predictions can not exceed.

Most growth functions are developed independently often using data from one or more sources and are subsequently tested using data from other sources, which is a valid approach, reflecting practical use. Many authors have taken this approach with Oltjen et al. (1986b), Keele et al. (1992), Di Marco et al. (1989), Wellock et al. (2003a), and Hoch and Agabriel (2004a) developing their models and then subsequently testing these models with data taken from selected studies in Oltjen et al. (1986a), Williams et al. (1992a), Di Marco and Baldwin (1989), Wellock et al. (2003b) and Hoch and Agabriel (2004b). Arnold and Bennett (1991a) compared outputs from four growth models when they were presented with hypothetical production situations, such as different diets (e.g. high concentrate diet vs high roughage diet). Arnold and Bennett (1991b) then evaluated the usefulness of these models by comparing experimentally measured growth and chemical body composition data with model simulated data when the models were given information concerning the diet and production characteristics (eg. hormone status, sex, breed, etc). Generally, growth functions are rarely compared in collective groups with the same dataset(s).

Any functions used for optimisation of growth pathways must use the available information sources, to accurately predict animal performance in any production circumstances before confidence can be placed in such a process. Therefore, the ultimate test of the models in this study is their ability to use available information (feed intake and age) and parameter estimates from other sources (average population parameters) to accurately predict animal performance. The current study uses criteria A, B and C listed below to narrow down the models available in the literature. The ability of the remaining models to accurately predict future animal performance is tested with criteria D, using two independent datasets that contain information concerning animal age and daily feed intake as well as parameters estimated in external populations.

3.2. Materials and Methods

3.2.1. Criteria for Selecting Suitable Growth Functions

In the context of optimising tactical management decisions, any functions selected for predicting animal performance need to contain sufficient flexibility to operate in different scenarios and need to make predictions that agree with the reality of beef production. A number of criteria exist that, if satisfied, allow functions to meet these needs.

A) Model Inputs:

As mentioned above, in an ideal situation information concerning age, feed intake, genetics, prevailing environment and growth history would be available for models to use when predicting future growth. Rarely is information of this type available in extensive production systems. The most basic information required by any model to make a prediction of growth is a measure of time. Age is the most readily available and commonly used information source for this purpose. Manipulation of the nutritional environment is a quicker and easier means than other alternatives, such as animal breeding, to alter the growth trajectory of animals to improve profit (Meszaros 1999) and efficiency (Ball et al. 1997). Consequently, growth needs to be predicted for various feeding conditions to ascertain if nutritional manipulations are having the desired effect on performance and ultimately efficiency and profit.

B) Growth Prediction from an Early Age:

The efficiency of beef production is determined by performance at all degrees of maturity, not only later maturities often associated with lot feeding. Consequently, conception is an ideal starting age for prediction because the potential then exists to manipulate an animal's entire growth pathway. However, given the difficulty associated with measuring and/or manipulating foetal growth, prediction and subsequent manipulation of performance from parturition would be desirable.

C) Number of Estimable Parameters:

Wellock et al. (2004a) discuss, in the context of predicting potential growth of the pig, the desirability of a growth function that contains as few parameters as possible. The ease of understanding and use of such a function along with a decrease in the error associated with parameter estimation and subsequent use are advantages to be gained from satisfying criteria of this nature. Having as few as possible estimable parameters in a growth model is one form of the long established law of parsimony, commonly referred to as Occam's Razor (Sweatt 1999) and is related to the following criterion of robustness.

D) Accuracy and Robustness:

The acceptability of any of the growth models tested during this study is determined by two components. The first is the accuracy of prediction, which is determined using a goodness of fit criterion that compares the observed body weights with predicted body weights. The second component is the robustness of the growth model. Robustness, in this study, is taken as the ability of a model to accurately predict body weights across a wide range of production conditions (Gribble 2001). Robustness can be compromised by using too many parameters, especially where the design and amount of data are limiting.

3.2.2. Feeding and Growth Data

The testing procedure used during the current study was designed to test both the fit of individual models to data and the transportability of their parameter estimates for predictive purposes with other data. In order to achieve this goal two datasets were

used. The first dataset (Trangie) was used for both fitting the models and testing their predictive abilities for animals from the same population that were not used for model calibration. The second dataset (CRC) was used for testing the predictive ability of the models in a population that is different from the dataset used for model calibration. This second dataset tests the robustness of the models but their ranking should be interpreted with caution due to the use of only one external dataset. The details of each dataset are presented below.

Trangie:

The requirement for functions to consider feed intake when predicting animal performance demands that data for both feed intake and growth be used to test functions. The test dataset also needs to span a substantial portion of the growth trajectory in order to be able to appropriately gauge the fit of the functions. The data used to test the various functions under consideration was taken from a serial slaughter experiment conducted by NSW Agriculture at the Agricultural Research Centre, Trangie, New South Wales. The 106 Angus steers used during the experiment were born in 1986 and 1987. Details concerning the establishment and maintenance of the selection lines are reported by Parnell et al. (1997).

Animals were slaughtered at different degrees of maturity throughout the experiment ranging from birth to maturity. Consequently, only 58 of the original 106 animals entered the feedlot phase of the experiment due to 24 animals being slaughtered at birth and another 24 animals being slaughtered at weaning (7 months). Additionally one animal was also excluded from the analysis due to large quantities of missing data. Data for the remaining 57 animals consisted of weekly live weights and weekly dry matter (DM) intakes of steers grown from approximately 7 months of age until considered mature at approximately 3 years and 8 months. Steers were considered to have reached maturity when weekly live weight measurements showed they had effectively stopped growing. These animals were grown on a pelleted diet consisting of 50% ground Lucerne hay, 45% cracked wheat and 5% cottonseed meal which provided 10.9 MJ ME/kg DM. Individual animals had access to the diet from an automatic feeding system (Herd 1991) 24 hours a day, with the programmed conditions that one kilogram of feed were available per feeding session and any

animal that had eaten in the previous half an hour was denied access. This potentially allowed 48 feeding sessions per day. Other details concerning this experiment and generation of this data are reported by Perry and Arthur (2000).

Beef CRC:

The data used as the external testing set was taken from an experiment established at the Agricultural Research centre, Trangie, New South Wales, independent from the experiment described for the Trangie dataset. The 96 Angus steers selected in the experiment were born in 2001 and were the result of 2.4 generations of selection for and against residual feed intake (RFI) plus an intermediate unselected line. For details concerning the establishment of these lines refer to Arthur et al. (2001). The steers entered the CRC for Cattle and Beef Quality "Tullimba" Research feedlot (Armidale, NSW), after backgrounding, at approximately 20 months of age weighing an average of 462kg (Hegarty et al. 2005). There were 12 steers accommodated within eight feedlot pens that each contained an automated feed-intake recorder (Ruddweigh, Guyra, NSW) (Bindon 2001a) allowing individual feed intakes to be recorded. The steers undertook a standard induction program following which the animals were given *ad libitum* access to a finishing ration. The ration consisted of 75% grain, 10% sorghum hay, 5% protein pellets and molasses with vitamin and mineral supplements. The diet contained 12.1 MJ ME/kg DM and had a DM digestibility of 82% (Herd 2005, pers. comm.). Individual feed intakes of 91 steers, following the removal of 5 steers due to inappetence, were recorded for a 10-week RFI test with unfasted live weights recorded weekly. For any further details relating to this experiment and generation of this data refer to Hegarty et al. (2005).

3.2.3. Growth Functions

Models in the literature that satisfy criteria A and B listed above included those developed by Parks (1970a), Freer et al. (1997), the model extended from the function of Kinghorn (1985) and a version of the model presented by Amer and Emmans (1998) that was extended to include rumen digestion and nutrient partitioning. The model developed by Soboleva et al. (1999) with heat production extensions (Oltjen et al. 2000), was not considered due to its inability to predict growth from neither birth

(Kinghorn 2003, pers. comm.) nor conception and the large number of estimable parameters. The Brody (1945), Richards (1959), von Bertalanffy (1957) and Logistic (Robertson 1908) functions as well as the function developed by Moore (1985) were also not considered due to their inability to consider feed intake. However, to illustrate the value of adding feed intake data to age data when predicting performance, the Gompertz (1825) function was included. A polynomial that considered both age and feed intake was also tested to compare the predictive ability of linear functions with that of non-linear growth models.

Given the above description of the data used for testing, any components contained within the original models that consider pasture consumption, lactation, environmental conditions, mobility (e.g. energy expended grazing) as well as male and female differences were excluded from the current testing. The differences between lines in both datasets were not considered; rather the animals within each dataset were treated as a single population. The form of each growth model/function used during testing is subsequently presented along with their respective estimable parameters.

