Chapter 4: Models for Predicting Body Composition

4.1. Introduction

Reducing the costs of production and the environmental impact production has while increasing the precision with which the quantity and quality of saleable product is estimated are challenges that are faced by both animal scientists and producers in the beef industry (Oddy et al. 1997a). These challenges need to be met not only to secure the financial future of beef enterprises but also to secure the environmental sustainability of individual producers and the industry as a whole. In attempting to meet these challenges, meat producers (sheep and cattle in particular) have come to the realisation that they now need to optimise their use of inputs whilst maximising efficiency, in contrast to past objectives of simply maximising output (Ball et al. 1997). The number of markets serviced by the Australian beef industry and the fact most beef enterprises supply more than a single market further complicate attempts to meet these challenges.

The preferences of consumers vary between markets, and consumers within any one market will have opinions as to what constitutes quality (Egan et al. 2001). However, regardless of the market there appear to be common criteria or "attributes of quality", that are partitioned into retail and consumption characteristics. Production operations are most readily able to impact upon retail characteristics including the quantity and distribution of fat, fat colour and even portion size. Thus, the quality of beef carcasses and their commercial value is dependent upon the distribution of lean, fat and bone as some parts of the carcass are more valuable than others (Kempster et al. 1976). In order to maintain viability, increasing pressure is placed on beef enterprises to produce a product (i.e. the carcass and its components) that meets these market criteria. The time required for animal breeding to make the changes necessary to increase consumer acceptability and consequently market access makes it relatively ineffective in the short term (Meszaros 1999). However, as discussed by Ball et al. (1997), nutritional manipulation can be used in the short term to make any required alterations.

As discussed in chapter 3, any nutritional manipulation used to alter animal growth should be conducted in an optimal manner, particularly when attempting to alter body

composition, so market specifications can be met and efficiency maintained and/or improved. Any optimisation procedure is reliant upon the mathematical functions employed to describe the system, thus function(s) that adequately describe body composition are required when manipulating body composition. As discussed in chapter 2, there are two distinct ways that empty body composition can be viewed. One is from a chemical perspective where the empty body is partitioned into lipid, water and lipid-free dry matter, and the other is from a physical perspective where the empty body is partitioned into carcass and non-carcass, which are further partitioned, in the case of carcass, into muscle, bone and fat (these perspectives of body composition are illustrated in Figure 4.4). The nature of the market criteria described above makes functions that have the capacity to predict physical composition more beneficial from a producer's perspective than models that predict chemical composition. However, there is scope to use functions that are driven by chemical composition to predict physical composition.

The limited number of models available for predicting physical body composition is discussed in chapter 2. The model developed by Soboleva et al. (1999) does not have the capacity to predict growth from approximately conception or birth and in its current form only partitions the empty body weight between muscle, viscera and fat without differentiation into carcass and non-carcass quantities, which would be more beneficial from a production perspective. The model developed by Sainz and Hasting (2000) only predicts the development of fat depots within an animal which again offers limited benefits in a production context. Consequently, of the physical composition models discussed in chapter 2, those developed by Song and Dinkel (1978b) are the only ones considered during the remainder of this chapter. However, it is recognised that the other models could have valuable contributions to make in future developments of physical body composition models.

An array of studies have used allometric equations to explore the developmental patterns of various body components in relation to the whole body (Butterfield et al. 1983a; Butterfield et al. 1984b; Thonney et al. 1987b). The growth model used by Amer and Emmans (1998) is based on the allometric relationships between chemical body components (Emmans 1988; Emmans and Kyriazakis 1995). The lack of models available for predicting physical body composition and the successful application of

allometric equations for predicting whole body growth provides the impetus for investigating the use of allometric equations for predicting body composition during *ad libitum* growth.

The aim of this chapter is to parameterise five alternative approaches that use allometric equations for predicting physical body composition. Three of the approaches include using direct relationships between body components and EBW, using the degree of maturity of EBW as a measure of component growth and using a hierarchical approach based on the degree of maturity of EBW. The two remaining approaches are based on allometric relationships between whole empty body protein and body component protein contents. These five different allometric approaches will have their abilities to predict physical body composition tested in comparison to the two models developed by Song and Dinkel (1978b).

4.2. Materials and Methods

4.2.1. Development and Parameterisation of Body Composition Models

In the study of de Lange (2003), the EBW of pigs is rationalised into six main physical components including muscle, fat, visceral organs, bones, blood and skin. This represents sensible partitioning of the body based on biological function and chemical composition. Thus the allometric models developed and parameterised in this study are done so on this basis except: 1) carcass fat (including kidney and channel fat) is grouped with carcass muscle (including the tail) to constitute "flesh" and 2) all visceral, lymphatic, vascular tissues along with non-carcass fat and head flesh are grouped as "viscera" (see below for explanation of alternative groupings). Thus each model uses five body pools to constitute EBW; these being flesh, bone, viscera, skin and blood. The datasets used for both model development and testing contain data from British bred steers (Shorthorn, Angus) thus removing any breed differences in body composition that would influence parameter estimates.

Development Data

The data used to estimate parameters for the allometric body composition models was taken from two serial slaughter trials conducted at the University of Minnesota

(Haecker 1920) and University of Missouri (Moulton et al. 1921) in the 1920's. Both experiments were designed to investigate the changes that occur in growth patterns and body composition of steers between early life (e.g. less than one month of age) and maturity. These changes were investigated from both physiological and chemical perspectives. At the time of slaughter the empty body was initially dissected into anatomical groups (e.g. liver, brain, muscle, bone, etc) in Moulton's study. However, in Haecker's study carcass fat deposits were group with carcass lean and visceral fatty deposits were grouped with the visceral organs. These groups were subsequently analysed to obtain their chemical composition, which was summed to obtain the chemical composition of the whole empty body. Datasets of this nature are rare for beef cattle and allow compositional changes to be followed simultaneously from physical and chemical perspectives as animals' progress towards maturity. This data also allows for the parameters of allometric models that use chemical composition of body components to predict physical composition to be estimated.

The experiment conducted by Haecker (1920) included 47 steers with approximately 3 steers slaughtered every 100 (~ 45 kg) pounds between 100 (~ 45 kg) and 1500 (~ 680 kg) pounds live weight. All animals were fed on a diet of corn, oats, bran, flour middlings and linseed meal with corn silage and prairie hay as roughage. This diet was fed to appetite such that the animals could be considered as fed *ad libitum*. All data recorded in this experiment were reported as pounds (lbs) and converted to kilograms for the purposes of this study. The data obtained from this experiment was used for parameterising the different allometric composition functions described below.

The experiment conducted by Moulton et al. (1921) involved a total of 29 steers across three feeding levels. Animals were fed high, medium or low levels of nutrition with these groups containing 10, 10 and 9 animals, respectively. The high nutrition group were offered the ration *ad libitum*. The medium nutrition group were fed to a level that would "allow them to achieve maximum growth without storing excess quantities of fat". The animals in the low nutrition group were fed to achieve distinctly retarded growth with a growth rate of approximately 0.23 kg (~ 0.5 lbs) per day considered adequate to keep the animals in the desired body condition (Moulton et al. 1921). One animal from each nutritional group was slaughtered at intermittent

ages up to 4 years of age with the initial group being slaughtered at 3 months of age. Animals fed on a high level of nutrition had slaughter weights of 110 kg at 3 months of age to 880 kg at 4 years of age. The weight ranges for the medium and low nutrition groups were 87 to 550 kg and 85 to 460 kg, respectively. All data in this experiment were reported in kg but only the data from the high nutrition group were used for model development and parameterisation because this group was the only group to achieve *ad libitum* growth.

