Chapter 5: Model Parameters for Cohorts

5.1. Introduction

Two key factors influence the efficiency of animal production, these being the efficiency with which individual animals produce the desired product and how efficiently the system produces these individuals (Kinghorn 1985). Thus, it becomes apparent that the efficiency of individual animals is a key factor in determining the overall efficiency of a production system. Recognising this, Knap (1995) discussed reasons why between-animal variation should be incorporated into growth models when simulating different production systems. However, many of the growth simulation models currently used only represent a perceived 'average' animal, with no consideration given to between-animal variation, based on the assumption that the deterministically simulated response of this animal to a given treatment or condition is the same as the response of the population (Wellock et al. 2004b) or selected cohort. This is only possible if all individuals in the cohort have an equal growth potential, are at the same stage of development and respond in the same manner to all prevailing stressors. In contrast, Pomar et al. (2003) found that the mean response of a cohort differed in magnitude and shape to that expected for an 'average' individual. This in turn implies that deviations from mean growth model parameter values have non-linear consequences due to the non-linear nature of the growth models. Thus, Pomar et al. (2003) made the conclusion that stochastic models that properly represent populations or cohorts (i.e. take between-animal variation into consideration) are needed in circumstances where the models are to be used for predicting nutrient requirements of different genotypes and sexes or for economic optimisation of production.

Parameterisation of growth models to obtain the most accurate predictions and thus their most appropriate application is not an easy process due to the difficulty associated with measuring the underlying physiological traits (Doeschl-Wilson et al. 2006) let alone repeatedly measuring such traits. For example, the protein content of an animal at maturity (P_m) is required by the growth model presented by Wellock et al. (2003a). Methods have been proposed for estimating difficult to measure model parameters, termed "inverted modelling" by Knap (2003) and "reverse simulation" by Bourdon (1998). Knap (2003) put forward the method of algebraically reworking

model equations to make the desired parameters the dependent variables. However, this method has several shortcomings including that many differential equations contained in growth models are difficult to invert analytically and problems of this type are ill-posed, have either no solution, a series of non-unique solutions or unstable solutions relative to inputs (Tikhonov and Arsenin 1977). Baldwin (1976) proposed an iterative inverted modelling method for estimating parameters that involves assigning initial parameter values, computing model outputs, comparing these outputs with experimental data, obtaining an error estimate, allowing a computer routine to then systematically adjust parameter values until computed and experimental differences are minimised (see Figure 5.1).

In one sense this approach was used during model validation in chapter 3 where growth model parameters were estimated initially for individual animals from growth and feed intake data and then averaged to obtain growth model parameter means and standard deviations. This approach has two shortcomings. The first is the time required to obtain parameter estimates for each individual prior to calculating the population parameters (e.g. approximately 24 hours per model for 57 animals). The second is the fact that growth models tend to be developed to represent perceived 'average' animals, not individuals. The time required to obtain the parameter estimates is partly a function of the number of data points used by this technique. Between 15 and 165 live weight and feed intake data points per animal were used to estimate the growth model parameters.

There is an alternative that takes advantage of the fact that growth models tend to be developed to represent perceived 'average' animals and allows for between-animal variation to be incorporated into growth models. This method iteratively tests growth model parameter means and standard deviations, generating sampled sets of input parameters for a whole cohort, until differences between predicted model outputs and production characteristics are minimised. The computational time required by this method is dramatically reduced for two reasons. Firstly, the quantity of data required by this method can be much lower because points need only be sampled at given intervals (e.g. 250, 450 and 650 days of age, rather than every 7 days). Secondly, there is only one optimisation for the whole cohort rather than one optimisation per cohort member.

There are two important steps in the process outlined by Baldwin (1976). They are how systematic adjustments are made to parameter values and the sampling method used to calculate the model outputs. The non-linear nature of growth simulation models as well as the non-linear interactions between the models and their input parameters requires that a heuristic is used that has the capacity to deal with such characteristics when systematically adjusting growth model parameters (e.g. DE, GA or simulated annealing). The sampling method used would influence the accuracy of any results obtained from it. Sampling error associated with stochastic random sampling from parameter distributions would result in decreased accuracy of estimates unless a generous number of samples were taken. Potentially, this problem could be overcome if stochastic random sampling is replaced by deterministic sampling, a method proposed by Kinghorn et al. (1993a). This method does not have the problem of sampling error and requires only a finite number of samples, leading to robust parameter estimates with zero standard errors.

The aim of this chapter is to compare the accuracy and speed of using deterministic and random sampling during inverted modelling for estimating average growth model parameters and their standard deviations for a cohort of animals. The prediction accuracy of both methods will also be compared to the method used in chapter 3 when parameters are estimated from all available data and only using partial data. The method used in chapter 3 will be referred to as Estimating Individual Parameters (EIP) in the remainder of this study. The phrase 'deterministic and random sampling' is referred to as Estimating Population Parameters (EPP) in the remainder of this study for ease of reading.

5.2. Materials and Methods

5.2.1. Feeding and Growth Data

Trangie

The data used during this study were the same data used in chapters 3 and 4. The data were 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. The 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). One animal was also excluded from the analysis due to large quantities of missing data. The 58 animals that entered the feedlot were grown on a pelleted diet which provided 10.9 MJ ME/kg DM via access to an automatic feeding system (Herd 1991) 24 hours a day, with the programmed condition that any animal that had eaten in the previous half an hour was denied access. This feeding system allowed animals to eat to appetite and thus the animals could be considered to have attained *ad libitum* growth.

The growth data collected from the remaining 57 animals consisted of live weights from approximately 7 months of age until considered mature at approximately 3 years and 8 months. The steers were considered to have reached maturity when weekly live weight measurements showed that they had effectively stopped growing. Other details concerning this experiment and generation of these data are reported by Perry and Arthur (2000). The live weight data were averaged across ages to obtain estimates of live weights and standard deviations at 250, 450, 650 and 1250 days of age. The phenotypic correlations between the live weights at these ages were also calculated. The lack of a recorded pedigree within this experiment meant that no genetic parameters were able to be estimated and so these data only represent phenotypic parameters.

CRC

The CRC dataset used in chapter 3 was also used in this study to test the transportability of the parameters estimated using EPP. These data were 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 in the experiment were born in 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 8 pens of 12 steers accommodated in the feedlot.

The steers undertook a standard induction program following which the animals were given *ad libitum* access to a finishing ration containing 12.1 MJ ME/kg DM and a DM digestibility of 82% (Herd 2005, pers. comm.). For any further details relating to this experiment and generation of this data refer to Hegarty et al. (2005).