Freer Model:

The growth model developed by Freer et al. (1997) and the updated version (Freer et al. 2002) contain functions that depend on an animal's stage of development. The standard reference weight (*SRW*) is the starting point from which normal weight (*N*), using Brody's growth rate parameter (C_{n1}) and the allometric scalar of Taylor (1968), is modelled:

$$N = SRW - \left(SRW - W_{Birth}\right).\exp\left(\frac{-C_{n1}.t}{SRW^{0.27}}\right) \quad \text{(kg)} \tag{3.1}$$

where t is time in days from birth and W_{Birth} is birth weight. SCA (1990) define SRW as an animal's base weight (live weight excluding fleece and conceptus) when skeletal development is complete and condition score is in the middle of the range (Freer et al. 1997). An animal's stage of development (Z) is then modelled using N and SRW.

$$Z = \frac{N}{SRW} \tag{3.2}$$

The total metabolisable energy intake (MEI_{Total}) of an animal is modelled in GrazFeed using the metabolisable energy intakes of pasture (MEI_f) and supplement (MEI_{Sup}), determined from the quality and quantity of each consumed. The testing process uses feed intake of a ration, thus only MEI_{Sup} is used to model total ME intake.

$$MEI_{Total} = MEI_{Sup} = (13.3DMD_S + 24.3EE_s + 1.32).I_S \quad (\text{MJ ME}) \tag{3.3}$$

where DMD_s is the DM digestibility of the supplement (%), EE_s is the ether extract of the supplement (gg^{-1}) and I_s is kg of DM intake in a time period. The ME required for maintenance (ME_m) is modelled in GrazFeed using the total ME intake in conjunction with the energy needed for maintenance metabolism (E_{met}) and grazing (E_{graze}), consequently only total ME intake and E_{met} are used.

$$ME_m = \left(\frac{E_{met}}{k_m}\right) + 0.09MEI_{Total} \quad (\text{MJ ME day}^{-1}) \tag{3.4}$$

The ME required for maintenance metabolism is modelled as:

$$E_{met} = 0.36Wt_{t-1}^{0.75}.\max\left(\exp\left(-8\text{x}10^{-5}.t\right), 0.84\right) \quad (\text{MJ ME day}^{-1}) \tag{3.5}$$

where Wt_{t-1} is weight from the previous day. The efficiency of energy use for maintenance (k_m) is defined as:

$$k_m = 0.5 + \left(0.02\frac{M}{D_{Solid}}\right) \tag{3.6}$$

where $\frac{M}{D_{Solid}}$ is the ME of DM of the diet. The relative feeding level (L) in excess of maintenance is modelled using MEI_{Total} and ME_m:

$$L = \left(\frac{MEI_{Total}}{ME_m} \right) - 1 \tag{3.7}$$

The effective degradability of protein in the diet and composition of gain are subsequently modified with this term during modelling of growth from the nutrients available using the equations contained in the Appendix. This information allows the modelling of empty body gain (*EBG*) and if required composition of gain.

$$EBG = \left(\frac{NE_g}{EVG} \right) \quad (\text{kg}) \tag{3.8}$$

where NE_g is the net energy available for gain and *EVG* is the energy contained in body weight change of growing animals. *EBG* is then used to increment live weight for each time period.

$$Wt_t = Wt_{t-1} + 1.09(EBG.\Delta t) \quad (\text{kg}) \tag{3.9}$$

where Δt is the number of days in a time period, Wt_{t-1} is the live weight prior to Δt and Wt_t is the live weight after Δt.

Extended Amer and Emmans Model:

The prediction of body weight, using the model presented by Amer and Emmans (1998), is based on the body being divided into four chemical components, these being protein, fat, water and ash. The unconstrained growth of each of these components is expressed as a function of the degree of maturity of protein contained in the body. The degree of maturity of protein in the body is represented by the following form of the Gompertz equation:

$$u_t = \exp\left(-\exp\left(G_o - (B_s.t)\right)\right) \tag{3.10}$$

where u_t is the degree of maturity of protein in the body, t is time, G_o is the initial condition derived from the ratio of the initial protein content (P_o) and mature protein

content (P_m). B_s is the scaled rate parameter used to express the general rate parameter in metabolic time. G_o and B_s are derived as follows:

$$G_o = \log_e\left(-\log_e\left(\frac{P_o}{P_m}\right)\right) \tag{3.11}$$

$$B_s = \frac{B^*}{P_m^{0.27}} \quad \left(\text{day}^{-1}\right) \tag{3.12}$$

where B^* is a general rate parameter. The initial body protein is estimated using the Newton-Raphson iteration method as presented in the Appendix and used in the pig growth model developed by Wellock et al. (2003a). The potential weights of each chemical body component depend upon the relationship defined by Emmans (1988), that states the degree of maturity of one chemical component is a power function of the degree of maturity of another chemical component and relies on the premise that B^* is identical for each component. This allows for the weights of the chemical body components to be predicted using:

$$P_t = u_t.P_m \quad (\text{kg}) \tag{3.13}$$

$$A_t = S.P_t \quad (\text{kg}) \tag{3.14}$$

$$L_t = u_t^{bl}.Q.P_m \quad (\text{kg}) \tag{3.15}$$

$$H_t = u_t^{bh}.R.P_m \quad (\text{kg}) \tag{3.16}$$

where P_t, A_t, L_t and H_t are the weights of protein, ash, lipid and water in the body at time, t. The ratios of ash, water and lipid to protein at maturity are represented by S, Q and R respectively, with S and R taking the values of 0.25 and 3.2, respectively (Amer and Emmans 1998). The power constants for lipid and water in the relationships described above are bl and bh with the values of 3 and 0.855, respectively (Amer and Emmans 1998). The derivatives of the above functions correspond to the unconstrained maximum growth rates of protein $\left(\frac{dP}{dt}_{\max}\right)$, ash $\left(\frac{dA}{dt}_{\max}\right)$ and water

$\left(\frac{dH}{dt}_{\max}\right)$ while the derivative of equation (3.15) corresponds to the desired rate of lipid deposition $\left(\frac{dL}{dt}_{des}\right)$. These are given by:

$$\frac{dP}{dt}_{\max} = B_s.P_m.u_t.\ln\left(\frac{1}{u_t}\right) \quad \left(\text{kg day}^{-1}\right) \tag{3.17}$$

$$\frac{dA}{dt}_{\max} = B_s.S.P_m.u_t.\ln\left(\frac{1}{u_t}\right) \quad \left(\text{kg day}^{-1}\right) \tag{3.18}$$

$$\frac{dL}{dt}_{des} = B_s.Q.P_m.u_t^{bl}.\ln\left(\frac{1}{u_t^{bl}}\right) \quad \left(\text{kg day}^{-1}\right) \tag{3.19}$$

$$\frac{dH}{dt}_{\max} = B_s.R.P_m.u_t^{bh}.\ln\left(\frac{1}{u_t^{bh}}\right) \quad \left(\text{kg day}^{-1}\right) \tag{3.20}$$

where B_s and u_t are as defined in equations (3.12) and (3.10), respectively. The degree of maturity of ash in the whole empty body is modelled in parallel to the degree of maturity of protein. During periods of nutritional limitation where protein is catabolised due to insufficient supply to meet maintenance needs desired protein deposition is predicted as above. When nutritional limitations are removed and a protein deficit relative to ash weight exists the desired protein deposition rate is modelled as a function of the degree of maturity of ash until this discrepancy is removed. The desired protein deposition is modelled in this manner to allow ash growth to occur at its normal rate whilst corrections in protein and lipid deposition are occurring, following Kyriazakis and Emmans (1992c).

$$\frac{dP}{dt}_{\max A} = \left(B_s.P_m.uA_t.\ln\left(\frac{1}{uA_t}\right)\right) + \left(ActA_t.\left(A:P_n - A:P_a\right)\right) \quad \left(\text{kg day}^{-1}\right) \tag{3.21}$$

where uA_t is the degree of maturity of ash in the empty body, $ActA_t$ is the actual ash content of the empty body, $A:P_n$ is the current ash to protein ratio in the empty body and $A:P_a$ is the desired ash to protein ratio, taken as 0.25.

The effective energy scale (Emmans 1994) is used for determining both the quantity of energy available in the feed eaten and the quantity of energy required by the animal to achieve its desired protein and lipid growth rates. The quantity of energy required on day, t (EN_t) is predicted with:

$$EN_t = MR_t + \left(z_P . \frac{dP}{dt}_{\max} \right) + \left(z_L . \frac{dL}{dt}_{des} \right) \quad \left(\text{MJ day}^{-1}\right) \tag{3.22}$$

where z_P and z_L are the energy costs of protein and lipid deposition on the effective energy scale provided $\frac{dL}{dt}_{des}$ is positive and are taken as 50 and 56 (MJ/kg), respectively. MR_t is the predicted maintenance requirement of the animal at time, t (Emmans and Fischer 1986). To allow comparison of maintenance requirements between animals of different mature sizes, the maintenance value is made proportional to $P_m^{0.73}$ (Emmans 1997) following Brody's (1945) rule for scaling mature maintenance needs.

$$MR_t = z_M . P_m^{0.73} . u_t \quad \left(\text{MJ day}^{-1}\right) \tag{3.23}$$

where z_M is the energy constant for maintenance, given as 1.65 and is considered to be constant across animals and diets. The quantity of effective energy (EE) contained in a kilogram of feed is determined using:

$$EE = 1.15ME - 3.84 - 4.67DCP \quad \left(\frac{\text{MJ}}{\text{kg DM}}\right) \tag{3.24}$$

where ME is the metabolisable energy and DCP is the digestible crude protein content of the feed. The ideal protein derived from feed is based on the ideal digestible crude protein (IDCP) scale similar to that used by Wellock et al. (2003a) and the rumen degradable protein system used by Freer et al. (1997) and SCA (1990). The quantity of ideal protein needed to meet the potential protein growth and maintenance needs is calculated as:

$$P_{req} = P_{Main} + \left(\frac{\frac{dP}{dt}_{max}}{k_{DPLS}} \right) \quad \left(\text{kg day}^{-1}\right) \tag{3.25}$$

where k_{DPLS} is the efficiency of use of ideal protein for growth (0.7) (SCA 1990) and prediction of protein maintenance (P_{Main}) needs follows the same form as that used for predicting maintenance energy needs:

$$P_{Main} = Z_{MP}.P_m^{0.73}.u_t \quad \left(\text{kg day}^{-1}\right) \tag{3.26}$$

where z_{MP} is the protein constant for maintenance given as 0.004 and is also considered to be constant across animals and diets. The actual protein growth and consequently whole body growth of an animal is determined by the quantity of digestible protein that leaves the stomach in the form of either microbial protein or undegraded protein, which can include protein from milk that bypasses digestion in the rumen. The quantity of digestible microbial protein ($DPLS_m$) synthesised during fermentation is predicted from the metabolisable energy intake (MEI), calculated as the product of ME content and feed intake (I_s), and the digestibility of the microbial protein, taken as 0.6 (Freer et al. 1997).