Allometric Composition Functions

The allometric equation developed by Huxley (1932), widely used to relate the growth of body components (Y) to the whole body (X), takes the form:

$$Y = aX^b \tag{4.1}$$

where b is the differential growth ratio (allometric coefficient), a is a constant and X can be actual body weight or body component measurements or it can be expressed as the degree of maturity of the whole body or a body component. The allometric function makes the assumption that the ratio of relative growth rates of X and Y are constant throughout growth. When transformed on a log-log scale, every percentage change in X is accompanied by b% change in Y. Thus a body component expressed as a percentage of another component decreases (b<1), remains constant (b=1) or increases (b>1) as this component increases. The rapid and complex changes that occur during foetal and early postnatal growth present problems that allometry struggles to deal with (Berg and Butterfield 1976) but within the interval of 0.25 to 0.75 of mature body weight, allometry describes the growth of numerous body components with high success. Advantages of allometric equations include (i) stable linear solutions following log-log transformation, (ii) straight-forward biological interpretation and (iii) simple stable derivatives (Schinckel 1999).

Equation (4.1) forms the basis of the development and parameter estimation of the body composition models described below. Some of the approaches require that equation (4.1) be rearranged when predicting body composition.

Actual EBW (ActEBW) Model:

Numerous studies have used allometric equations to compare the developmental patterns of different body components directly to the developmental pattern of the whole empty body (McPhee and Trappett 1987; Moughan et al. 1990; Perry and Arthur 2000; Sørensen et al. 2003b). This allometric approach uses equation (4.1) to model the direct relationship between empty body weight (X) and body component weight (Y), where a and b are as described above. Figure 4.1 illustrates the simple direct relationships between body components and EBW. Figure 4.1 also demonstrates that non-carcass estimates are obtained by summing viscera, blood and skin with flesh and bone contained in Head/Tail/Feet. Carcass estimates are simply the sum of the remaining flesh and bone. Linear regressions are used in each allometric model to partition flesh and bone between carcass and non-carcass depots (described below).

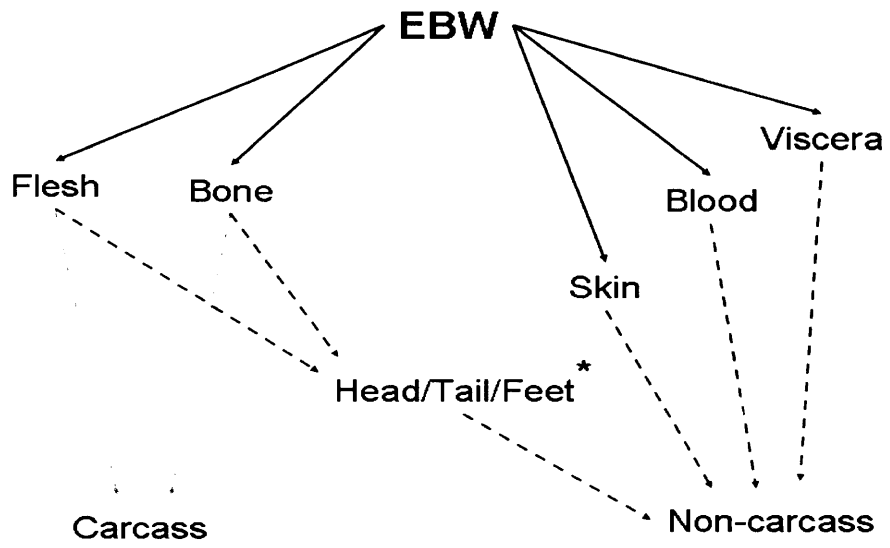

Figure 4.1: Diagrammatic representation of the allometric relationships between body component weights and empty body weight. * Prediction of Head/Tail/Feet is described below.

Degree of Maturity (DOM) Model:

Every component within the body can be partitioned the same way as body weight, i.e. into an adult value and degree of maturity (Taylor and Murray 1987). The equation:

$$u_y = u_x^b \tag{4.2}$$

is used to describe the degree of maturity of a body component (u_y) in relation to the degree of maturity of the whole body (u_x). The allometric coefficient, b, describes the maturing pattern of the body component relative to the whole body. As illustrated in Figure 4.2, b values <1 indicate early maturing components where as b values >1 indicate late maturing components and components with b values = 1 mature at the same rate as the whole body.

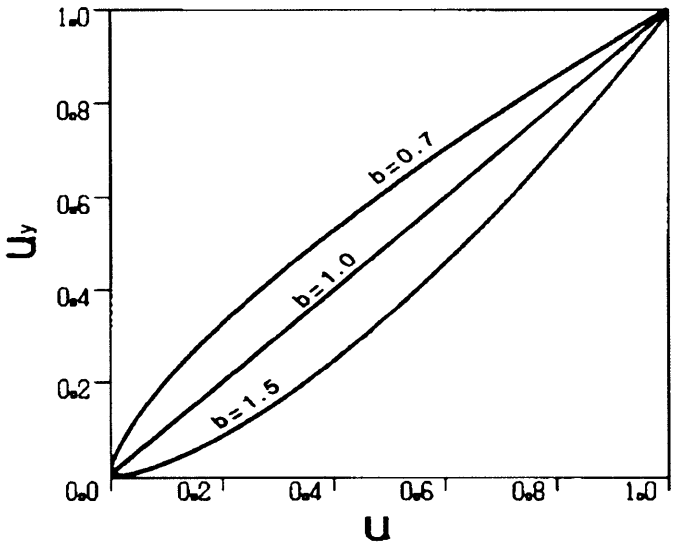

Figure 4.2: Allometric square illustrating the maturing patterns associated with b values of <1, =1 and >1, taken from Taylor and Murray (1987).

Allometric relationships of this type have been widely used for analysing growth patterns of both physical and chemical body components. Body components analysed include wool, bone, total fat, total muscle and visceral organs of different species including goats (Thonney et al. 1987a; Thonney et al. 1987b, 1987c), large and small

strains of Australian Merino rams (Butterfield et al. 1983a; Butterfield and Thompson 1983; Butterfield et al. 1983b; Butterfield et al. 1983c) and Australian Dorset Horn rams and wethers (Butterfield et al. 1984a; Butterfield et al. 1985; Butterfield et al. 1984b). A study involving Australian Merino sheep selected for high and low weaning weight (Thompson et al. 1985a) used this allometric approach for analysing chemical body composition whilst other authors use it as the basis for modelling chemical composition of body weight (Emmans 1988; Emmans and Fischer 1986; Emmans and Kyriazakis 1995).

This allometric approach can be represented by the schematic in Figure 4.1 except EBW is replaced by degree of maturity of EBW (uEBW). A variation on equation (4.1) is used when predicting body composition with this approach.

$$Y = Z_i.MatEBW.X^b \quad (\text{kg}) \tag{4.3}$$

where X is the degree of maturity of EBW, $MatEBW$ is mature EBW and Z_i is the ratio of the weight of body component i and EBW at maturity. The mature EBW was taken as being 1500 lbs (~ 610 kg), which is the live weight of the last animal slaughtered in Haecker's (1920) experiment.