5.2.2. Parameter Estimation

Growth Model

The most desirable growth models contain few parameters (Ferguson and Gous 1993), which helps reduce error likely to be associated with parameter estimation. The growth model presented by Amer and Emmans (1998) and tested in chapter 3 was chosen for comparing EPP. This model contains only three parameters that are affected by genotype (i.e. that are not biological constants) (Amer and Emmans 1998; Wellock et al. 2004b) and assumes that these parameters explain the biological variation seen when animals are exposed to environmental conditions that are not limiting (possible ramifications of this assumption are discussed in the discussion relating to environmental temperatures). These are mature protein content (P_m), lipid to protein ratio at maturity (Q) and a general rate parameter (B^*). The model takes the same form as that presented in chapter 3 in equations (3.10) to (3.16). The Newton-Raphson iteration method used to estimate initial body protein content takes the same form as equation (3.101) in the Appendix.

Estimation of Model Parameters

As briefly outlined above, the parameter estimation procedure is an iterative process that follows the system proposed by Baldwin (1976). It proceeds as follows: "assign initial values to unknown model parameters; compute, using these parameters and input data, model outputs (i.e. body weight means, standard deviations and correlations in the current study); compare these computed estimates to experimental data to calculate an error; iteratively adjust parameter values in a systematic manner until the differences between computed estimates and real data are minimised." This process is shown graphically below in Figure 5.1. The parameters being estimated in this study were the mean and standard deviations of input parameters from the growth

model described above. The parameters were used to minimise the differences between the predicted means, standard deviations and correlations of growth model live weight outputs and experimental data at the above mentioned ages.

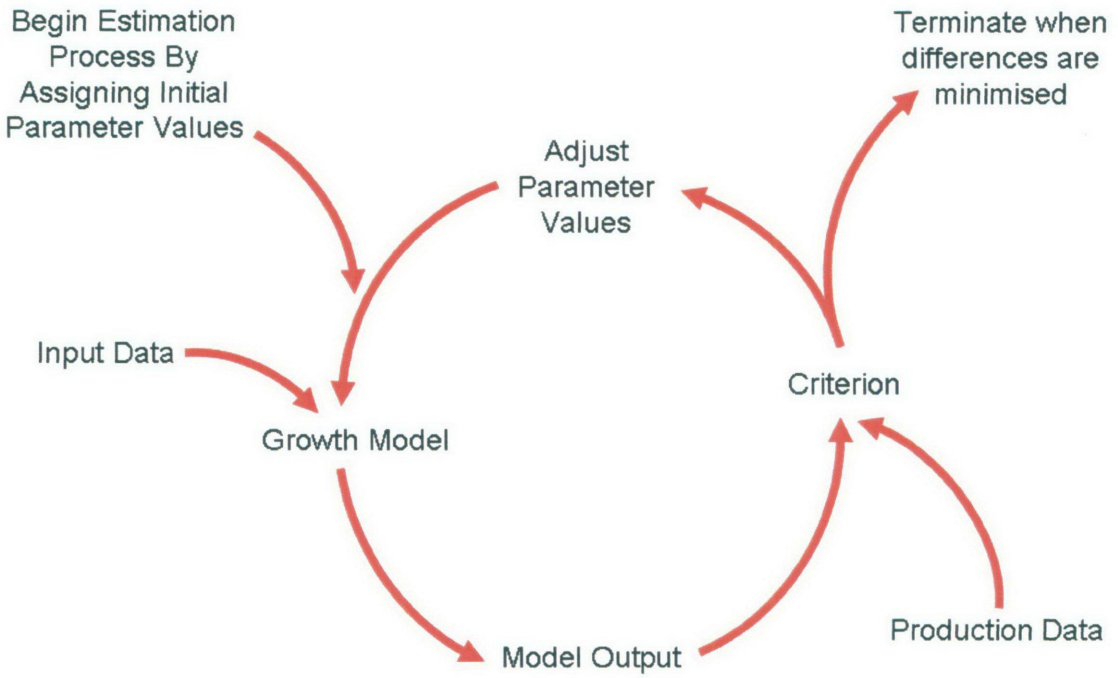

Figure 5.1: Graphical description of the parameter estimation process followed when testing deterministic and random sampling.

Generating Growth Model Outputs

The mean and standard deviations of the growth model input parameters were used to produce a simulated population and live weight outputs (e.g. means and standard deviations) from the growth model that are then compared to those of the Trangie data. The parameters for each observation taken during EPP were derived using:

$$P_{i,j} = \mu_i + x_j.\sigma_i \tag{5.1}$$

where $P_{i,j}$ is the value of the *ith* growth model parameter for the *jth* observation, μ_i is the population mean for the *ith* growth model parameter, x_j is the *jth* observation, generated using deterministic or random sampling as described below in 'Sampling Methods' and σ_i is the standard deviation of the *ith* growth model parameter. The

comparison between sampling methods conducted in this study was based on 2000 observations and 729 observations being taken by random and deterministic sampling, respectively. A constraint, $P_{i,\min j} > 0$ where $P_{i,\min j}$ is the value of the *ith* parameter for the minimum observation, was imposed to prevent parameter estimates falling below zero. This constraint prevented biologically and mathematically illegal operations from occurring. The constraint on the mature protein parameter (P_m) was increased to, $P_{i,\min j} > P_o$ where P_o is initial protein content, to prevent mature protein content from being estimated as lower than the initial protein content.

Differential Evolution

The systematic adjustment of the growth model parameter means (μ_i) and standard deviations (σ_i) in equation (5.1) above was conducted using Differential Evolution (DE) (Price and Storn 1997). The criterion used by DE for determining the error between predicted model outputs and the experimental data was weighted residual sums of squares (WRSS).

$$WRSS = \sum \left(z_i . \left(\hat{Y}_i - Y_i \right) \right)^2 \tag{5.2}$$

where $\hat{Y}_i$ is the model predicted component, i, Y_i is component i taken from the experimental data, and z_i is the weighting applied to component, i. The weightings (z_i) were used to remove bias associated with the difference in scale between live weights and correlations e.g. a difference of 20 kg between experimental and model predicted live weights has 100 times the influence on an unweighted criterion than a difference of 0.2 between correlations. The weightings applied were 10^{-3}, 6.67 x 10^{-3} and 1 for average live weights, standard deviations and correlations between the live weights. Parameter estimation using EPP was replicated 10 times and the values presented in the results for the growth model parameters, model outputs, criterion and runtime were averaged across these 10 replicates. Experience showed that an acceptably low level of between replicate variation in DE convergence was achieved following 5,000 DE generations.

Sampling Methods

The successful application of estimating growth model parameter means and standard deviations using this process is reliant on the sampling of observations from the assumed distributions of the model parameters. The methods tested for sampling the observations (x_j) in equation (5.1) are discussed below.

Random Sampling

Simple stochastic random sampling was used where n observations were selected from the assumed normal distribution of each parameter given by the parameter's mean and standard deviation (Figure 5.2a). Once sampled, each observation (x_j) had an equal influence on the ensuing parameter estimation process.