$$MCP = \frac{(8.4MEI)}{1000} \quad \left(\frac{\text{kg}}{\text{MJ ME}}\right) \tag{3.27}$$

$$DPLS_m = 0.6MCP \quad \left(\frac{\text{kg}}{\text{MJ ME}}\right) \tag{3.28}$$

The quantity and quality of protein that leaves the rumen undegraded is subsequently calculated as the difference between total crude protein intake and protein degraded in the rumen.

$$RDPI = RDP\%.CP\%.I_s \quad \left(\frac{\text{kg}}{\text{kg of feed intake}}\right) \tag{3.29}$$

$$UDPI = CPI - RDPI \quad \left(\frac{\text{kg}}{\text{kg of feed intake}}\right) \tag{3.30}$$

where RDP% is the rumen degradability of the feed protein and CP% is the crude protein content of the diet. The contribution each protein pool makes to total digestible protein leaving the stomach is calculated from:

$$DPLS = \left(v_{udp}.D_{udp}.UDPI\right) + \left(DPLS_m.v_{mcp}\right) \quad (\text{kg}) \tag{3.31}$$

where v_{udp} is the biological value of the undegraded protein, v_{mcp} is the biological value of microbial protein, taken as 0.8 (McDonald et al. 2002) and D_{udp} is the degradability of the undegraded protein component of the feed protein.

$$D_{udp} = 0.9\left(1 - \left(\frac{ADIP_s}{UDP_s}\right)\right) \tag{3.32}$$

where $ADIP_s$ is the acid detergent insoluble protein (g/g DM) and UDP_s is the rumen indigestible protein (g/g DM) content of the feed. The biological value of the undegraded protein is calculated from the estimated amino acid profile of the undegraded protein. This amino acid profile is calculated from the UDP% of each feed component (Freer et al. 1997) and its amino acid profile is taken from NRC (1996). The DPLS is subsequently used to predict the quantity of protein deposition that will be supported by the protein available from the animal's diet.

$$\frac{dP}{dt} = k_{DPLS}.\left(DPLS - P_{Main}\right) \quad \left(\text{kg day}^{-1}\right) \tag{3.33}$$

with the constraint that if $\frac{dP}{dt} > \frac{dP}{dt}_{\max}$ then $\frac{dP}{dt} = \frac{dP}{dt}_{\max}$. In the situation where *DPLS* is inadequate for protein maintenance then protein is catabolised to meet these needs.

$$\frac{dP}{dt} = \left(\frac{\left(LP\%.MEE_t\right)}{23.8}\right) + MP_t \quad \left(\text{kg day}^{-1}\right) \tag{3.34}$$

MEE_t is the quantity of effective energy needed for maintenance above that provided by the diet, MP_t is the quantity of ideal protein needed for maintenance above that provided by the diet, 23.8 is the heat of combustion of protein and $LP\%$ is the proportion of effective energy for maintenance obtained from protein catabolism.

$$LP\% = -\left(\left(\frac{\alpha P}{EI_{PMain}}\right).EI_a\right) + \alpha P \tag{3.35}$$

where αP is the proportion of energy in the animal that is contained in protein, EI_{PMain} is the effective energy needed for protein maintenance and EI_a is the actual quantity of effective energy eaten by the animal in the current time period. The surplus or deficiency of energy after maintenance and protein deposition needs have been taken into consideration is used to predict lipid deposition.

$$\frac{dL}{dt} = \frac{\left(EI_a - MR_t - \left(b_P.\frac{dP}{dt}\right)\right)}{b_L} \quad \left(\text{kg day}^{-1}\right) \tag{3.36}$$

where b_P is the cost of protein retention (MJ/kg) and is assumed to be 50. When lipid deposition is positive b_L is the cost of lipid retention (MJ/kg) with the value of 56, however when lipid deposition is negative, b_L assumes the value of 39.6 MJ/kg, which is the heat of combustion of lipid (Emmans 1994). In the situation where protein catabolism takes place ($\frac{dP}{dt}$ negative) lipid retention is predicted using:

$$\frac{dL}{dt} = \frac{\left(MEE_t - \left(23.8\left(\frac{dP}{dt}.MP_t\right)\right)\right)}{39.6} \quad \left(\text{kg day}^{-1}\right) \tag{3.37}$$

A lipid to protein ratio is used to prevent lipid catabolism from depleting lipid stores below a minimum quantity required for survival i.e. that needed for cell membranes, hormone and ATP production (Frandson et al. 2003). The ratio used to constrain empty body lipid content, $L:P_{\min} = 0.2P_t$, is intermediate to the values of 0.4 and 0.1 used by Bridges et al. (1992a) and Wellock et al. (2003a) and is stated as the ratio of lipid to protein in the protoplasm of the cell (Frandson et al. 2003). This value is also

similar to the average lipid to protein ratio of new born calves (Haigh et al. 1920), which would be expected to have minimal quantities of excess lipid. If lipid catabolism takes the lipid to protein ratio below this constraint, protein deposition is adjusted to maintain the minimum ratio.

The deposition of water and ash is predicted from the deposition of protein. In the case that protein deposition is positive, ash deposition is predicted as:

$$\frac{dA}{dt} = 0.25\frac{dP}{dt} \quad \left(\text{kg day}^{-1}\right) \tag{3.38}$$

Whenever protein deposition is negative or during periods of rehabilitation following negative protein deposition, ash deposition is predicted as:

$$\frac{dA}{dt} = 0.045\frac{dP}{dt} \quad \left(\text{kg day}^{1}\right) \tag{3.39}$$

Regardless of whether protein deposition is positive or negative, the deposition of water is predicted as:

$$\frac{dH}{dt} = \frac{dP}{dt}.R.b_h.\left(\frac{ActP_t}{P_m}\right)^{bh-1} \quad \left(\text{kg day}^{-1}\right) \tag{3.40}$$

The mass of each chemical body component at the beginning of the current time interval is incremented by the predicted growth of the component during the current time period, where Δt is the number of days in a time period. Empty body weight at the end of the current time period is predicted by summing each of the body components.

$$ActP_t = ActP_t + \left(\frac{dP}{dt}.\Delta t\right) \quad (\text{kg}) \tag{3.41}$$

$$ActL_t = ActL_t + \left(\frac{dL}{dt}.\Delta t\right) \quad (\text{kg}) \tag{3.42}$$

$$ActA_t = ActA_t + \left(\frac{dA}{dt}.\Delta t\right) \quad (\text{kg}) \tag{3.43}$$

$$ActH_t = ActH_t + \left(\frac{dH}{dt}.\Delta t\right) \quad (\text{kg}) \tag{3.44}$$

$$ActEBW_t = ActP_t + ActL_t + ActA_t + ActH_t \quad (\text{kg}) \tag{3.45}$$

Following Wellock et al. (2003a), full body weight is predicted by:

$$Wt_t = \frac{ActEBW_t}{0.95} \quad (\text{kg}) \tag{3.46}$$

The untested nature of some of the assumptions made in the extensions added to the base model of Amer and Emmans (1998) could suggest that the model may not function sensibly. However, in an attempt at demonstrating that the model does indeed function sensibly, the partitioning of ME as ME intake increases from 0 to *ad libitum*, between maintenance, protein deposition, lipid deposition and heat loss is presented in Figure 3.1.

Figure 3.1 is based on a 300 kg animal with a mature weight of 750 kg. The diet provided adequate protein when fed *ad libitum* and was based on diets commonly used throughout Australian feedlots for short-fed markets. The diet consisted of 80% grain (60% Sorghum, 20% Barley), 15% roughage (Sorghum hay), 2.5% protein supplement (Cottonseed meal), 1% molasses and 1.5% mineral supplement (Savage 2005, pers. comm., 5 November). The diet was estimated to have a dry matter (DM%) content of 88.8%, DM digestibility of 77% and to contain 11.84 MJ ME/kg DM, 10.6% crude protein that had a rumen degradability of 78% using the feed characteristics contained in GrazPLAN (Freer et al. 1997).