Hierarchical Degree of Maturity (HDOM) Model:

This approach is also based on degree of maturity of EBW, however in contrast to the DOM approach; a hierarchical system is established with EBW being partitioned between Carcass/Head/Tail/Feet (CHTF) and Blood/Skin/Viscera (BSV) (Figure 4.3). These components are further partitioned with CHTF consisting of bone and flesh, with BSV consisting of skin, blood and viscera. Each stage in the model is represented by an allometric relationship (e.g. $CHTF \sim a_1.\mu_{EBW}^{b_1}$ and subsequent to this $Bone \sim a_2.\mu_{CHTF}^{b_2}$). Equation (4.4) is used to predict body component weight in each stage of this model:

$$Y = Z_i.MatCom.X^b \quad (\text{kg}) \tag{4.4}$$

where Z_i is the ratio of body component weight to weight of the component above it in the hierarchy at maturity (e.g. ratio between mature weights of CHTF and EBW). X is the degree of maturity of the component higher in the hierarchy and MatCom is the mature weight of this component (e.g. degree of maturity and mature weight of EBW when predicting CHTF). EBW, CHTF and BSV at maturity were taken as being 610, 450 and 160 kg, respectively, from Haecker's (1920) experiment which represent the weight of each trait in the last animal slaughtered.

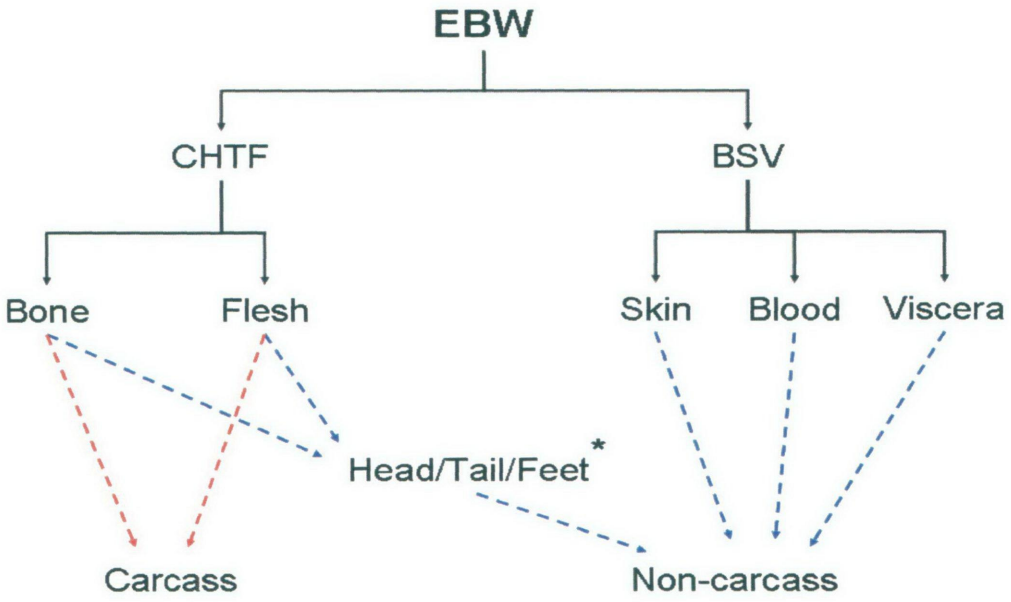

Figure 4.3: Hierarchical organisation of allometric relationships using degree of maturity of the previous stage as the basis (e.g. $Bone \sim a_2.\mu_{CHTF}^{b_2}$). * Prediction of Head/Tail/Feet is described below.

The rationale for investigating this approach was that it may reduce extrapolation and error associated with using EBW in the two approaches described previously. Studies have performed analysis of body composition using similar approaches. Butterfield et al. (1983a) investigated the growth pattern of total muscle in relation to live weight and in a subsequent paper the growth patterns of individual muscle groups were analysed in relation to total muscle (Butterfield et al. 1983c).

Chemical Degree of Maturity (ChemDOM) Models:

The two approaches described below are somewhat of an extension of the DOM approach except they use chemical composition of the empty body as the starting point from which physical body composition is predicted (Figure 4.4). The whole empty body is partitioned into five body components as described above. These are:

- Flesh (includes fat and muscle)
- Bone
- Skin
- Viscera
- Blood (can potentially be incorporated into viscera)

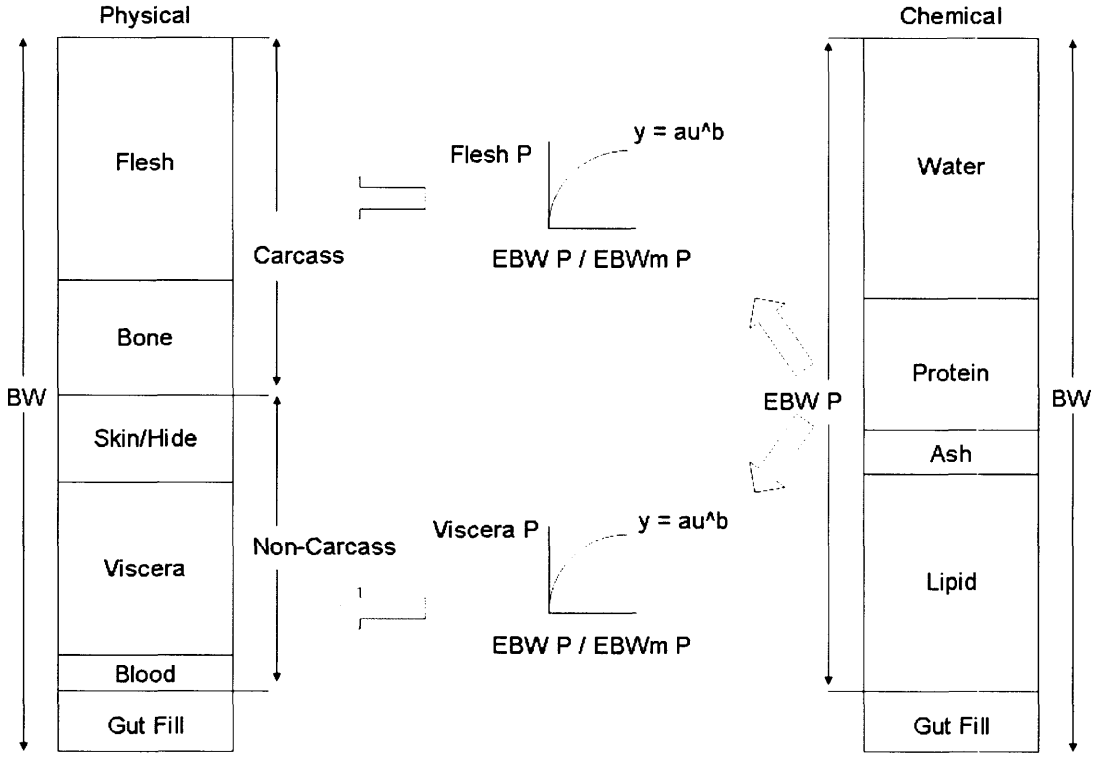

Figure 4.4: Physical and chemical perspectives of empty body composition including an illustration of the approaches taken to predict physical body composition from chemical composition using allometric relationships (where EBW P is the protein content of the EBW, etc).