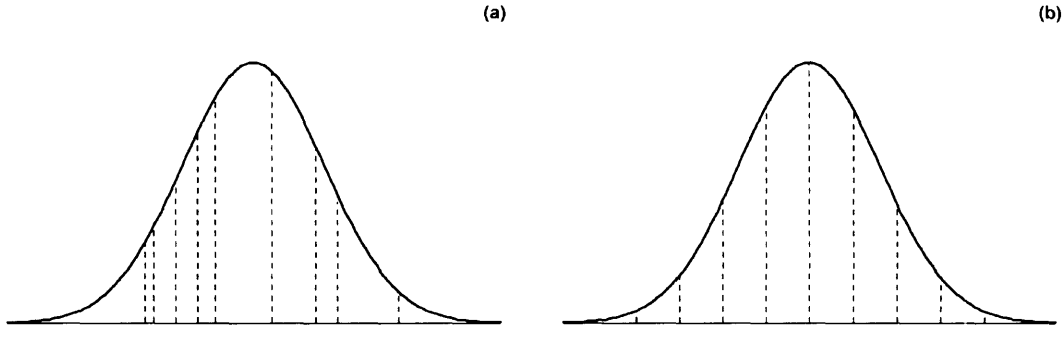

Figure 5.2: Comparison of random (a) and deterministic (b) sampling from a true normal distribution.

Deterministic Sampling

Deterministic sampling is a fully repeatable method that gives the properties of an infinite population but only requires finite computational resources (Kinghorn et al. 1993b). It is an alternative to stochastically selecting many observations and calculating parameter estimates. Deterministic sampling systematically samples observations from an assumed true distribution and weights the observations by the number or density of observations at that point (Mackinnon et al. 1996) to eliminate bias in the parameter estimates. It draws values of a variable, X, at fixed points, x_i

across the true distribution of X (Figure 5.2b). The expected number or density of observations with the value x_i equals the height of the density function at x_i multiplied by the interval between x_i and x_{i+1} and the number of observations in the population. An example would be if a population of size 100 with a distribution of N(0,1) were sampled at intervals of 0.1 between -7 and 7, then the expected number of observations at x_i is equal to 100 x 0.1 x h_i where h_i is the height of the normal distribution at x_i (Mackinnon et al. 1996), calculated from the standard normal density. During this study observations were taken at 1 standard deviation intervals and it was found that sampling to 4 standard deviations either side of the growth model parameter means (as shown in Figure 5.2b) produced robust results.

The assumption that the input parameters of the growth model have true normal distributions is made. However, deterministic sampling is not constrained to function only in environments that contain parameters with normal distributions. Deterministic sampling could be applied equally successfully in circumstances where parameter distributions take other forms, such as uniform distributions.

Using stochastic methods in objective functions during search processes has the inevitable property that certain parameter values may appear to have superior performance but in reality are not the global optimum for the problem. These values could be considered "lucky" as they have a more variable impact on model outputs, giving greater potential for selection bias, as a search algorithm will always seek to maximise the prevailing criterion. Deterministic methods do not suffer from this problem when used in objective functions because they are fully repeatable and thus replicates give identical answers. Figure 5.3 illustrates how stochastic methods can produce variable outcomes that can result in selection bias (blue diamonds) compared to the consistent outcomes of deterministic methods (black line). Deterministic methods identify the true global optimum (purple dot) while stochastic methods can identify those that are not (green dots).

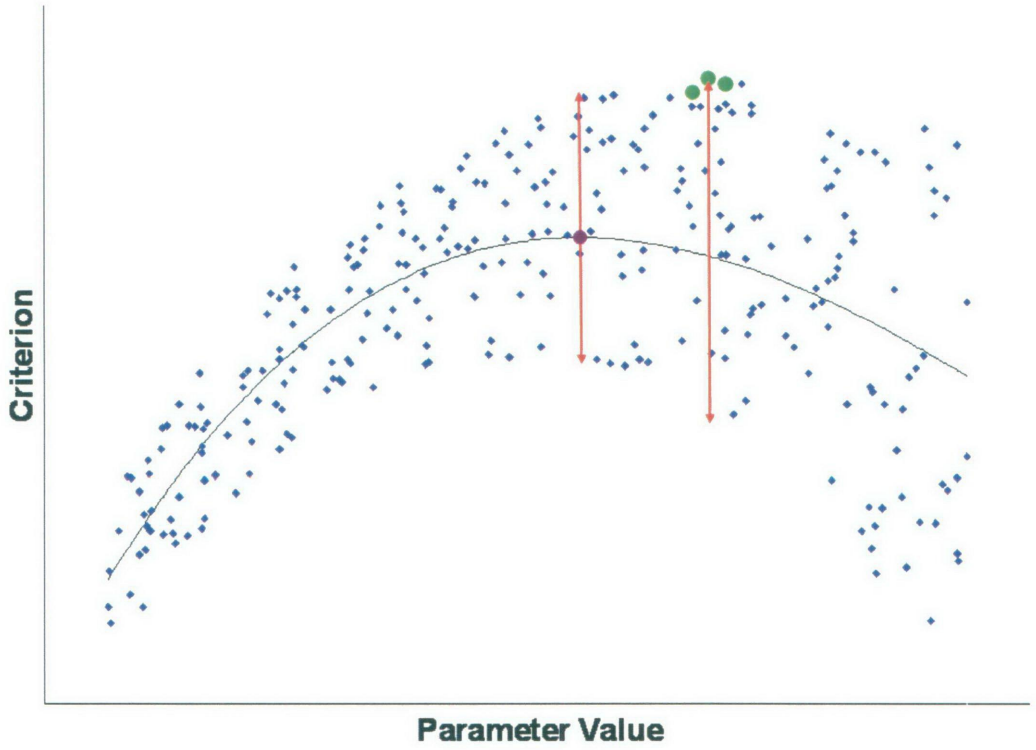

Figure 5.3: Variable criterion values produced by stochastic random sampling (♦) that produces upward selection bias (●) in comparison to deterministic methods (—).

Computing Platform

All analyses were programmed using Microsoft Visual Basic .NET in the Microsoft .NET Framework 1.1 (Copyright © Microsoft Corporation, 2003) and were run on a 3.06 GHz Mobile Intel Pentium personal computer with 512 MB of RAM to allow runtime comparisons between EPP.

5.2.3. Predictive Ability

The predictive ability of the parameters estimated by EPP was compared to those made using EIP. This contained two steps that used two independent datasets. The first step used prior information concerning average parameter estimates made using the sampling procedures described above along with feed intake and age information contained in the Trangie dataset. The second step used the parameter estimates described above but tested them with the Beef CRC dataset. This second step was

designed to test the transferability of parameter estimates to unrelated animals grown in unrelated experimental conditions. To remove any confounding effects of sex or breed, the data used during this step of testing were obtained from Angus steers only. The results obtained using the Beef CRC dataset should be taken with some degree of caution as this was the only suitable alternative dataset available. Testing of alternative datasets could well lead to different conclusions.