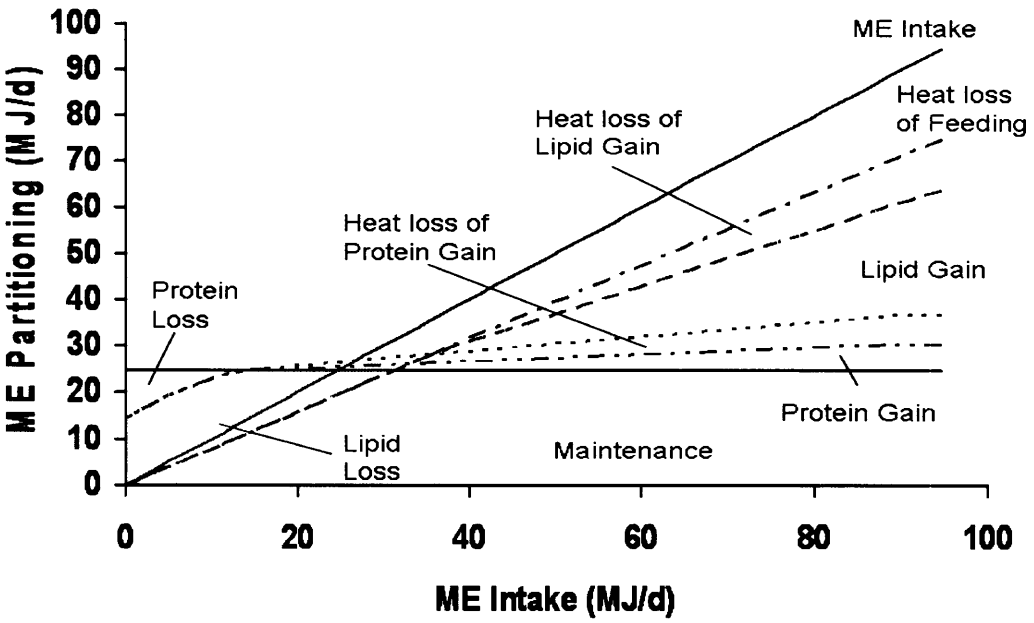

Figure 3.1: Partitioning of ME with increasing ME intake for a 300 kg steer consuming a short-fed feedlot ration commonly used in Australian feedlots.

At maintenance ME intake (25 MJ/d) the model predicts a gain in body protein and a loss in body lipid, which is a shortcoming of many partitioning models (Emmans and Kyriazakis 1997). The ME intake at which point protein deposition ceases and protein catabolism begins is approximately 13 MJ/d. As ME intake decreases below 13 MJ/d towards 0 MJ/d the quantity of energy obtained from protein catabolism to meet animals requirements increases according to equation (3.35) presented above. When 0 ME intake occurs the proportion of energy required for maintenance that is obtained from protein catabolism is equal to the proportion of total energy in the whole body that is contained in protein. Increasing ME intake above maintenance increases the rate of protein deposition until the point where lipid deposition begins at an ME intake of approximately 34 MJ/d. The consequences of changing ME intake on a 300 kg steer appear to agree in broad terms with the concepts presented by Black (1974) (Figure 2a) and Fowler (1978) (Figure 2) for a 5 kg lamb and a 60 kg pig, respectively. The form ME partitioning takes, as seen in Figure 3.1, is generally the same regardless of body weight.

Kinghorn Model:

A standard reference growth curve (analogous to the "Standard Reference Weight" found in SCA (1990)) is formed from the base function developed by Kinghorn (1985) and is defined as:

$$Wt_t = 0.000065\left(L_m.\left(1-\exp\left(-\left(\frac{0.4t}{L_m}\right)\right)\right)\right)^{3.337} \quad \text{(kg)} \tag{3.47}$$

where t is age in days from conception, Wt_t is weight at time, t. The power parameter, 3.337 was estimated from Taylor's (1980) mean growth curves of nine mammalian species, and L_m is mature length, which is defined as:

$$L_m = \left(\frac{A_m}{0.000065}\right)^{\left(\frac{1}{3.337}\right)} \quad \text{(cm)} \tag{3.48}$$

where A_m is mature weight. With relative ease the base model can be converted to a time-step model that predicts weight at time, t as a function of the previous weight (Wt_{t-1}) and the time elapsed between Wt_t and Wt_{t-1}:

$$Wt_t = 0.000065\left(\left(\frac{Wt_{t-1}}{0.000065}\right)^{\frac{1}{3.337}} + \exp\left(-0.4\Delta t.\left(\frac{0.4t}{L_m}\right)\right)\right)^{3.337} \quad \text{(kg)} \tag{3.49}$$

where Δt is the number of days in the time period between Wt_t and Wt_{t-1}. The term $\exp\left(-\frac{(0.4t)}{L_m}\right)$ in the base model is defined as the animal's "drive to grow" that varies between one at conception and zero at maturity. During restricted feeding, an animal's drive to grow can be based on its age or weight.

$$Grow\max Time = \exp\left(-\left(\frac{0.4t}{L_m}\right)\right) \quad \text{(kg)} \tag{3.50}$$

$$Grow\max Weight = \exp\left(-\left(\frac{0.4t_{Expect}}{L_m}\right)\right) \quad (\text{kg}) \tag{3.51}$$

where age as expected from weight (t_{Expect}) during *ad libitum* feeding is defined as:

$$t_{Expect} = -1\left(\frac{L_m}{0.4}\right).\log\left(1-\left(\frac{L_{t-1}}{L_m}\right)\right) \quad (\text{days}) \tag{3.52}$$

where L_{t-1} is an animal's length at time, t-1. A linear interpolation between GrowmaxTime and GrowmaxWeight determines an animal's overall drive to grow:

$$Grow\max = MatCoe.Grow\max Time + (1 - MatCoe).Grow\max Weight \quad (\text{kg}) \tag{3.53}$$

where *MatCoe* is a maturation coefficient. Appetite increases when animals have restricted intake for a period of time, are modelled by:

$$Grow\max W = Grow\max + AppFact.(1 - CS) \quad (\text{kg}) \tag{3.54}$$

where *AppFact* is the appetite factor which scales the relation between *CS* and Appetite. A value of 1 was found to give sensible patterns of response to previous nutritional restriction. *CS* is an animal's condition score modelled by:

$$CS = \frac{Wt_{t-1}}{0.000065L_{t-1}^{3.337}} \tag{3.55}$$

Replacing $\exp\left(-\frac{(k.t)}{L_m}\right)$ in the time-step model with *GrowmaxW* and subtracting the previous weight (Wt_{t-1}), models *ad libitum* growth.

$$AdlibG = 0.000065\left(\left(\frac{Wt_{t-1}}{0.000065}\right)^{\frac{1}{3.337}} + (0.4Grow\max W.\Delta t)\right)^{3.337} - Wt_{t-1} \quad (\text{kg}) \tag{3.56}$$

The feed intake required to realise this *ad libitum* growth is modelled by the sum of the maintenance requirements of average body weight and the product of net food conversion ratio and *ad libitum* growth within a time period.

$$AdlibF = \Delta t.m.\left(Wt_{t-1} + \frac{AdlibG}{2}\right)^{0.75} + NFCRT.AdlibG \quad (\text{kg}) \qquad (3.57)$$

where the convention used by SCA (1990) for estimating maintenance needs in relation to body weight ($W^{0.75}$) is followed, with m and $NFCRT$ being defined as:

$$m = \frac{0.03}{DMD} \qquad (3.58)$$

$$NFCRT = \frac{NFCR}{DMD} \qquad (3.59)$$

where $NFCR$ is the net food conversion ratio parameter and DMD is the digestibility of the nutrient intake. A linear extrapolation is made between *ad libitum* growth and maintenance to produce a measure of the weight loss when no food is eaten.

$$ZeroFoodGrowth = -1\left(\frac{AdlibG}{NFCRT.AdlibG}\right).\left(\Delta t.m.\left(\frac{Wt_{t-1}}{2}\right)^{0.75}\right) \quad (\text{kg}) \qquad (3.60)$$

This relationship simplifies to give weight loss during starvation modelled as:

$$ZeroFoodGrowth = -1AdlibG.\left(\frac{\Delta t.m.Wt_{t-1}^{0.75}}{NFCRT.AdlibG}\right) \quad (\text{kg}) \qquad (3.61)$$

Ad libitum growth and feed intake are then used with starvation weight loss in a linear interpolation to model growth in a time period.

$$Growth = ZeroFoodGrowth + (AdlibG - ZeroFoodGrowth).\left(\frac{I_s}{AdlibF}\right) \quad (\text{kg}) \qquad (3.62)$$

where I_s is feed intake (kg) in a time period. The weight of an animal following this growth is simply the addition of growth and the previously calculated weight.

$$Wt_t = Wt_{t-1} + Growth \quad (\text{kg}) \tag{3.63}$$

The increase in length of an animal over time is modelled, in a similar manner to weight, and used for estimating age as expected from weight during *ad libitum* feeding. Firstly, *ad libitum* growth in length is modelled:

$$AdlibLGrow = 0.4Grow\max.\Delta t \quad (\text{cm}) \tag{3.64}$$

Following which the increase in length possible from actual feed intake is modelled and added to the previously calculated length (L_{t-1}).

$$L_t = L_{t-1} + AdlibGrow.\left(\frac{I_s}{AdlibFood}\right) \quad (\text{cm}) \tag{3.65}$$

Parks Model:

Weight (Wt_t) at time, t predicted by the Parks (1982) model is defined as:

$$Wt_t = (A - W_o).\left(1 - \exp\left[-\frac{(AB)F_t}{A}\right]\right) + W_o \quad (\text{kg}) \tag{3.66}$$

where A is mature weight, W_o is birth weight, AB is a growth efficiency factor and F_t is feed intake defined as:

$$F_t = C.\left\{t - t^*.\left(1 - \frac{D}{C}\right).\left[1 - \exp\left(-\frac{t}{t^*}\right)\right]\right\} \quad (\text{kg}) \tag{3.67}$$

where t is time in days from the start of the feeding and growth data, C is mature feed intake, D is feed intake at time zero and t^* is Brody's (1945) time constant. The feed intake function described above indicates that feed intake data is not used in the same manner by the Parks model as it is used by the Freer, Amer or Kinghorn models to

predict growth. The Parks model uses a fitted curve to describe feed intake and predicts growth from this function rather than using real feed intake data.