The quantity of protein (P_i) partitioned into body component, i is determined using the allometric relationship between protein content of that body component and the

degree of maturity of the protein content of the empty body. The protein contained in each body component is predicted as follows:

$$P_i = W_i.P_m.\left(U_t^b\right) \quad \text{(kg)} \tag{4.5}$$

where P_m is the mature protein content of the empty body, W_i is the ratio of protein in component i to empty body protein at maturity, b is the allometric coefficient of that relationship and U_t is the degree of maturity of protein in the empty body at time, t, calculated as:

$$U_t = \frac{ActP_t}{P_m} \tag{4.6}$$

where $ActP_t$ is the protein content of the whole empty body at time, t. The ash content (A_i) of the body components is predicted from the protein content (P_i) of each body component (as predicted above) using allometric relationships based on the degree of maturity of protein contained in each body component (U_{ti}).

$$A_i = S_i.P_{mi}.\left(U_{ti}^b\right) \quad \text{(kg)} \tag{4.7}$$

where P_{mi} is the protein content and S_i is the ash:protein ratio at maturity of body component, i. The water content (H_i) of each body component is also predicted from the protein content of each component, using allometric relationships based on the degree of maturity of protein contained in each body component.

$$H_i = R_i.P_{mi}.\left(U_{ti}^b\right) \quad \text{(kg)} \tag{4.8}$$

where R_i is the water:protein ratio at maturity of body component, i. The lipid content (L_i) of each component is again predicted from the protein content of each body component, using allometric relationships based on the degree of maturity of protein contained in each body component.

$$L_i = Q_i.P_{mi}.\left(U_{ti}^b\right) \quad \text{(kg)} \tag{4.9}$$

where Q_i is the lipid:protein ratio at maturity of body component, *i*. During the remainder of this study the model using this form of the lipid to protein relationship is referred to as the ChemDOM1 model. An alternative means of estimating these lipid to protein relationships that adds flexibility to the model is to make these parameters a function of 1) the Lipid/Protein ratio of the mature empty body $(L_m : P_m)$, 2) the ratio of the protein content of the body component and protein content of the empty body at maturity $(P_{mi} : P_m)$ and 3) the ratio of lipid in the respective body component to empty body lipid content at maturity $(L_{mi} : L_m)$, in the following manner:

$$Q_i = \frac{L_m : P_m . L_{mi} : L_m}{P_{mi} : P_m} \tag{4.10}$$

where L_m is the lipid content of the mature empty body, P_m is the protein content of the mature empty body, L_{mi} is the lipid content of the *ith* mature body component and P_{mi} is the protein content of the *ith* mature body component. When the Lipid/Protein ratio of the mature empty body is available (discussed below) all that remains to be estimated is the ratio between the lipid content of the body component and the lipid content of the empty body at maturity because the ratio between the protein content of the body component and protein content of the empty body at maturity are already estimated above. The small number of animals contained in Haecker's (1920) experiment resulted in the ratios of body component lipid content to empty body lipid content at maturity being taken as the ratios displayed by the animal slaughtered at 1500 lbs (~ 610 kg). Studies conducted by Wright and Russel (1984) illustrate the existence of differential partitioning of lipid between different breeds of mature cows. This phenomenon is not new and has been illustrated with an example using dairy breeds that deposit higher quantities of lipid intra-abdominally compared to beef breeds (Kempster 1981). These findings indicate that the ratio between body component lipid content and empty body lipid content at maturity maybe affected by genotype and thus could change between breeds. Throughout the remainder of this study the model using this form of the lipid to protein relationship is referred to as the ChemDOM2 model.

The predicted total weight of each body component in both models is subsequently calculated as the sum of each of the chemical components that form that particular physical body component.

$$Fl_t = P_{Fl} + A_{Fl} + H_{Fl} + L_{Fl} \quad (\text{kg}) \tag{4.11}$$

$$Bo_t = P_{Bo} + A_{Bo} + H_{Bo} + L_{Bo} \quad (\text{kg}) \tag{4.12}$$

$$V_t = P_V + A_V + H_V + L_V \quad (\text{kg}) \tag{4.13}$$

$$Bl_t = P_{Bl} + A_{Bl} + H_{Bl} + L_{Bl} \quad (\text{kg}) \tag{4.14}$$

$$Sk_t = P_{Sk} + A_{Sk} + H_{Sk} + L_{Sk} \quad (\text{kg}) \tag{4.15}$$

where Fl_t, Bo_t, V_t, Bl_t and Sk_t are the total weights of flesh, bone, viscera, blood and skin in the empty body.

Non-Carcass Flesh and Bone:

Each of the composition models proposed above partition the empty body into five different body components; however in practical terms the first major division of any animal upon slaughter is made between the carcass and non-carcass components. Linear regression analysis was applied to the data of Moulton et al. (Moulton et al. 1922) in order to make an estimate of the partitioning of flesh and bone between the carcass and non-carcass components.

Statistical Analysis

Estimation of all allometric coefficients and linear regressions were conducted using the statistical package R (R Development Core Team 2004). Parameter estimation used a linear log-log form of equation (4.1), following Moughan et al. (1990):

$$\log Y = \log a + b.\log X \tag{4.16}$$

where log Y is the logarithm of Y, log X is the logarithm of X, log a is the intercept term and b is the allometric coefficient. This type of transformation allows variation in Y to be equalised at each X, which is an assumption of least-squares regression (Schinckel 1999). Estimation of a from equation (4.1) is undertaken by back transformation of log a (e.g. $a = \exp(\log a)$). Estimation of the Z_i, W_i, S_i, R_i and Q_i coefficients described above is undertaken by dividing the back transformation of log a by the mature weight of component X (e.g. when estimating Z_i for bone using the degree of maturity of CHTF in the HDOM model, $Z_{Bone} = \frac{\exp(\log a)}{Mature\ CHTF}$).

4.2.2. Validation of Body Composition Models

Validation Data

The carcass composition models presented above were tested for their ability to fit body composition data 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 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 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 condition 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.

Prior to slaughter the steers were fasted for 24 hours and weighed. During the slaughter process components of the gastro-intestinal tract had any contents emptied along with all omental and mesenteric fat removed. The non-carcass components were weighed separately and then bulked into the following depots: viscera (all organs plus thoracic fat), non-carcass fat (omental, mesenteric, kidney-channel and testicular), other non-carcass components (head, tail and non-carcass portions of the legs) and hide. The carcasses were halved with each weighed and stored at -20°C until analysed. Upon thawing the right half of the carcass was dissected into muscle, bone, subcutaneous and intermuscular tissue which were then weighed and multiplied by two to obtain whole carcass quantities. Other details concerning the experiment and generation of the data are reported by Perry and Arthur (2000).

Due to how the models were developed by Song and Dinkel (1978b), all composition models were tested initially with the composition data partitioned into "bone", "muscle" and "non-carcass", which included all non-carcass components. This testing phase is called T1 in the remainder of the study. Once the two Song and Dinkel (1978b) models were removed, the viscera and non-carcass fat data were grouped as "viscera" (except for the kidney-channel fat) while hide, blood and other non-carcass components were grouped as "remainder". The carcass data were again grouped into "bone" and "flesh" where flesh contained muscle along with subcutaneous, intermuscular and kidney-channel fat. This testing phase is called T2 in the remainder of the study.

Estimating Input Parameters for Composition Models

The ChemDOM models use the quantity of protein in the mature empty body as the basis from which they predict chemical composition of the body components. No information was available from the Trangie experiment regarding protein content of animals at maturity. Mature protein content is one estimable parameter in the growth model presented by Amer and Emmans (1998) and tested in chapter 3. Another estimable parameter is the lipid to protein ratio of the empty body at maturity, used by the ChemDOM2 model. Consequently, this model was used as a means of estimating both these parameters. In order to achieve this, the model was fitted to live weight

data for each animal using Differential Evolution (Price and Storn 1997) in an identical manner to that conducted in chapter 3, with the assumption that growth was *ad libitum* and consequently animals were attaining their growth potential. To allow the model to be fitted to live weights, following Wellock et al. (2003a) and in a similar manner to that used by Freer et al. (1997), the modification:

$$BW = \frac{EBW}{0.95} \quad (\text{kg}) \tag{4.17}$$

was made to obtain estimates of live weight (BW) from model EBW estimates. This modification was also used for estimating live weight at slaughter and mature live weight required by the two models developed by Song and Dinkel (1978b). The estimate of mature EBW was also used in the DOM and HDOM models. An exercise was conducted during T1 to compare the accuracy of using actual EBW measurements made prior to slaughter with EBW estimates made using the growth model to test the compatibility of growth and composition models. During T2 only actual EBW measurements made prior to slaughter were used as inputs to the composition models.