The importance that previous growth of animals has on future growth has been highlighted in chapters 2 and 3. The predictive ability of parameters estimated by EPP was compared in this context. EIP was used to make parameter estimates when using only the first 37 data points for each animal in the Trangie dataset. The predictive ability of the estimated parameters was then tested across all the data points for each animal. Five of the 57 animals were excluded from this process due to only 15 data points being recorded for these animals. The maximum age reached in the first 37 data points by any of the 52 animals tested was 530 days. Consequently, to avoid the influence of data from extreme ages, EPP only used average body weights and standard deviations at 250 and 450 days of age, along with the correlation between these two ages, to obtain growth model parameter estimates.

Growth Model

The growth model used to test the predictive abilities of each set of parameter estimates was the extended version of that used to make the parameter estimates (section 5.2.2). The model takes the same form as that presented in chapter 3 in equations (3.10) to (3.46). The Newton-Raphson iteration method used to estimate initial body protein content takes the same form as equation (3.101) in the Appendix.

During predictive testing a constraint was placed on the starting protein content to prevent it from exceeding the estimated mature protein content (P_m in the 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 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 given live weight.

Model Fit Across Individual Animals

The Mean Squared Error (MSE) was used to compare the predictive abilities of each set of parameters, as predicted by optimising equation (5.2), averaged across animals to take into account the different quantities of data available for each animal. MSE is defined as:

$$MSE = \frac{\left[\sum\left(\hat{Y}_t - Y_t\right)^2\right]}{n - np} \tag{5.3}$$

where $\hat{Y}_t$ is the model predicted live weight at time, t, Y_t is the observed live weight data at time t, n is the number of data points for each animal and np is the number of input parameters in the model under consideration (3 in the growth model used during this study). The MSE was averaged across animals to make a comparison of the predictive ability of each set of estimated parameters. An R^2 was also calculated and averaged across animals to compare the predictive ability of the estimated parameter sets.

$$R_A^2 = 1 - \left(\frac{df}{df - np}\right).\left(\frac{SSE}{SST}\right) \tag{5.4}$$

where SSE is the sum of squares of error and SST is the total sums of squares. Confidence intervals of 95% were generated around the average predictions of each set of parameters for comparison with averaged live weight from both the Trangie and Beef CRC datasets in the following manner (Hogg and Craig 1995):

$$CI = Xb \pm 1.96\left(\frac{\sigma_e}{w_t}\right) \tag{5.5}$$

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

$$\sigma_e = \sqrt{\frac{\left[\sum_t \left(w_t \cdot \left(\hat{Y}_t - Y_t \right)^2 \right)\right]}{df_e}} \tag{5.6}$$

where df_e is the total 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:

$$w_t = \frac{1}{\left(\frac{Y_t}{\max Wt} \right)} \tag{5.7}$$

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

5.3. Results

5.3.1. Parameter Estimation

The testing of EPP was conducted to compare the performance of each method in terms of the required computational time, the difference between observed and predicted data as well as the variation in model outputs and estimated parameters between replicates. Table 5.1 displays the average parameter estimates and the between replicate variation along with the WRSS for each sampling method. The WRSS indicates that deterministic sampling performed with a higher accuracy that approached statistical significance (p=0.077) than random sampling. All the parameters estimated by random sampling had higher variation between replicates which indicate it performed less consistently reducing the confidence that can be placed in these estimates.

Table 5.1: Weighted residual sums of squares (WRSS), growth model parameter estimates and standard deviations averaged across 10 replicates presented with the between replicate variation.

	Sampling Method	
Parameters	Deterministic	Random
Pm	120.143 ± 0.053	120 ± 0.458
Pm SD	20.64 ± 0.02	31.276 ± 0.561
Q	0.3707 ± 0.0011	0.3724 ± 0.002
Q SD	0.0008 ± 0.0005	0.0043 ± 0.0056
B*	0.01781 ± 0.0000185	0.0179 ± 0.000072
B* SD	0.0012 ± 0.000022	0.0018 ± 0.000048
WRSS	0.019 ± 0.0000026	0.01917 ± 0.00036

The patterns of protein and lipid accretion predicted by the parameter means given in Table 5.1 are illustrated in Figure 5.4. Predictions made by the parameters estimated by deterministic sampling are obscured by the predictions made by random sampling. The variation seen around these patterns was produced by taking parameter values that are two standard deviations either side of the parameter mean (e.g. $\bar{X} \pm 2SD$) and then appling all possible combinations of these values for each sampling method. Greater variation for both protein and lipid accretion rates is clearly evident for the parameters estimated by random sampling. The greater amount of variation produced by random sampling reduces confidence in the parameter estimates as it allows parameter values to reach levels that would be unexpected in cattle. This is particularly the case for P_m where values of approximately 25 kg are within three standard deviations of the mean and would not be expected to be seen in Australian production conditions. The early maturing pattern of protein and late maturing pattern of lipid evident for both sets of parameters estimates are sensible and what would be expected.

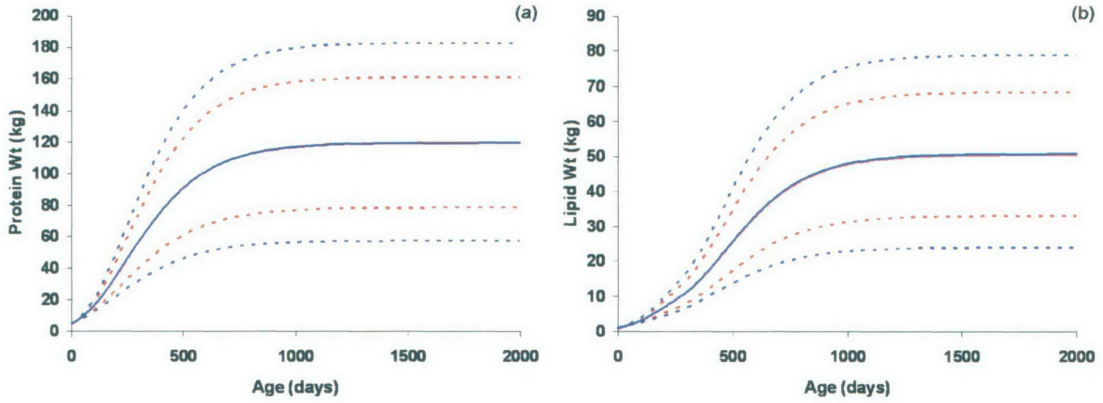

Figure 5.4: Comparison of the predicted protein (a) and lipid (b) accretion patterns and their variation produced by using parameter estimates 2 standard deviations from the means given in Table 5.1 for random (—) and deterministic (—) sampling.