Polynomial Function:

Weight (Wt_t) predicted by the polynomial function was defined as:

$$Wt_t = a + b.t + c.t^2 + d.I_s + e.I_s^2 \quad (\text{kg}) \tag{3.68}$$

where t is age in days from conception and I_s is feed intake of a time period.

Gompertz Model:

Weight (Wt_t) predicted by the Gompertz (1825) function is defined as:

$$Wt_t = A.\left(\exp\left(-\exp\left(G_o - (B.t)\right)\right)\right) \quad (\text{kg}) \tag{3.69}$$

where t is age in days from birth, A is mature weight, B is a growth rate parameter and G_o is defined as:

$$G_o = \ln\left(-\ln\left(\frac{W_o}{A}\right)\right) \tag{3.70}$$

where W_o is birth weight.

The growth models described above contain different numbers of total and estimable parameters (Table 3.1). The Gompertz and Freer models both contain 2 estimable parameters with these two being the only parameters contained in the Gompertz model while the Freer model contains 50 parameters in total.

Table 3.1: The number of constants, fitted and total parameters contained in each of the growth models described above.

Model	No. Constants	No. Fitted Parameters	Fitted Parameters	Total No. Parameters
Polynomial	0	5	a, b, c, d, e	5
Gompertz	0	2	A, B	2
Parks	0	5	A, AB, C, D, t*	5
Kinghorn	6	3	A_m, MatCoe, NFCR	9
Amer	20	3	P_m, B*, Q	23
Freer	48	2	SRW, C_{nl}	50

3.2.4. Model Validation

Model performance testing adopts the approach of using training and test datasets to assess the ability of each model to satisfy the two components of criterion D. The feed intake and growth data from the training dataset are used for making model parameter estimates on an individual animal basis and assessing the goodness of fit achieved with these parameters. The ability of a model to predict future animal growth is assessed using an animal's age and feed intake data from the test dataset and average parameter estimates from the training dataset. The testing procedure is a replicated process with each being initiated by randomly allocating 28 and 29 animals to the training and test datasets, respectively.

Parameter Estimation:

The non-linear nature and complexity of some of the models under consideration make it difficult to develop algebraic solutions for parameter estimates. These difficulties were overcome by using a Differential Evolution (DE) algorithm (Price and Storn 1997), which has the ability to make unbiased parameter estimates for non-linear problems and can use a goodness of fit criterion (e.g. residual sums of squares (RSS) in the current applications). The parameter estimation process was made an iterative process due to missing weight records in the dataset. An Expectation Maximisation (EM) algorithm was constructed to overcome this problem.

EM Algorithm:

Prior to the EM algorithm being initiated the feed intake and growth data were averaged by age and parameters estimated using the DE for the average population data. Missing weight records, for each animal, were replaced during the first EM iteration by predictions made with these initial parameters. Given these expected values, parameters were re-estimated for the growth and feed intake functions. The missing weight records were replaced in subsequent EM iterations by predictions made with parameter estimates from the previous iteration. Twenty iterations per animal were allowed for each model, after which the parameter estimates and fitness criterion remained unchanged with subsequent iterations.

Differential Evolution:

DE was used in both steps during the parameter estimation process. DE was used to make parameter estimates prior to the EM algorithm being initiated during which DE was found to always converge following 30,000 generations. DE was also used to make parameter estimates during the EM process. An adequate level of DE convergence was considered to occur after 3,000 generations per EM iteration, giving a total of 60,000 generations per animal for each model. The fitness criterion used by the DE to generate parameter estimates based on individual animal data was the RSS, defined as:

$$RSS = \sum \left(\hat{Y}_t - Y_t \right)^2 \tag{3.71}$$

where t is time, $\hat{Y}_t$ is model predicted weight at time, t and Y_t is weight data at time, t.

Parameter Constraints:

A potential problem associated with using DE for making parameter estimates is interdependency between parameters. When DE is given free reign in the parameter space it will explore areas that result in either illegal functions being evaluated (e.g. log(-1)) or unrealistic parameter estimates being made (e.g. mature weight estimates in the range of 100,000 kg), simply in an attempt at minimising the objective function. In an attempt at resolving this issue constraints were placed on the parameter space of

all models explored by DE, with the exception of the polynomial for which no 'biologically sensible' limits could be defined. To maintain consistency between models, common parameters were treated in an identical manner, mature weight (A, A_m, SRW) being the most obvious was constrained between 100 and 1200 kg. An effort was also made to keep any constraints on parameter estimates as least stringent as possible to allow as large a parameter space as possible to be searched.

Model Prediction:

Comparison of the predictive abilities of the models tested was separated into two stages. The initial stage includes dividing the Trangie dataset into training and test datasets as discussed above. This prediction procedure uses prior information concerning average parameter estimates made using the training dataset and information contained in the test dataset (i.e. individual feed intake and age data). Twenty replications of this prediction procedure were performed to provide an indication of the predictive abilities of each function when applied to different animals in the same population, for which common parameter values might be expected. The second stage uses a second dataset, the CRC dataset, whose information was obtained from a feedlot experiment conducted at the CRC for Cattle and Beef Quality "Tullimba" Research feedlot (Armidale, NSW). This second testing procedure was designed to test the transferability of parameter estimates made during parameter estimation to unrelated animals grown in unrelated experimental conditions. To remove any confounding effects of sex or breed, the data used during this stage of testing was obtained from Angus steers alone.

During testing of the Amer model a constraint was placed on the starting protein condition to prevent it from exceeding the average estimated mature protein content (P_m in the Amer model, described above). The main purpose of this constraint was to allow the model to run completely without committing any illegal mathematical operations. It was envisaged that this constraint would not improve this model's predictive ability; if anything it was considered that it would reduce it, because animals are constrained to lower body protein contents than would be expected for their body weight.

Model Fit Across Individual Animals:

Comparison of models during the parameter estimation and prediction procedures was conducted in an identical manner. The Mean Squared Error (MSE) was used to compare the fit of the models across animals to take into account the different quantities of data used for different animals. MSE is defined as:

$$MSE_{model} = \frac{\left[\sum\left(\hat{Y}_t - Y_t\right)^2\right]}{n - np} \tag{3.72}$$

where $\hat{Y}_t$ is the model predicted weight at time, t, Y_t is the observed weight data at time, t, n is the number of data points for each animal and np is the number of parameters fitted in the model under consideration. The MSE was averaged across animals to make a comparison of the average fit of each model tested. An adjusted R^2 (R_A^2), following Kinghorn (1987) was also calculated and averaged across animals to compare the fit of models.

$$R_A^2 = 1 - \left(\frac{df}{df - np}\right) \cdot \left(\frac{SSE}{SST}\right) \tag{3.73}$$

where SSE is the sum of squares of error, SST is the total sums of squares, df is the degrees of freedom (number of data points for each animal). Confidence intervals of 95% were generated around the average prediction of each model for comparison with averaged live weight from both datasets in the following manner (Hogg and Craig 1995):

$$CI = Xb \pm 1.96\left(\frac{\sigma_e}{w_t}\right) \tag{3.74}$$

where Xb represents the average model prediction, σ_e represents the error standard deviation (SD) which is given by:

$$\sigma_e = \sqrt{\frac{\left[\sum_t \left(w_t . \left(\hat{Y}_t - Y_t \right)^2 \right)\right]}{df_e}} \tag{3.75}$$

where df_e is the degrees of freedom minus the number of parameters in the model (df - np) and w_t is a weighting used to take into account changing error SD as live weight increases over time, given by:

$$w_t = \frac{1}{\left(\frac{Y_t}{\max Wt} \right)} \tag{3.76}$$

where Y_t is weight data at time, t and $maxWt$ is the maximum predicted weight achieved across the growth trajectory.

3.3. Results

3.3.1. Parameter Estimation

The parameter estimation procedure was an exercise designed to establish how accurately the selected feeding and growth functions fit feeding and growth data of individual animals. The polynomial model provided the best average fit to the live weight data (Table 3.2). As the complexity of the growth model increased (moving down through Table 3.2) it can be observed that the level of fit to the live weight data decreased, with the exception of the Parks model which had a superior fit to the Gompertz model. A comparison of models with similar levels of complexity but different degrees of freedom (eg. polynomial vs Gompertz or Amer vs Freer) reveals that models containing more estimable parameters produced higher average fits to the live weight data. Comparison of models with similar degrees of freedom reveals that model complexity reduces their capacity to fit data (eg. Gompertz vs Freer). The SD of MSE also supports these trends with the Parks and polynomial models having the lowest variances and the Freer model having the largest variance. These trends are also supported by the average error SD of the predicted weights (σ_e). The adjusted R^2 values possess limited variation indicating all models have a high level of fit to the live weight data.

Table 3.2: The MSE, SD of the MSE, adjusted R^2 values and error SD (σ_e) averaged across animals from parameter estimation are presented for each model tested along with their respective degrees of freedom (*df*).