Model Fit across Individual Traits and Animals

The testing procedure used during model testing was similar to the testing procedure used in chapter 3. The Mean Squared Error (MSE) was used to compare the fit of the models to the body composition data. MSE is defined as:

$$MSE_{\text{model}} = \frac{\sum\left(\hat{Y}_i - Y_i\right)^2}{df - 1} \tag{4.18}$$

where $\hat{Y}_i$ is the model predicted weight of component, i, Y_i is weight data of component i and df is the degrees of freedom, 4 in this case. The MSE_{model} was averaged across animals to make a comparison of the average fit of each model tested. MSE was also used to compare the average fit of the models to individual traits. In this case MSE is defined as:

$$MSE_{\text{model. component}} = \frac{\sum\left(\hat{Y}_i - Y_i\right)^2}{df - 1} \tag{4.19}$$

where $\hat{Y}_i$ is the model predicted component weight for animal, i, Y_i is the component weight data of animal, i and df is the degrees of freedom, 57 in this case. R^2 values were also calculated to compare the fit of the models across both animals and components.

$$R^2 = 1 - \left(\frac{SSE}{SST}\right) \tag{4.20}$$

where SSE is sums of squares of error and SST is the total sums of squares.

4.3. Results

4.3.1. Development and Parameterisation of Body Composition Models

Actual EBW (ActEBW) Model:

Table 4.1 contains the parameters and standard errors estimated for the allometric relationships in the ActEBW model. The R^2 values for each relationship are also presented. As described above, log a in Table 4.1 is the intercept term of equation (4.16) and a is the constant in equation (4.1). The allometric coefficients (b) reveal that flesh matures later than the empty body whilst the remaining components mature earlier. The R^2 values indicate that all relationships had a high goodness of fit but the flesh/EBW relationship was fitted with the highest accuracy followed by the viscera/EBW relationship. The blood/EBW and skin/EBW relationships were fitted with the lowest accuracy.

Table 4.1: Estimated parameters (± s.e.) and R^2 values for the allometric relationships contained in the ActEBW model.

Body Component	Log a	a	b	R^2
Flesh	-1.37 ± 0.03	0.25	1.14 ± 0.005	0.999
Bone	-0.27 ± 0.12	0.76	0.71 ± 0.02	0.987
Viscera	-1.75 ± 0.12	0.17	0.97 ± 0.02	0.994
Blood	-1.76 ± 0.15	0.17	0.76 ± 0.03	0.984
Skin	-1.67 ± 0.17	0.19	0.84 ± 0.03	0.983

Degree of Maturity (DOM) Model:

The parameters and standard errors estimated for the allometric relationships contained in the DOM model are presented in Table 4.2 along with the R^2 values for each relationship. The allometric coefficients (*b*) in Table 4.2 are identical to those contained in Table 4.1 because both the ActEBW and DOM models use the approach displayed in Figure 4.1, except the DOM model replaces EBW with degree of maturity of EBW. The ratios of the body components to EBW at maturity (Z_i) in Table 4.2 indicate that 63% of the EBW is made up of flesh. Bone and viscera constitute 12% and 15% of mature EBW while only 3% and 7% of EBW are made up of blood and skin, respectively. The R^2 values in Table 4.2 are identical to those contained in Table 4.1 which is also a consequence of both models using the approach displayed in Figure 4.1.

Table 4.2: Estimated parameters (± s.e.) and R^2 values for the allometric relationships contained in the DOM model.

Body Component	Log a	Z_i	b	R^2
Flesh	5.96 ± 0.006	0.63	1.14 ± 0.005	0.999
Bone	4.3 ± 0.03	0.12	0.71 ± 0.02	0.987
Viscera	4.5 ± 0.03	0.15	0.97 ± 0.02	0.994
Blood	3.12 ± 0.03	0.03	0.76 ± 0.03	0.984
Skin	3.73 ± 0.04	0.07	0.84 ± 0.03	0.983

Hierarchical Degree of Maturity (HDOM) Model:

Table 4.3 contains the parameters and standard errors estimated for the allometric relationships in the HDOM model along with the R^2 values for each relationship. The

first stage in the model indicates that CHTF is later maturing and constitutes 75% of the EBW at maturity while BSV is early maturing and constitutes 25% of the EBW at maturity. The R^2 values indicate both relationships were fitted with a high degree of accuracy. In the second stage of the model the allometric coefficients reveal that flesh matures later than CHTF while bone matures earlier. The allometric coefficients for blood and skin indicate they mature earlier than BSV whilst viscera matures later. Flesh constitutes 84% and bone 16% respectively of CHTF at maturity whilst BSV is composed of 58% viscera, 27% skin and 15% blood at maturity. The R^2 values indicate that the relationships between flesh/CHTF and viscera/BSV were fitted with the highest accuracy with the other relationships being fitted with lower accuracy. The relationships between CHTF/EBW and BSV/EBW were also fitted with high accuracy.

Table 4.3: Estimated parameters (± s.e.) and R^2 values for the allometric relationships contained in the HDOM model.

Body Component	Log a	Z_i	b	R^2
Stage 1:				
CHTF	6.12 ± 0.006	0.75	1.04 ± 0.005	0.999
BSV	5.04 ± 0.02	0.25	0.9 ± 0.01	0.997
Stage 2:				
Flesh	5.94 ± 0.005	0.84	1.1 ± 0.004	0.999
Bone	4.29 ± 0.03	0.16	0.69 ± 0.02	0.987
Viscera	4.54 ± 0.02	0.58	1.08 ± 0.02	0.997
Blood	3.15 ± 0.03	0.15	0.84 ± 0.03	0.984
Skin	3.77 ± 0.03	0.27	0.93 ± 0.03	0.987

Chemical Degree of Maturity (ChemDOM) Models:

Table 4.4 contains the estimated parameters and standard errors for the allometric relationships between protein content of the body components and protein content of the empty body. The R^2 values for each relationship are also presented. Similar to Table 4.1, the allometric coefficients (*b*) in Table 4.4 reveal that protein content of flesh matures later than empty body protein content whilst the protein content of the remaining components mature earlier. The protein content of flesh at maturity constitutes 57% of total empty body protein whilst only 9% and 4% are contained in

viscera and blood, respectively. Bone and skin contain 18% and 12% of the empty body protein. The R^2 values indicate that the relationship between flesh protein content and empty body protein content was fitted with the highest accuracy followed by the viscera/EBW, bone/EBW and blood/EBW relationships. The relationship between skin protein content and EBW protein content was fitted with the lowest accuracy.

Table 4.4: Estimated parameters (± s.e.) and R^2 values for the allometric relationships between protein content of the body components and the whole empty body.