Table 5.2 compares the average and standard deviation of live weight at 250, 450, 650 and 1250 days of age, taken from the Trangie experiment data, with the outputs produced by EPP. The averages and standard deviations are similar for both methods with a tendency for deterministic sampling to produce results that are slightly closer to the overall distributions of the experimental data. Also evident in Table 5.2 is the difference between the predicted live weights and the experimental data particularly at 450, 650 and 1250 days of age. The age-weight correlations produced by both EPP were essentially identical (Table 5.3) but again there is disparity between some of the experimental and predicted correlations (e.g. correlations for 250-450 and 650-1250).

Table 5.2: Comparison of the average weight and standard deviation outputs made by deterministic and random sampling with data taken from the Trangie experiment.

	Age (days)			
	250	450	650	1250
Mean:				
Trangie	231.61	379.96	498.13	663.33
Deterministic	240.74 ± 0.24	418.33 ± 0.24	524.30 ± 0.12	604.17 ± 0.28
Random	240.82 ± 0.78	418.29 ± 0.56	524.17 ± 0.37	603.81 ± 1.34
SD:				
Trangie	32.02	57.83	76.30	99.38
Deterministic	25.28 ± 0.04	54.69 ± 0.03	77.35 ± 0.02	102.16 ± 0.10
Random	25.18 ± 0.18	54.58 ± 0.13	77.34 ± 0.07	102.28 ± 0.13

The results shown in Tables Table 5.2 and Table 5.3 illustrate that random sampling produces greater variation in model outputs between replicates than deterministic sampling. Generally, the between replicate variation ranges from 1.5 to 4 times greater for random sampling than deterministic sampling, with a few extreme cases where it is up to 12 times greater (e.g. correlations for 250-450 and 450-650). This reinforces the uncertainty that is associated with parameter estimates made using random sampling. The small amount of variation between replicates seen for deterministic sampling reflects non-perfect convergence in the DE optimisation algorithm used.

Table 5.3: Comparison of correlations between weights at different ages produced by deterministic and random sampling with data taken from the Trangie experiment.

Correlations	Trangie	Deterministic	Random
250-450	0.870	0.928 ± 0.0001	0.928 ± 0.0012
250-650	0.862	0.841 ± 0.0002	0.841 ± 0.0015
250-1250	0.746	0.716 ± 0.0003	0.716 ± 0.0012
450-650	0.938	0.979 ± 0.00007	0.979 ± 0.0009
450-1250	0.913	0.923 ± 0.0002	0.923 ± 0.0019
650-1250	0.919	0.982 ± 0.00003	0.982 ± 0.0001

The results presented in the tables above are a consequence of the way each method samples from the parameter space. Figure 5.5 illustrates that deterministic sampling provides a much more even coverage of the parameter space preventing any one segment from being over or under represented. In comparison, the distribution of observations taken during random sampling is represented by a cluster in the central area of the parameter space with the extremities being represented by only a few observations. Although not presented, another important point to note is that Figure 5.5b doesn't change between replicates where as Figure 5.5a is unique to each replicate.

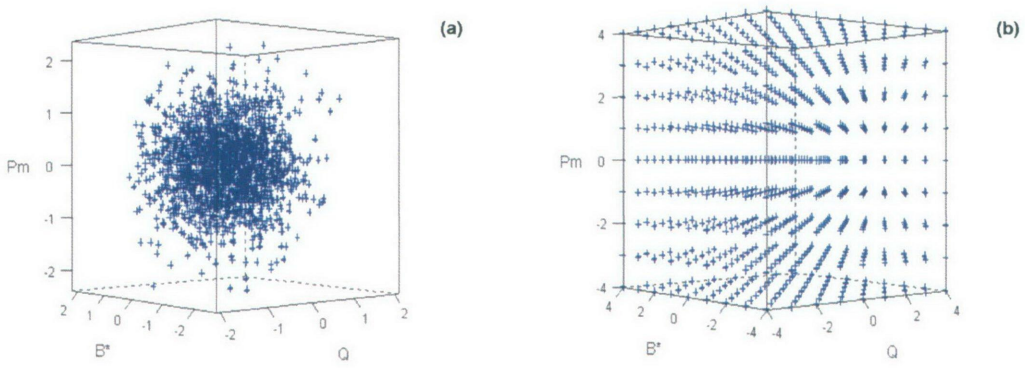

Figure 5.5: Distribution of the 2,000 (a) and 729 (b) observations taken across the parameter space by random (a) and deterministic (b) sampling, respectively.

The patterns of selected observations seen in Figure 5.5 are the result of selecting different numbers of observations for each sampling method. Deterministic sampling selected observations at 1 standard deviation intervals for 4 standard deviations either side of the growth model parameter means (i.e. 9 sampling points per parameter). Given that three growth model parameters were sampled, the total number of observations equates to 729 (i.e. 9^3). Using 2,000 observations random sampling was able to obtain a WRSS that was inferior, at a level that approached statistical significance (p=0.077), compared to the WRSS obtained using deterministic sampling. Consequently, the greater number of data points required by random sampling resulted in approximately three times the computational resources being required (Table 5.4) to perform at this level in comparison to deterministic sampling.

Table 5.4: Number of sampled observations and optimisation runtime (seconds) for 5,000 DE generations when estimating parameters with deterministic and random sampling.

	Sampling Method	
	Deterministic	Random
No. Observations	720	2,000
Time (sec)	10817	31284

5.3.2. Predictive Ability

The ultimate purpose of procedures such as EPP is to estimate parameters that can be used to accurately predict animal performance. The predictive abilities of the parameters estimated during this study were tested by applying the parameters to each animal in the Trangie dataset. The parameters estimated by deterministic sampling were found to have a slightly inferior predictive ability than those estimated by random sampling as illustrated by the MSE, SD of MSE, R^2 and error SD values in Table 5.5. However, as might be expected from the amount of raw data used for EIP, both sets of estimated parameters had inferior predictive abilities compared to the parameters estimated by EIP. EIP calculated average population parameters and their standard deviations after firstly estimating the parameters for individual animals from live weight and feed intake data. The two step nature of this parameter estimation process and the quantity of data used has implications on the error structure of the estimated parameters in terms of reducing the amount of error expected compared to that produced by EPP.

Table 5.5: The MSE, SD of MSE, R^2 and error SD (σ_e) values averaged across animals using the Trangie dataset are presented to compare the predictive ability of the parameters estimated by EIP with those estimated using deterministic and random sampling.