Model	df	Average MSE	MSE SD	R_A^2	σ_e
Polynomial	5	233.12	144.67	0.9991	16.34
Gompertz	2	389.46	242.53	0.9984	21.61
Parks	5	272.07	139.04	0.9988	18.31
Kinghorn	3	737.64	1757.04	0.9975	23.77
Amer	3	1547.30	2113.26	0.9928	36.22
Freer	2	3311.75	4956.23	0.9874	52.65

The average error SDs are reproduced in Figure 3.2 to illustrate the confidence intervals associated with fitting the data and for comparison of the average curve of each model with the average data from the Trangie dataset. The polynomial, Parks and Gompertz functions form a tight band around the average data. The Kinghorn model has a slightly wider band with the Freer and Amer models having the widest bands. Figure 3.2 suggests that the models all tend to have average predictions that under-estimate the average data with the exception of the Amer model which slightly over-predicts.

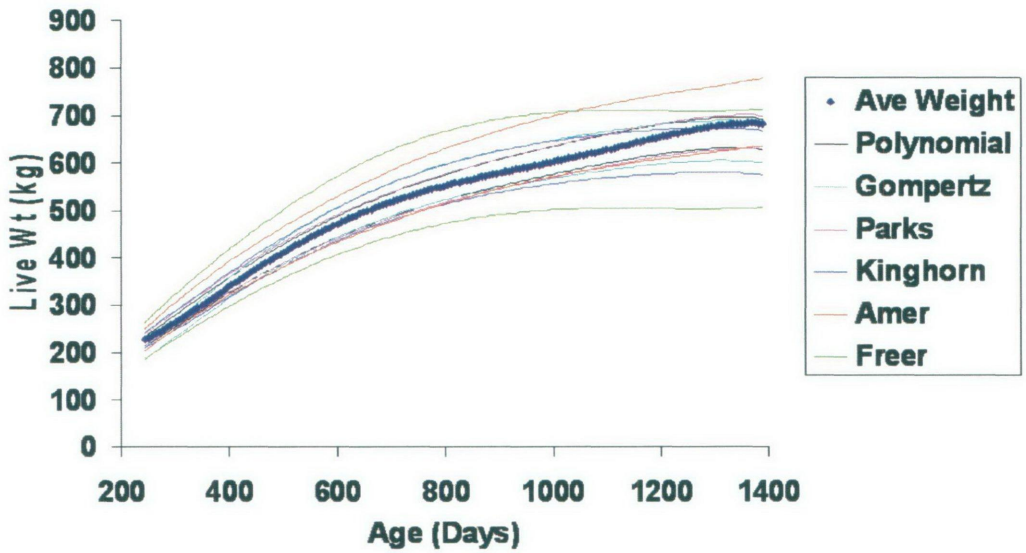

Figure 3.2: Average confidence intervals of fitted models in comparison to the Trangie data averaged across animals.

3.3.2. Model Prediction

The first stage of the model prediction procedure was designed to test the ability of the selected models to predict growth given age, feed intake data and average parameter estimates derived from a different population. The polynomial model produced the poorest average predictive ability when compared to the Trangie live weight data (Table 3.3). All other models predictive abilities were substantially better with the Kinghorn model producing the most accurate predictions followed by the Amer, Freer, Parks and Gompertz models respectively, when comparing MSE. The degrees of freedom of the models appear to have a small effect on their predictive abilities. Generally, models with lower degrees of freedom have higher predictive abilities (eg. polynomial vs Gompertz) but the effect of degrees of freedom on predictive ability is less significant than the effect of model complexity (eg. Gompertz vs. Freer). The SD of MSE supports this trend with the polynomial model having the greatest SD and the Kinghorn model having the smallest. The adjusted R^2 values tend to agree with these trends except for a small amount of re-ranking, between the Amer and Freer models and the Gompertz and Parks models, which can be attributed to the degrees of freedom of the models. In general models that take larger quantities of information into consideration (eg. age and feed intake vs. age alone) produced superior predictions, which is what was expected at the beginning of the study.

Table 3.3: The MSE, SD of the MSE, adjusted R^2 values and error SD (σ_e) averaged across animals and replicates from model prediction testing using the Trangie, training and test datasets, are presented for each model tested along with their respective degrees of freedom (*df*).

Model	df	Average MSE	MSE SD	R_A^2	σ_e
Polynomial	5	20129.68	21342.25	0.8899	128.81
Gompertz	2	5940.51	7606.41	0.9667	72.54
Parks	5	5341.77	7983.75	0.9666	65.06
Kinghorn	3	3169.19	3228.17	0.9861	53.49
Amer	3	4302.40	4182.82	0.9815	65.22
Freer	2	4568.50	5746.52	0.9829	61.86

The average error SDs are reproduced in Figure 3.3 to illustrate the confidence intervals associated with the predictive ability of each model in comparison to the average data from the Trangie dataset. In contrast to Figure 3.2, the Polynomial produces the widest confidence interval that also follows an inappropriate trajectory in comparison to the average Trangie data. The remaining models produce smaller confidence intervals that follow trajectories that agree with the average data. Within these models the Kinghorn model produces the tightest confidence intervals followed by the Freer, Parks, Amer with the Gompertz having the largest. Figure 3.3 suggests that the Kinghorn, Freer and Gompertz models under-predict the average data particularly as an animal's age increases whilst the Parks model tends to over-predict as age increases. The Amer model has the most accurate predictions at older ages but it tends to over-predict growth at ages below approximately 700 days.

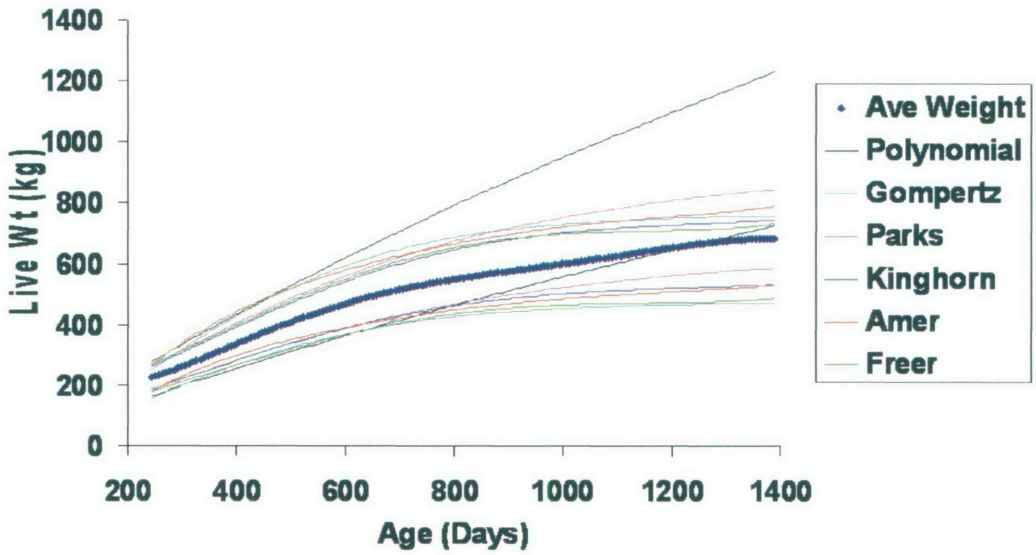

Figure 3.3: Average confidence intervals from model prediction testing using the Trangie, training and test datasets in comparison to the Trangie data averaged across animals.

The second stage of the model prediction procedure was designed to test the transferability of parameter estimates between unrelated populations of animals grown in an unrelated set of experimental conditions. The general trend was for prediction accuracy to increase as the complexity of the growth models increased

(Table 3.4), with the exception of the polynomial and Gompertz models. The degrees of freedom of the models appear to have little effect on their predictive abilities. The best and worst performed models both have 2 degrees of freedom with the remaining models dispersed between these. The adjusted R^2 values and weighted SD agree with this general trend. The SD of MSE also tends to agree with this trend with the exception of the Amer model. One explanation for this discrepancy is the restriction placed on initial protein content during the testing procedure, as discussed above.

Table 3.4: The MSE, SD of the MSE, adjusted R^2 values and error SD (σ_e) averaged across animals and replicates from model prediction testing using the Beef CRC dataset are presented for each model along with their respective degrees of freedom (*df*).

Model	df	Average MSE	MSE SD	R_A^2	σ_e
Polynomial	5	6313.02	7807.67	0.9839	72.39
Gompertz	2	7311.89	7393.91	0.9816	79.81
Parks	5	5025.29	2970.89	0.9863	70.00
Kinghorn	3	2845.62	1915.56	0.9922	52.15
Amer	3	2192.92	3338.69	0.9947	41.01
Freer	2	1680.68	1478.00	0.9954	38.70

The average error SDs are once again used to illustrate the confidence intervals associated with the predictive ability of the models (Figure 3.4). The overwhelming characteristic of the confidence intervals in Figure 3.4 are the flat trajectories of the Kinghorn, Parks, Gompertz and Polynomial models. At younger ages the average predictions of these models seem to agree well with the average CRC data, however, as age increases they underestimate weight. The Amer and Freer models are the only models that have predictive trends that are in agreement with the averaged data. However, in a similar manner to Figure 3.3 these models tend to predict more accurately at different ages. The Freer model seems to over-predict at older ages whilst the Amer model seems to under-predict at younger ages and have more appropriate estimates when the experiment ceased.