Body Component	Log W	W_i	b	R^2
Flesh (W_{Fl})	4 ± 0.01	0.57	1.12 ± 0.01	0.998
Bone (W_{Bo})	2.84 ± 0.02	0.18	0.84 ± 0.01	0.993
Viscera (W_V)	2.15 ± 0.02	0.09	0.89 ± 0.02	0.994
Blood (W_{Bl})	1.48 ± 0.03	0.04	0.91 ± 0.02	0.989
Skin (W_{Sk})	2.44 ± 0.04	0.12	0.92 ± 0.04	0.98

Linear regression analysis of ash content as a percentage of lipid free dry matter on degree of maturity of whole empty body protein produced non-significant slopes for flesh ($p>0.15$) and skin ($p>0.5$) indicating that the ratio of ash to protein in these tissues remained constant at all degrees of maturity. Consequently, the allometric relationships between ash and protein contained in flesh and skin simplify to linear relationships:

$$A_i = S_i.P_i \quad (\text{kg}) \tag{4.21}$$

where ash (A_i) is predicted as a percentage (S_i) of the protein content (P_i) of flesh and skin (predicted using the allometric relationships in Table 4.4). The coefficients from the linear regressions used to predict ash content of flesh and skin are presented in Table 4.5. The parameters and standard errors estimated for the allometric relationships between ash and protein in bone, viscera and blood are also presented in Table 4.5 along with their respective R^2 values. The allometric coefficients indicate that the ash contents of bone and blood mature later than their protein contents whilst the ash content of viscera matures earlier than the protein content. The ash content of viscera and blood at maturity is 5.5% and 4.3% of the protein content, respectively whilst the ash content of bone is 105.7% of the protein content. The R^2 values indicate

that the ash:protein relationships in bone and blood were fitted with the highest accuracy while the relationship in viscera was fitted with a slightly lower accuracy.

Table 4.5: Estimated parameters (± s.e.) and R^2 values for the allometric relationships between ash and protein contents of bone, viscera and blood along with the coefficients for the linear regressions between ash and protein in flesh and skin.

Body Component	Log S	S_i	b	R^2
Flesh (S_{Fl})	-	0.045	-	-
Skin (S_{Sk})	-	0.027	-	-
Bone (S_{Bo})	2.82 ± 0.02	1.057	1.2 ± 0.03	0.994
Viscera (S_V)	-0.76 ± 0.03	0.055	0.87 ± 0.03	0.988
Blood (S_{Bl})	-1.66 ± 0.02	0.043	1.12 ± 0.02	0.994

The parameters and standard errors estimated for the allometric relationships between water and protein contents of the body components are presented in Table 4.6 along with the R^2 values for each relationship. The allometric coefficients indicate that the water content of all body components mature earlier than their protein contents. The ratios between water and protein content in the body components at maturity range from 1.4 for bone to 4.4 for viscera. The water:protein relationships in flesh and blood were fitted with the highest accuracy followed by the relationships in viscera and skin. The water:protein relationship in bone was fitted with the lowest accuracy.

Table 4.6: Estimated parameters (± s.e.) and R^2 values for the allometric relationships between water and protein contents of the body components.

Body Component	Log R	R_i	b	R^2
Flesh (R_{Fl})	5.21 ± 0.02	3.3	0.91 ± 0.01	0.997
Bone (R_{Bo})	3.09 ± 0.02	1.4	0.67 ± 0.03	0.982
Viscera (R_V)	3.62 ± 0.02	4.4	0.85 ± 0.02	0.993
Blood (R_{Bl})	2.85 ± 0.01	3.9	0.9 ± 0.01	0.997
Skin (R_{Sk})	3.29 ± 0.03	2.2	0.95 ± 0.03	0.988

Table 4.7 contains the estimated parameters and standard errors for the allometric relationships between lipid and protein contents of the body components used in the ChemDOM1 model. The R^2 values for each relationship are also presented. Analysis of the lipid contents revealed that blood contains negligible lipid and thus the

assumption was made that blood contains no lipid. The allometric coefficients in Table 4.7 reveal that the lipid content of all body components mature at a later stage of development than their protein contents. The ratios between lipid and protein at maturity vary considerably between body components. The quantity of lipid contained in skin is 48% of the protein content whilst the lipid contained in bone is 81% of its protein content. In contrast, the quantity of lipid contained in flesh is 284% of its protein content and the lipid content of viscera is 520% of its protein content. The R^2 values indicate the lipid:protein relationship in flesh was fitted with the highest accuracy whilst the relationship in skin was fitted with the lowest accuracy.

Table 4.7: Estimated parameters (± s.e.) and R^2 values for the allometric relationships between lipid and protein contents of the body components used in the ChemDOM1 model.

Body Component	Log Q	Q_i	b	R^2
Flesh (Q_{Fl})	5.06 ± 0.06	2.84	2.08 ± 0.05	0.993
Bone (Q_{Bo})	2.54 ± 0.05	0.81	1.27 ± 0.06	0.971
Viscera (Q_V)	3.79 ± 0.09	5.2	2.29 ± 0.1	0.978
Skin (Q_{Sk})	1.22 ± 0.17	0.48	1.78 ± 0.17	0.898

The degree of maturity of protein in each body component is the basis from which lipid content is predicted in the ChemDOM2 model, thus the allometric coefficients are identical to those contained in Table 4.7. The estimated ratios between lipid content of the body components and lipid content of the empty body at maturity used in the ChemDOM2 model are presented in Table 4.8. This model also makes the assumption that blood contains no lipid. Partitioning of lipid at maturity within the body is quite biased toward flesh and viscera with small quantities of lipid partitioned to bone and skin. Flesh contains 70% of the lipid contained in the whole empty body at maturity, viscera contains 23% while bone and skin only contain 5% and 2% respectively.

Table 4.8: Estimated ratios between lipid content of the body components (L_{mi}) and lipid content of the whole empty body (L_m) at maturity used in the alternative allometric relationships contained in the ChemDOM2 model.

Body Component	$L_{mi}:L_m$
Flesh (Q_{Fl})	0.70
Bone (Q_{Bo})	0.05
Viscera (Q_V)	0.23
Skin (Q_{Sk})	0.02

Non-Carcass Flesh and Bone:

Linear regression analysis of carcass and non-carcass bone on degree of maturity of empty body protein content produced non-significant slopes ($p>0.1$). This indicates that at any degree of maturity, 71% of bone is contained in the carcass and the remaining 29% in the non-carcass. Linear regression analysis of carcass and non-carcass flesh on degree of maturity of empty body protein produced significant slopes ($p<0.001$), thus linear regression functions are used to partition flesh between carcass and non-carcass. The coefficients for partitioning flesh along with the R^2 values are presented in Table 4.9 and indicate the vast majority of flesh is contained in the carcass.

Table 4.9: Linear regression parameters (± s.e.) and R^2 values for predicting flesh contained in carcass and non-carcass components of the empty body.

	Intercept	Slope	R^2
Carcass	0.998 ± 0.0001	0.001 ± 0.0001	0.83
Non-Carcass	0.002 ± 0.0001	-0.001 ± 0.0001	0.83

4.3.2. Validation of Body Composition Models

The testing procedure compared the predictive abilities of the five allometric models developed and parameterised in this study with the abilities of the two models developed by Song and Dinkel (1978b). During the T1 phase of testing comparisons were made between model accuracy when predictions were made using either EBW estimates made with the growth model presented by Amer and Emmans (1998) or actual EBW measurements made prior to slaughter.

When body composition was predicted during T1 using EBW estimates made with the Amer and Emmans (1998) growth model, the ActEBW model produced the highest average accuracy of prediction (Table 4.10). The ChemDOM1 model, that uses the ratio of lipid to protein in body components at maturity, produced the least accurate predictions. The two models developed by Song and Dinkel (1978b) produced predictions that were superior to the ChemDOM1 model but were inferior to the other models. The DOM and HDOM models performed at comparable levels, with both being inferior to the ChemDOM2 model which was in turn inferior to the ActEBW model. Both the SD of MSE across animals and R^2 values tend to support these trends with some re-ranking of the R^2 values between the DOM, HDOM and ChemDOM2 models.

Table 4.10: The MSE, SD of MSE and R^2 values averaged across animals for all the body composition models tested in T1 when using EBW estimates made by the growth model presented by Amer and Emmans (1998).