	Average MSE	MSE SD	R^2	σ_e
EIP	4302.4	4182.82	0.982	65.22
Deterministic	10886.37	8710.28	0.9508	105.9
Random	10857.78	8693.56	0.951	105.76

The average error SDs are reproduced in Figure 5.6 to illustrate the confidence intervals associated with the predictive abilities of the estimated parameters in comparison to the average data from the Trangie dataset. Across the whole growth trajectory, the confidence intervals for the parameters estimated by EPP are inferior to the confidence interval produced by EIP. In the initial stages of the growth trajectory this inferiority is only slight. However, this inferiority dramatically increases along the growth trajectory particularly in the upper confidence interval. Towards the end of the growth trajectory the inferiority tends to decrease in the upper confidence interval and increase in the lower confidence interval. As would be expected from the results

in Table 5.5 the confidence intervals for EPP are nearly identical and thus follow very similar trajectories in Figure 5.6 thus making them hard to distinguish.

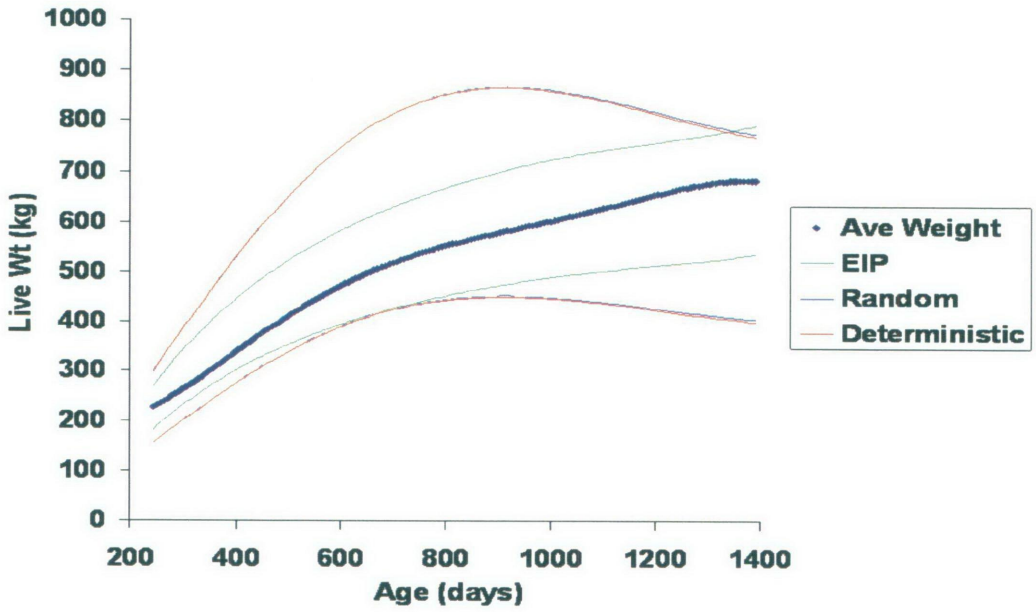

Figure 5.6: Confidence intervals of prediction when using the parameters estimated by EIP and those estimated with deterministic and random sampling in comparison to the Trangie data averaged across animals.

Another aspect to the acceptability of growth model parameter estimates is their transportability between unrelated populations of animals grown in unrelated environmental conditions. The results that tested this aspect of parameter acceptability are in contrast to the results presented above. The average MSE, SD of MSE, R^2 and error SD values in Table 5.6 indicate both sets of parameters estimated by EPP have greater predictive abilities in the Beef CRC dataset than the parameters estimated by EIP, with virtually no difference between those estimated using EPP.

Table 5.6: The MSE, SD of MSE, R^2 and error SD (σ_e) values averaged across animals using the Beef CRC dataset are presented to compare the transportability of the parameters estimated by EIP with those estimated using deterministic and random sampling.

	Average MSE	MSE SD	R^2	σ_e
EIP	2192.92	3338.69	0.9959	41.01
Deterministic	649.34	576.46	0.9985	24.74
Random	649	576.67	0.9985	24.73

The average error SDs are again used to illustrate the confidence intervals associated with the predictive ability of each set of estimated parameters (Figure 5.7). It can be seen that the confidence intervals for the parameters estimated by EPP are much smaller than the confidence interval of the parameters estimated by EIP. The parameters estimated by EIP tend to under predict weight at younger ages and make more appropriate estimates towards the end of the experiment. The estimates made using EPP appear to be in agreement with the experimental data at younger ages and could be considered to be slight over predictions at older ages. Again because the error SD's in Table 5.6 for EPP are similar their confidence intervals are hard to distinguish in Figure 5.7.

Table 5.7 contains the predictive ability of parameters estimated using the technique described by EIP and those estimated using EPP when only partial data is available. In contrast to Table 5.5, the MSE, SD of MSE, R^2 and error SD values indicate that parameters estimated using deterministic sampling have a greater predictive ability than parameters estimated by EIP or random sampling. It can also be seen that the parameters estimated with random sampling have an inferior predictive ability than those estimated using EIP. The difference between deterministic sampling and EIP is smaller than the difference between EPP.

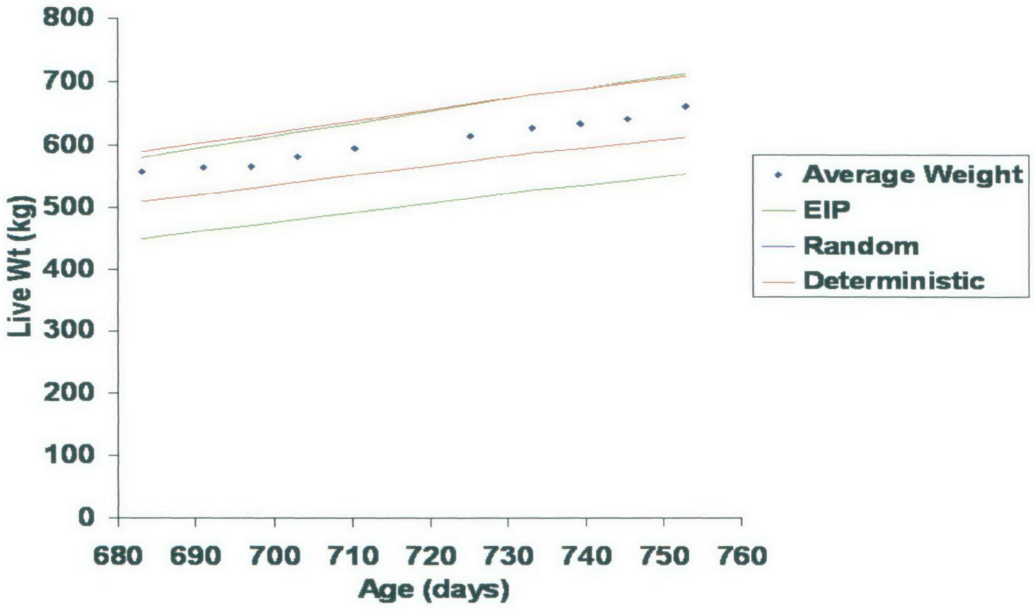

Figure 5.7: Confidence intervals of prediction when using the parameters estimated by EIP and those estimated with deterministic and random sampling in comparison to the Beef CRC data averaged across animals.