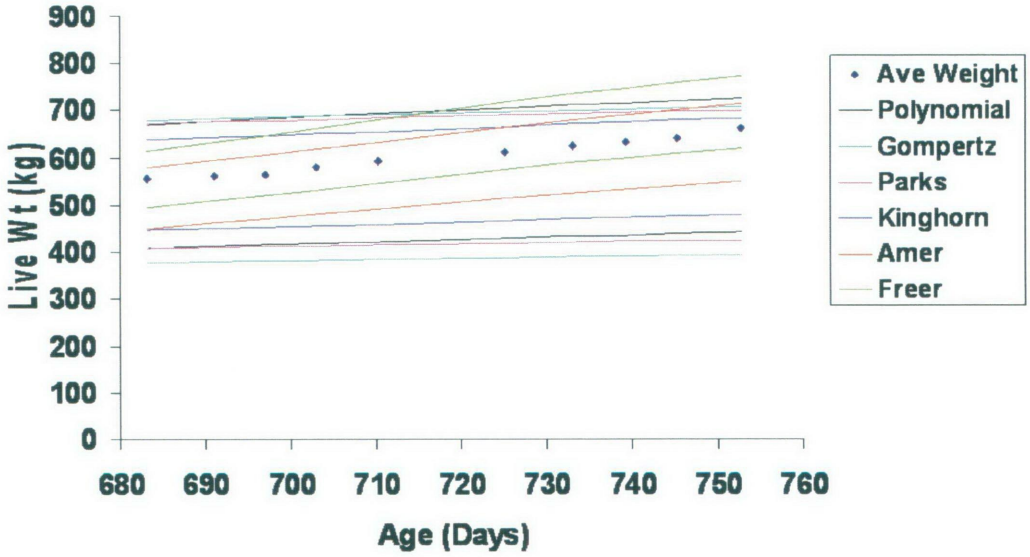

Figure 3.4: Average confidence intervals from model prediction testing using the Beef CRC dataset and parameters estimated from the Trangie dataset in comparison to the Beef CRC data averaged across animals.

3.4. Discussion

The purpose of selecting and testing various functions was to identify a model that had the ability to accurately predict performance given information relating to individual animal age and feed intake. The results from the parameter estimation procedure reveal the more simplistic models (polynomial, Gompertz) provide a higher level of fit than the more complex feeding and growth models (Freer, Amer). A plausible explanation for this occurrence is the inherent structure that exists in the feeding and growth models. These types of models are developed based on the growth and feeding characteristics of groups of animals almost always from many experiments and thus have a structure that broadly agrees with the average performance of such animals. However, a model such as the polynomial has no defined structure, and so it has the flexibility to fit to virtually any growth trajectory given sufficient parameters. Although the Gompertz function does have a defined structure, this structure is more simplistic than those of the Freer and Amer models, apparently allowing it more flexibility to fit growth trajectories.

When considering *ad libitum* growth, Wellock et al. (2004a) indicated the Parks model satisfied all their criteria but did not consider it further because it includes a food intake parameter. The valid reasoning behind this decision was they consider food intake is a consequence of potential growth rather than a contributor (Emmans and Kyriazakis 2001). In the current study the animals may not have actually achieved *ad libitum* feed intakes due to external influences (eg. high summer daytime temperatures) and inclusion of feed parameters in the Parks model may have allowed it to compensate for this to produce a better fit than the Gompertz function. Another explanation may be the degrees of freedom of the model. The Parks model contains 5 parameters whilst the Gompertz contains 2, which may allow the Parks model more flexibility to fit to the live weight data. The Kinghorn model produced an intermediate fit which is probably a result of the model's complexity being intermediate to the two groups of models discussed above.

Although parameter estimates made during model testing are not considered a criterion for selecting models, an interesting result was the number of animals whose parameter estimates were anchored against the search space boundaries, particularly for the Freer model (Table 3.5). The explanation for this occurrence maybe that the form of the model tested here was not developed for extended feedlot use (Freer, 2005, pers. comm.) and thus the DE attempts to compensate by estimating unrealistic parameters. This highlights the importance of setting parameter boundaries, but, as discussed previously, consistent boundaries were set across models. Also, this should not be taken to mean the Freer model is inappropriate for use in growth pathway optimisation but rather that this is one issue that could be addressed to take the model one step closer to the real system.

Table 3.5: The number of animals, out of the 57 animals contained in the Trangie dataset, whose estimates were anchored against the search space boundaries for each parameter in the models tested along with the number of animals who had more than 1 parameter anchored against the search space boundaries. The parameter numbers below represent the order that the parameters are listed in Table 3.1 (e.g. Freer Parameter No. 1 below is *SRW* from Table 3.1).

Model	Parameter No.					More than 1 Parameter
	1	2	3	4	5	
Polynomial	0	0	0	0	0	0
Gompertz	0	0	-	-	-	0
Parks	5	0	0	0	9	5
Kinghorn	10	0	9	-	-	1
Amer	2	38	28	-	-	28
Freer	37	47	-	-	-	28

This type of issue is related to the concept discussed by Michalewicz and Fogel (2000), when using heuristics such as DE, that you are only finding a solution for a model and any shortcomings of the model will be exploited to find a solution that minimises (or maximises, depending on the objective) the evaluation function. Thus, a model's structure is central to its optimisability; i.e. the model's ability to find sensible optimal parameters. Application of this concept to the optimisation of growth trajectories requires that models have internal limitations preventing unrealistic outcomes. An example is a model that contains no limitations on feed intake and thus when attempting to maximise biological efficiency allows a heuristic to nominate the outcome, "feed an animal nothing until the last moments prior to slaughter and then feed massive quantities to achieve the desired outcomes". Other internal limitations that models use to describe cattle growth may need to contain are maximum daily growth rates of components (e.g. protein), the maximum quantities of dietary components an animal can safely consume (e.g. maximum urea quantities in a ration (Gondro 2005)) and minimum feed intakes (e.g. preventing negative pasture intakes to allow greater concentrate intakes (Gondro 2005)). Another example of how a model's optimisability can be compromised that is specific to this study relates to which parameters are fitted during parameter estimation. If parameters that would normally act as internal constraints were selected for optimisation this could

potentially compromise the validity of the model reducing its ability to fit data and estimate sensible optimal parameters.

The predictive abilities of the models were tested using data from two independent experiments. The purpose of using the Trangie information was to test the transferability of parameter estimates between animal populations when controlling environmental, breed and sex effects. The most obvious result is the inaccurate predictions made by the polynomial and the limited agreement in the shapes of the average Trangie and polynomial predicted growth trajectories. This type of result is not unexpected as polynomials lack structure and parameters that have been sensibly inspired by the biological nature of the prevailing problem. Polynomials often behave rather badly at the periphery of the trajectory and extrapolation is generally considered a risky exercise. This means that they are much less likely to fit sensibly outside the range of the training data, especially due to the high-power functions involved.

The predictive ability of the remaining models was substantially higher than the polynomial. Within these models, generally those of higher complexity produced more accurate predictions (Freer more accurate than Gompertz). The exception is the Kinghorn model which is less complex than either the Amer or Freer models but produced more accurate predictions. The performance of this model is not surprising as firstly the model is based on a series of sound biological assumptions (Kinghorn 1985) related to growth characteristics of an average animal. Secondly, the model assumes that the diet is homogeneous, which is the case in the current scenario with the training and test datasets containing the same diet. Thus any influence nutritional factors had on the estimated parameters did not impede the functioning of this model. A conclusion that could be drawn from this result, and tested, is the possibility that the potential curve contained in this model, analogous to the Gompertz curve in the Amer model, could prove to be an appropriate basis for other feeding and growth models.

The purpose of using the CRC information was to test the transferability of parameter estimates between animal populations when controlling breed and sex effects but allowing the nutritional components of the environment to change. It should be noted

that only a single suitable alternative dataset was available. Other such datasets might well have led to different conclusions on model suitability and the following comments are made with caution. The Freer and Amer models were the only models capable of using average parameter estimates to produce growth patterns that were in general agreement with average growth data. Predictions of the remaining models followed a trajectory that indicated growth had reached a plateau. These results are somewhat expected given the estimated parameters are a function of the feed intake, including diet characteristics (MJ ME/kg, CP %), used to estimate them. The Amer and Freer models are the only models that consider dietary characteristics thus it would be expected that the effect diet characteristics have on parameter estimates is removed. Consequently, predictions using these models would be expected to have higher accuracy, meaning their parameter estimates are more transferable than the parameters of the other models. The Kinghorn model produced slightly lower prediction accuracy than the Amer and Freer models (Table 3.4). This result shows the potential for this model to perform more accurately if extensions were made, primarily to allow the model to more fully consider energetics of growth, dietary characteristics and nutrient partitioning or to use its core growth function within a model such as the Amer model.

The value of using feed intake information is also highlighted by the results from both model prediction tests. The Gompertz model that does not consider feed intake data performed consistently worse than the other models that do consider feed intake data, with the exception of the polynomial whose poor performance has been discussed above. The nature of the data used during testing, where animals were given access to ample feed to attain *ad libitum* feed intakes does not fully illustrate the value feed intake offers when predicting growth. The difference in predictive ability between the Gompertz model and the other models would be expected to increase if predictive testing were carried out with data where animals were feed restricted.