Model	Average MSE	MSE SD	R^2
ActEBW	675.49	596.18	0.987
DOM	839.83	701.55	0.984
HDOM	834.9	701.12	0.984
ChemDOM1	5177.59	4143.23	0.928
ChemDOM2	775.05	616.28	0.983
Song/Dinkel1	2984.15	1390.19	0.949
Song/Dinkel2	3540.57	1778.83	0.946

Predictions of body composition made by the most accurate (ActEBW) and three least accurate (ChemDOM1, Song/Dinkel1 and Song/Dinkel2) models from Table 4.10 are illustrated in Figure 4.5. The plots of model predictions versus observed weights for flesh, bone and non-carcass in comparison to the data versus data lines reveal that the ActEBW model consistently over predicts flesh and bone weight whilst its predictions of non-carcass weight are evenly distributed. Model 1 developed by Song and Dinkel under predicts flesh at lower observed weights while their model 2 predicts accurately at these observed weights. Both models consistently over predict flesh at high observed weights. Trends in the opposite direction are evident for non-carcass predictions made by these two models. These two models over predict bone weight at

higher observed weights and then dramatically over predict at lower observed weights. The predictions for flesh and non-carcass made by the ChemDOM1 model for animals older than 7 months of age at slaughter occur in two categories; one group that are over predictions and another that are under predictions. The predictions made for bone can also be grouped into two categories but the division is not as apparent as the division for flesh and non-carcass.

The prediction of body composition using actual EBW measurements made prior to slaughter produced re-ranking of the models (Table 4.11). The ChemDOM1 model again produced the least accurate predictions with the two models developed by Song and Dinkel (1978b) and the ChemDOM2 model maintaining their order of predictive accuracy. The ActEBW model's predictive ability was again superior to the ChemDOM2 model but in this instance was inferior to the DOM and HDOM models that again performed at comparable levels. The SD of MSE and R2 values support these trends in model predictive ability.

Table 4.11: The MSE, SD of MSE and R^2 values averaged across animals for all the body composition models tested in T1 when using actual EBW measurements taken prior to slaughter.

Model	Average MSE	MSE SD	R^2
ActEBW	183.32	128.2	0.996
DOM	154.2	133.09	0.996
HDOM	153.23	131.67	0.996
ChemDOM1	4140.51	3985.44	0.946
ChemDOM2	330.49	266.32	0.994
Song/Dinkel1	1664.51	831.9	0.97
Song/Dinkel2	1899.59	1110.61	0.972

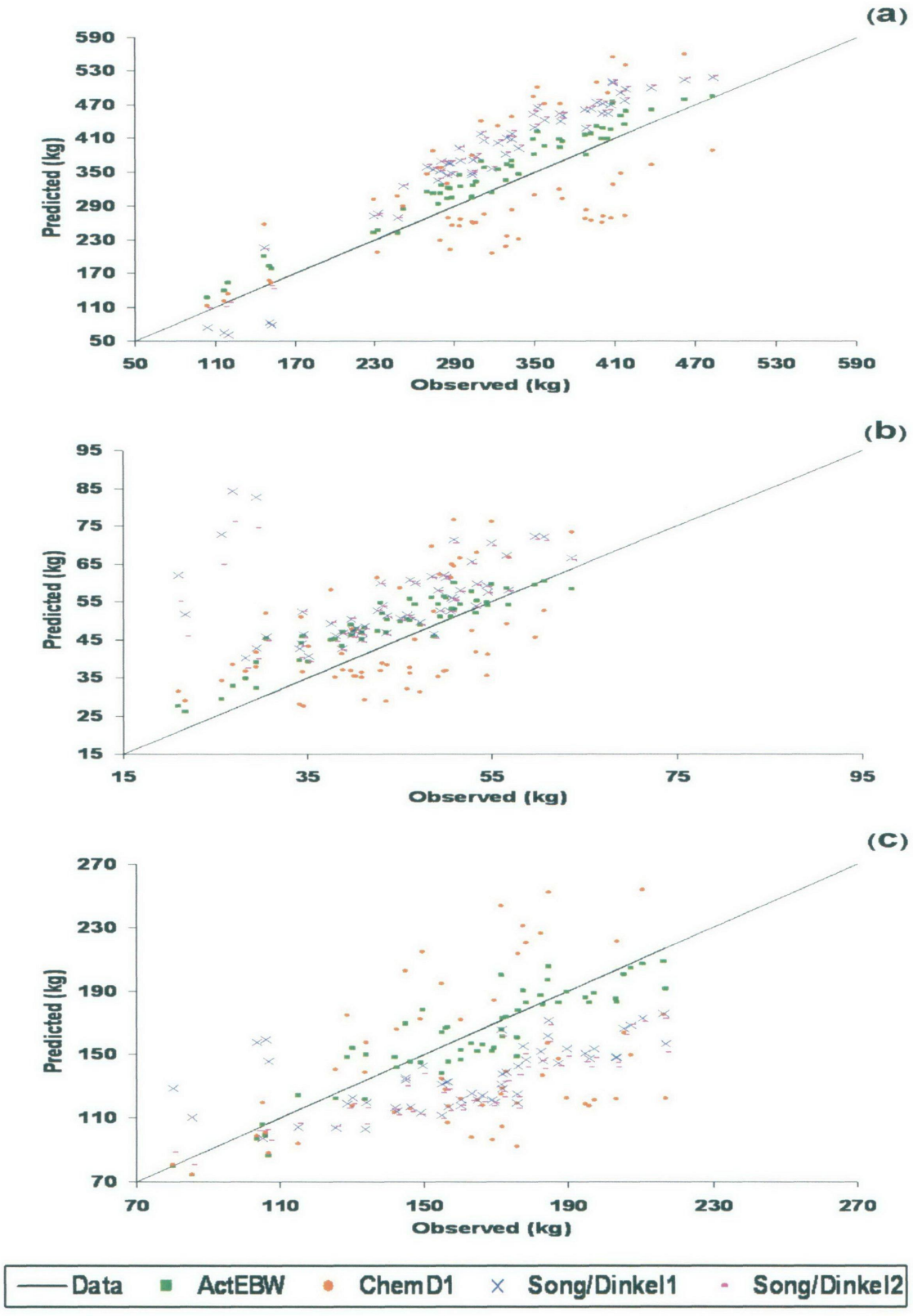

Figure 4.5: Observed vs predicted weight of flesh (a), bone (b) and other (c) for the ActEBW, ChemDOM1 and two Song and Dinkel (1978b) models tested during T1 using EBW estimates made by the growth model presented by Amer and Emmans (1998).

The predictions of body composition made by the ActEBW model and three least accurate (ChemDOM1, Song/Dinkel1 and Song/Dinkel2) models from Table 4.11 are illustrated in Figure 4.6. The plot of predicted flesh versus observed flesh weight indicates the ActEBW model predicts accurately while the ChemDOM1 model's predictions can again be placed into two categories (Figure 4.6a). Predictions made by the two Song and Dinkel models follow similar trends to those seen above in Figure 4.5a. The plot of predicted bone versus observed bone weight reveals that all models have a tendency to over predict at lower observed weights with the Song and Dinkel models over predicting more dramatically than the other two models. The predictions for all models tend to become more accurate as observed bone weight increases with the predictions made by the ChemDOM1 model being the most dispersed and both Song and Dinkel models appearing to still slightly over predict bone weight (Figure 4.6b). The ChemDOM1 model predictions of non-carcass weight can again be partitioned into two groups whilst the ActEBW model tends to consistently under predict. Model 1 developed by Song and Dinkel over predicts non-carcass at lower observed weights while their model 2 predicts accurately at lower observed weights. Both models consistently over predict non-carcass weight at higher observed weights (Figure 4.6c).