Table 5.7: The MSE, SD of MSE, R^2 and error SD (σ_e) values averaged across animals using the Trangie dataset are presented to compare the predictive ability of the parameters estimated using 37 data points and EIP with those estimated using deterministic and random sampling when only using data for 250 and 450 days of age.

	Average MSE	MSE SD	R^2	σ_e
EIP	5878.25	5701.69	0.9753	73.52
Deterministic	5790.99	5564.63	0.9757	72.89
Random	6423.59	6276.66	0.9731	75.97

The average error SDs are used to illustrate the confidence intervals associated with using the parameters estimated from partial data by each technique across the whole growth trajectory of animals in the Trangie dataset (Figure 5.8). The confidence intervals for each technique are similar in the initial stages of the growth trajectory but tend to separate towards the later stages with deterministic sampling having the smallest interval at the termination of the experiment. All parameter sets tend to make predictions that are relatively close to the average Trangie data up until approximately

700 days. Beyond this age all parameter sets tend to over predict growth with random sampling making the most dramatic over predictions.

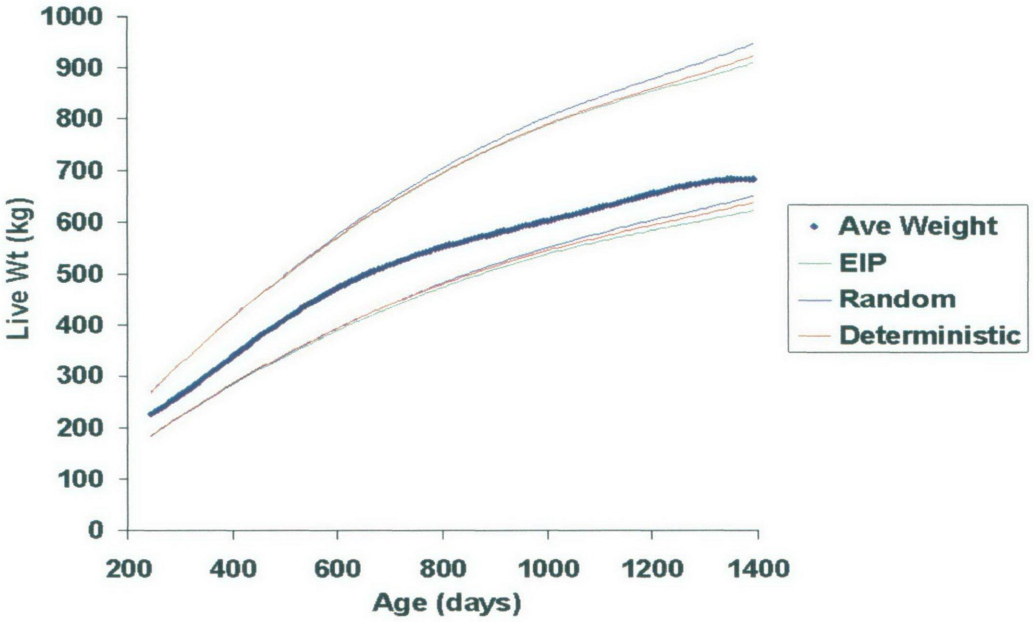

Figure 5.8: Trangie data averaged across animals in comparison to the confidence intervals of prediction when using the parameters estimated by EIP with 37 data points and those estimated with deterministic and random sampling using only data for 250 and 450 days of age.

5.4. Discussion

The purpose of this study was to compare the speed and accuracy of using EPP during inverted modelling for estimating growth model parameters for a population of animals. The optimisation criteria (Table 5.1) and model outputs presented in Tables Table 5.2 and Table 5.3 indicate that deterministic sampling had a higher accuracy than random sampling in relation to the average population data (i.e. average live weight, standard deviations and correlations at different ages). Figure 5.4 illustrates the higher amount of variation seen in protein and lipid accretion rates predicted by random sampling compared to deterministic sampling. This outcome supports the observation that less confidence can be placed in the estimates obtained from random sampling. The differences seen between the model outputs and the experimental data

in Tables Table 5.2 and Table 5.3 for both sampling methods could be taken to indicate that the model is not sufficiently representative of animal growth. However, these differences are a consequence of the model used not considering information from factors that have important influences on growth particularly the environmental conditions to which animals were exposed. The oscillations seen in the averaged Trangie data (Figures Figure 5.6 and Figure 5.8) are due to summer temperature extremes seen in western NSW (discussed in Chapter 3 and again below). The form of the growth model used during this study did not take feed intake, environmental temperatures or the interaction between these into consideration.

Tables Table 5.2 and Table 5.3 also reveal that greater variation is present in the model outputs predicted using random sampling. This is not a desirable outcome as it places uncertainty around these parameter estimates. This is confirmed in Table 5.1 by the variation around the estimated parameters. It can be clearly seen that the parameters and their estimated standard deviations have greater variation surrounding them than those estimated with deterministic sampling. The presence of between replicate variation around the parameter estimates made using deterministic sampling is attributable to terminating the sampling runs after 5,000 generations of the DE. However, the small size of this variation indicates that if given sufficient time the DE would produce results with zero between-replicate variation.

The reason behind the higher level of variation seen in the parameter estimates and model outputs produced by random sampling is explained in Figure 5.5a. This figure reveals that the sampling points taken by random sampling are clustered in the central portion of the parameter space. This results in large areas that are poorly covered in the sampling procedure while other areas could be considered as being well covered. Although not explicitly shown in the results, Figure 5.5a changes between replicates which the procedure is then forced to accommodate when estimating the parameters in order to produce a high level of fit during each replicate, thus contributing to the between-replicate variation.

The distribution of sampling points used by deterministic sampling, shown in Figure 5.5b, is in stark contrast to that seen for random sampling. The parameter space is sampled in an even manner with all regions being represented and no clustering or

sparse areas occurring. An important outcome of this sampling method is that the pattern seen in Figure 5.5b doesn't change between replicates. Given adequate DE generations to converge this reduces the variation in parameter estimates and model outputs to zero between replicates as the procedure is not required to accommodate sampling variation. Thus, greater confidence can be placed in the parameter estimates made using deterministic sampling.

The results presented in Tables Table 5.1, Table 5.2 and Table 5.3 for deterministic sampling were achieved by sampling 729 observations from the parameter space in comparison to the 2,000 observations required by random sampling. This highlights the major advantage of deterministic sampling, in that its computing costs are substantially lower than random sampling. Deterministic sampling required an average of 10 817 seconds to estimate the above parameters using 5,000 iterations of DE per replicate where as random sampling required 31 284 seconds (Table 5.4). This provides scope for deterministic sampling to be used to explore scenarios that would otherwise be impossible to explore with stochastic simulations that rely on random sampling (Mackinnon et al. 1996). The higher efficiency offered by deterministic sampling is particularly useful in combination with optimisation procedures that contain repetitious calculations.