One shortcoming of the current study is the assumptions made in the models tested, particularly the extensions made to the Amer model. Within this model the digestion of feed protein and efficiency of use for growth could be treated in different manners. An alternative approach for pigs proposed by Kyriazakis and Emmans (1992a; 1992b) and tested both qualitatively and quantitatively by Sandberg et al. (2005a; 2005b) uses

the relationship between ME and digestible crude protein content of the diet represented by a linear-plateau model that asymptotes at 0.814 to calculate an efficiency of protein use parameter. The Freer model tested above contains a function that adjusts feed intake for the level of feeding to account for changes in residence time (Freer et al. 1997) and thus rumen degradation of protein. This type of scenario is not currently considered in the extended Amer model and would be a desired addition. Improvements of this nature are a continual process and the ultimate for a feeding and growth model used during growth pathway optimisation would be to take advantage of a dynamic rumen model like the Cornell Net Carbohydrate and Protein System model (Fox et al. 2004) or the CSIRO ruminant model (Nagorcka and Zurcher 2002) that have the capacity to consider hourly variation in rumen activity. This type of improvement could also allow lag effects associated with diet changes to be modelled more accurately than past attempts, such as Keele et al. (1992). However, the quantity of information required by such a model may prevent it from predicting long term trends (e.g. growth over a week).

This study based prediction of growth on knowledge of age and feed intake. Other types of information, such as genetic information (both breed and family/EBV), prevailing environmental information (temperature, rainfall, wind speed) and growth history could also be used to predict future growth. The amount of information concerning the prevailing environment can be enormous and the manner in which this information is used is often difficult to discern. Few models, except the Freer model and the pig simulation models presented by Knap (1999) and Wellock et al. (2003a), consider this type of information when predicting animal performance. However, in the Australian environment this type of information can be especially important, particularly when beef cattle production is occurring in different climatological zones.

An attempt was made to take into account the effect summer temperatures were having on animal growth at Trangie. Figure 3.5 contains two animals whose weight data were smoothed with a 5th order polynomial using Sigmaplot version 7.0 (SPSS Inc, Chicago, ILL, USA) as a means of identifying if the animals were experiencing periodic (annual) depressions in weight gain, due to the effects of high summer temperatures. The arrows in Figure 3.5 highlight points in the trajectories where

depression of growth appears to be occurring; however in both cases the time between these arrows exceeds an annual cycle (365 days).

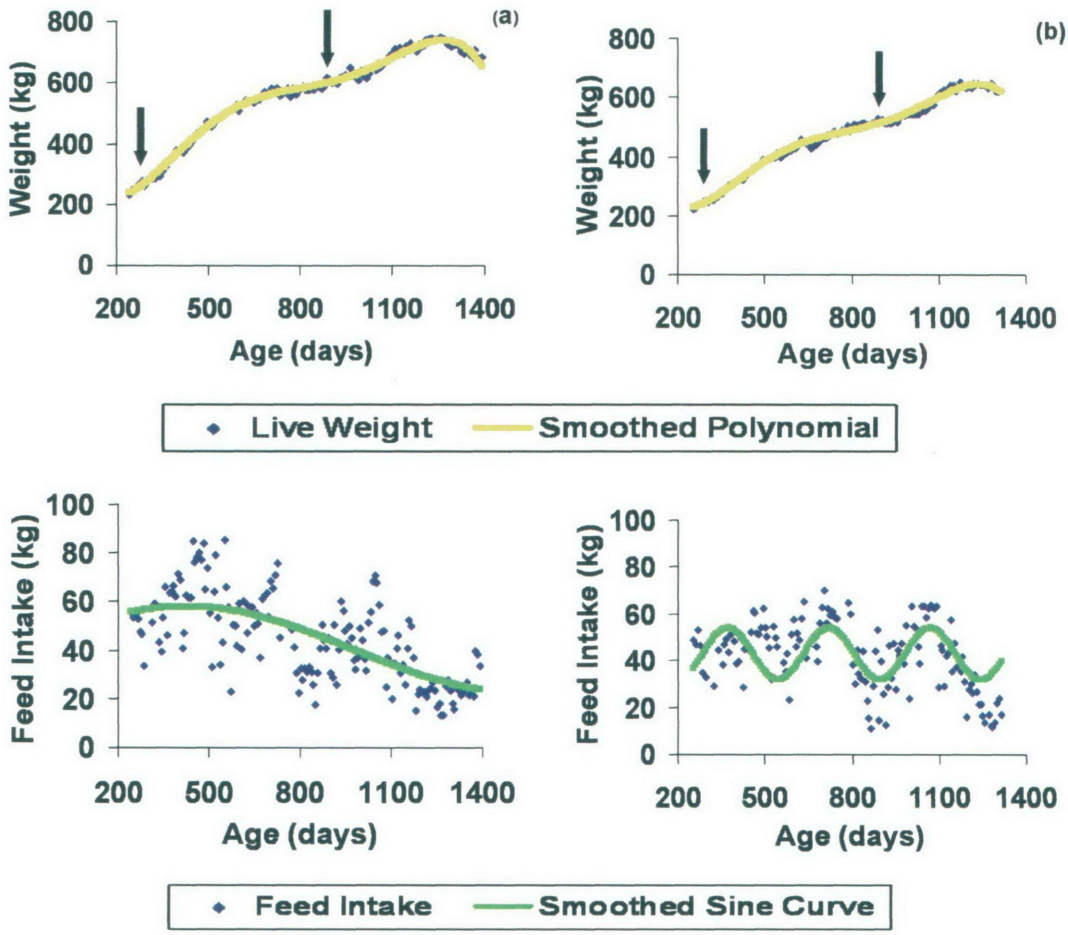

Figure 3.5: Smoothed weight and feed intake curves in comparison to actual data of 2 steers grown at the NSW Agriculture Research Centre, Trangie, New South Wales.

Visual inspection of Figure 3.5 shows some resemblance to a cyclic pattern in feed intakes can be discerned, with depressions corresponding approximately to the arrows indicated in the live weight figures. In an attempt at taking these patterns into consideration a 4 parameter sine curve was fitted to the feed intakes, using Sigmaplot version 7.0 (SPSS Inc, Chicago, ILL, USA), similar to that done in other studies (Thompson and Parks 1983; Thompson et al. 1985b).

$$f_t = f_o + a.\sin\left(\frac{2\pi}{(b.t)} + c\right) \tag{3.77}$$

where f_t is feed intake at time, t, f_o is the initial feed intake, a is the amplitude of the sine curve (kg/week), $\frac{2\pi}{b}$ is the frequency of the sine curve (radians/week) and c is the phase shift of the sine curve (radians). The animals depicted in Figure 3.5 were selected to demonstrate the extreme differences found in smoothing patterns. The addition of linear and quadratic terms to equation (3.77) did not in fact improve the goodness-of-fit. Based on the results of such smoothing the decision was made that a cyclic pattern of feed intake may exist but this pattern does not occur uniformly around an accepted feed intake curve of maximum intake reducing to an equilibrium intake at maturity (Kyriazakis and Emmans 1999) and thus was unable to be modelled appropriately.

Past feeding and growth of animals is important information in terms of the impact it has on future growth and in determining appropriate parameter estimates used during prediction of future growth. Testing the ability of functions to accurately predict growth given information concerning previous growth is an avenue that needs to be explored because of its direct relevance to optimising growth pathways. Any decisions made during an optimisation process are dependent upon predicted performance made using previous performance under given conditions that may include different feeding levels. Genetic information would also play an important role in predicting animal performance. The current study used only data from Angus steers, however the effects that sex and breed of an animal would have on their performance are not hard to envisage. Thus modelling these influences would be integral in determining if animals of different breeds and even sexes would have the capacity to follow desired growth trajectories. The expected impact such genetic factors would have on model parameter estimates can also be envisaged, for example expected mature body weights of cows would be lower than those of the steers used in this study and the mature lipid ratio (Q) in the Amer model would also be expected to be higher. Information from within breeds (eg. EBV of bull A vs EBV of bull B) would also help determine if animals of a particular lineage are capable of meeting desired endpoints and ultimately should also be used for predicting animal performance.

3.5. Conclusion

The model testing procedures used throughout this study show that functions with no or little inherent structure (polynomial, Gompertz) have a greater capacity to fit beef cattle growth data compared to feeding and growth models (Amer and Freer) whose internal structure is inherently rich. However, when the predictive abilities of these models are tested, internally rich models have the capacity to make more robust predictions when their estimated parameters are transferred to different populations. Given that only one external dataset was used for testing model robustness, the conclusion that feeding and growth models (Amer and Freer) are more appropriate than the other functions for predicting growth during optimisation of growth pathways is made with caution. Based on these conclusions and the irregularity of the parameter estimates made for the Freer model, the extended Amer model will be used in following chapters involving growth trajectory optimisation.

3.6. Recommendations

The limited availability of appropriate growth and feed intake datasets was a limitation in this study. Identification and/or development of more such datasets would improve this model testing process. Datasets of this type could also be used to validate the extensions made to the Amer and Emmans (1998) growth model for beef cattle. The models tested in this study had all information available to them during the parameter estimation process. The performance of these functions under limited data conditions needs to be tested and would shed more light on which function would be most appropriate for predicting animal performance during growth pathway optimisation. Future research also needs to explore the effect that genetic factors (e.g. sex, breed and EBV) have on growth model parameter estimates and if they could be used to assist the estimation process.