MacKinnon et al. (1996) pointed out that the computational requirements of deterministic sampling are increased when sampling occurs from higher orders of multivariate distributions rather than univariate distributions. Although the efficiency of deterministic sampling was still apparent during this study when sampling from multivariate distributions, it should be noted that only 3 parameters were being estimated. If the number of parameters estimated during these simulations were to exceed ~12 (e.g. 9^{12} = 2.82E+11 sample points) the efficiency of deterministic sampling would be lost resulting in random sampling becoming a more attractive alternative for estimating growth model parameters.

Scope exists for the use of quasi-random numbers during the sampling process to overcome this constraint of deterministic sampling. Quasi-random numbers are designed to provide a more uniform coverage of the sample space than random numbers by minimising the deviation of sample values from uniformity, using a

criterion called 'discrepancy' (Mascagni and Karaivanova 2002). This is achieved by removing the serial independence of subsequently generated values (i.e. making the sample points correlated) (Caflisch 1998) which eliminates clumping seen with random numbers. Mascagni et al. (2002) and Mascagni and Karaivanova (2001) have found that the convergence rate and accuracy of Monte Carlo methods have been increased by the use of quasi-random sequences. Using quasi-random numbers with the weighting strategy employed by deterministic sampling could provide a solution for simulations that contain too many estimable parameters for deterministic sampling to maintain its superior efficiency.

Ultimately, the purpose of parameter estimation methods is to find parameters that have the ability to accurately predict the potential and actual performance of animals in real production environments. The predictive abilities of the parameters estimated by EPP were tested in a manner similar to that used during the model testing conducted in chapter 3. Initially, the Trangie dataset was used to test the predictive ability of parameters when used in a single population where the environmental, breed and sex effects were controlled. The average parameters estimated by EIP were found to have a greater predictive ability than those estimated by deterministic or random sampling (Table 5.5). This is also reflected in the confidence intervals presented in Figure 5.6, where it can be seen that the parameters estimated by EPP over-predict growth across most of the growth trajectory. The higher predictive ability of the parameters estimated by EIP could be attributed to the greater amount of information available in comparison to the information available to EPP. EIP used between 15 and 165 live weight and feed intake data points per animal to estimate parameters whereas EPP only used the average live weights and standard deviations at 250, 450, 650 and 1250 days of age along with the correlations between these ages.

The dataset taken from the Beef CRC was used to test the transferability of parameter estimates between populations of animals when the nutritional components of the environment were allowed to change but the breed and sex effects were controlled. The predictive ability of the parameters estimated by EPP was higher than the parameters estimated by EIP (Table 5.6). The confidence intervals displayed in Figure 5.7 are much smaller for EPP than for the parameters estimated by EIP. The EIP parameter estimates tended to under predict live weight across the whole growth

trajectory with this under prediction being less significant at older ages. In contrast, the predictions made using the parameters estimated by EPP were in general agreement with the average live weight data with a slight tendency for over prediction to occur at older ages. However, these results should be taken with some degree of caution as this was the only suitable alternative dataset available and other such datasets may well lead to different conclusions. We have no dataset-level degrees of freedom to contrast different methods.

This difference in predictive ability of the parameters estimated by EIP and those estimated by EPP could be associated with the feed intake data used in chapter 3. The parameters estimated by EIP are directly influenced by the feeding circumstances animals were experiencing i.e. daily variation in each individuals feed intake directly affects the parameters estimated (discuss in chapter 3). EPP only used population estimates of live weights at certain ages which in a sense averaged out the daily variations in feed intake by only allowing it to influence parameter estimates through the live weight data. This allowed these parameter estimates more flexibility when dealing with animals that were experiencing different nutritional circumstances.

Future growth is impacted upon by the feeding levels experienced and growth achieved in an animal's past. The ability to accurately predict the growth outcomes of exposure to different environments given information concerning previous growth is important for production systems and has direct relevance to the optimisation of growth pathways, which may include the manipulation of feeding levels.

The predictive ability of parameters estimated by the methods described above when using partial data was tested. The results in Table 5.7 indicate that the set of parameters estimated by deterministic sampling had the highest predictive ability while the parameters estimated by random sampling had the lowest and those estimated using EIP were intermediate. The difference between deterministic sampling and random sampling is attributable to the sampling of observations. The uniform coverage of the parameter space that occurs during deterministic sampling provides stability where as the clustering and sparseness seen in random sampling has a greater influence when smaller quantities of data are used. Figure 5.8 demonstrates that the parameters estimated by each of the methods tend to over predict live weight

at ages greater than those used to estimate the parameters. This could be interpreted as indicating that during the initial stages of the experiment animals were attaining their growth potential and the parameters were estimated to reflect this situation. The over predictions could then be seen as a result of environmental suppression of growth at older ages which is not accounted for due to both a lack of environmental data and the inability of the growth model used to take such information into account. This scenario has been explored in Chapter 3 when an attempt was made to model the influence that annual oscillations in summer temperatures in western NSW have on realised growth (Figure 3.5).

The next logical step would involve the refinement of the parameter estimation methods to increase accuracy by including information from other sources. An initial improvement would involve the incorporation of how environmental temperatures influence feed intake and thus affect growth. This could take a form similar to that attempted and discussed in chapter 3. This study only used data that were obtained from Angus steers. Factors such as sex and breed would have important influences on the estimation of parameters for growth models. Examples of these influences are not hard to envisage and may include cows having lower mature protein contents (P_m) to reflect lower mature body weights and higher mature lipid to protein ratios (Q) than the steers in this study. Genetic information can play an important role in predicting animal performance. Within breed information would prove beneficial when augmented with available phenotypes for predicting the growth of different lineages of animals. Including these factors in the estimation of growth model parameters would help facilitate the drafting of cohorts for meeting the demands of different market endpoints.

5.5. Conclusion

The results from the testing conducted in this study demonstrate the impact that both the form of the growth model used and the information available has on parameters estimated by all methods tested. In particular the addition of environmental information (e.g. daily temperatures) would help increase the accuracy of the predictions made by the growth model. The results also indicate that deterministic sampling offers a more accurate and computationally efficient means of obtaining

parameter estimates for growth models than either random sampling or EIP. This is particularly the case when smaller quantities of recorded animal data are available and the number of model parameters is moderate (<10).

5.6. Recommendations

Deterministic sampling could be refined to address the loss in efficiency that occurs when the number of parameters being estimated exceeds approximately 12. Incorporation of quasi-random numbers with the weighting strategy used by deterministic sampling could provide a solution to this loss of efficiency. However, the performance of quasi-random numbers would need to be extensively tested in an environment such as this study before confidence could be placed in any parameter estimates and procedures that apply them.