Comparison of the R^2 values presented in Tables Table 4.10 and Table 4.11 for each body composition model make it clear that using actual EBW measurements made prior to slaughter improved predictions of body composition in comparison to using EBW estimates made with the growth model. A comparison of the plots presented in Figures Figure 4.5 and Figure 4.6 also support this result with Figure 4.6 being a frame shift down in comparison to Figure 4.5. This frame shift is of approximately the same magnitude for all the models. Consequently, the remaining model testing performed in this study was conducted using actual EBW measurements made prior to slaughter.

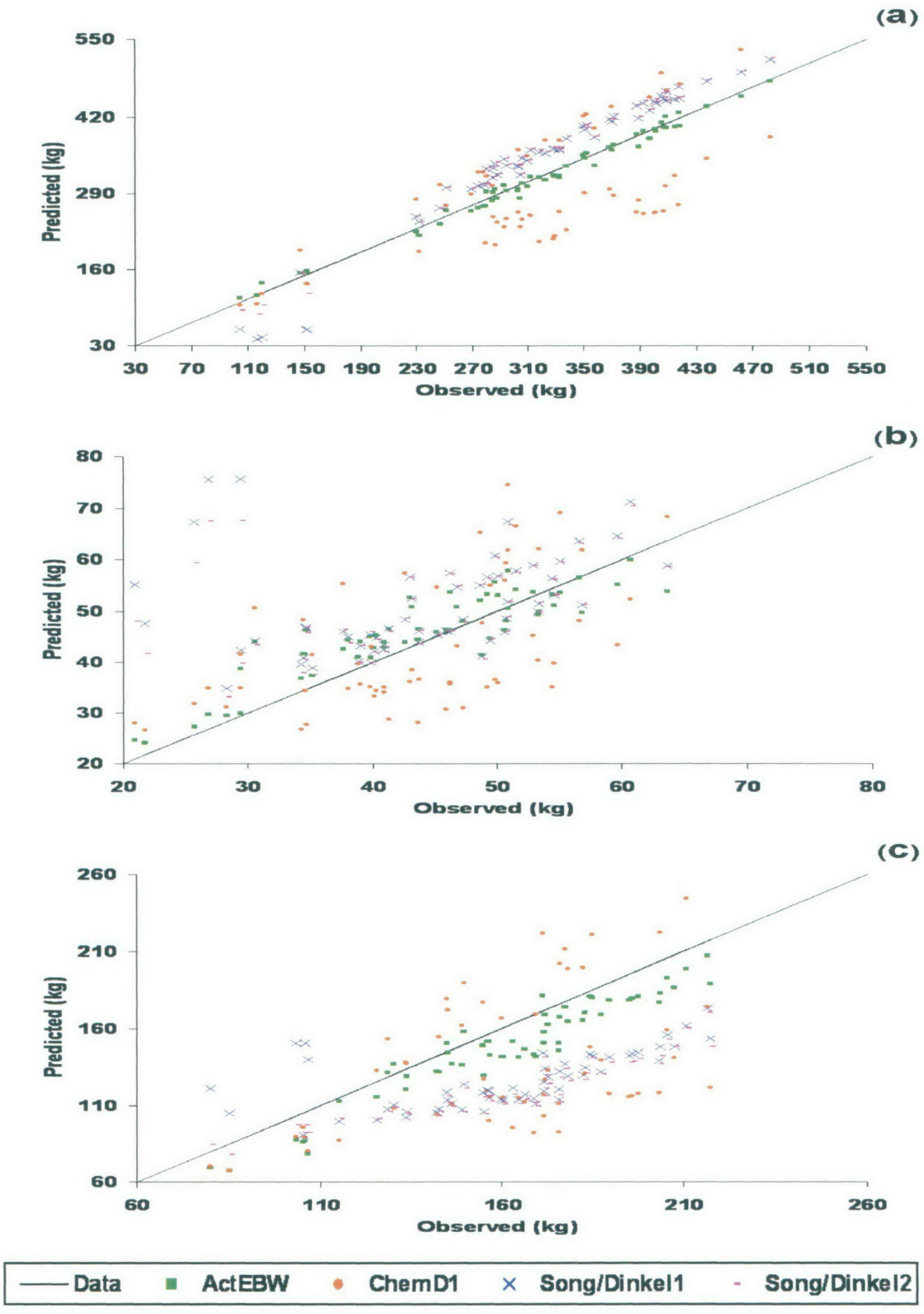

Figure 4.6: Observed vs predicted weight of flesh (a), bone (b) and other (c) for the ActEBW, ChemDOM1 and the two models developed by Song and Dinkel (1978b) tested during T1 when using actual EBW measurements taken prior to slaughter.

The results presented in Tables Table 4.10 and Table 4.11 also reveal that the two models developed by Song and Dinkel (1978b) and the ChemDOM1 model have lower predictive accuracies than the remaining models. The data illustrated in Figures Figure 4.5 and Figure 4.6 show that the predictions made by the two Song and Dinkel models are biased upward for flesh while they are biased downward for non-carcass. Their predictions of bone are extremely inaccurate at low observed bone weights. Their predictions improve in accuracy with increasing observed bone weight but never achieve the same level of accuracy as the ActEBW model. The ChemDOM1 model predictions form two distinct groups that are never as accurate as the predictions made by the ActEBW model. In an effort to further demonstrate the predictive abilities of the ActEBW, DOM, HDOM and ChemDOM2 models testing was expanded to include flesh, bone, viscera and remainder.

In comparison to Table 4.11, the results in Table 4.12 from T2 produced re-ranking amongst the ActEBW, DOM and HDOM models while the ChemDOM2 model maintained its inferior predictive ability. The ActEBW and HDOM models predictive abilities were comparable while the DOM model had an inferior predictive ability compared to these two. The SD of MSE and R^2 values support these trends in predictive ability.

Table 4.12: The MSE, SD of MSE and R^2 values averaged across animals for the ActEBW, DOM, HDOM and ChemDOM2 models tested in T2.

Model	Average MSE	MSE SD	R^2
ActEBW	149.72	84.36	0.995
DOM	188.69	110.92	0.994
HDOM	150.87	95.45	0.995
ChemDOM2	547.65	397.62	0.986

Re-ranking amongst the models that occurred between Tables Table 4.11 and Table 4.12, primarily the ActEBW and DOM models, is attributable to the accuracy with which each model predicts different body components. The results shown in Table 4.11 illustrate that the predictive ability of the DOM model was superior to that of the ActEBW model. The results presented in Table 4.13 indicate that the predictive superiority of the DOM model is due to its ability to make more accurate predictions

of non-carcass weight even though the ActEBW model predicts bone and flesh with higher accuracy. The reason for this is because the differences in ability of the two models to predict bone and flesh are not as large as the difference in their abilities to predict non-carcass weight. The ChemDOM2 model predicts all traits with lower accuracy than the DOM or HDOM models but predicts non-carcass weight with a higher accuracy than the ActEBW model.

Table 4.13: The MSE, SD of MSE and R^2 values for each trait predicted in T1 averaged across animals for the ActEBW, DOM, HDOM and ChemDOM2 models.

Model	Bone		Flesh		Non-Carcass	
	Average MSE	R^2	Average MSE	R^2	Average MSE	R^2
ActEBW	25.58	0.987	88.92	0.999	258.68	0.991
DOM	47.67	0.977	106.5	0.999	159.75	0.994
HDOM	46.09	0.977	108	0.999	157.85	0.994
ChemDOM2	50.89	0.975	414.62	0.996	207.26	0.993

When predicting viscera and remainder as opposed to non-carcass weight as a whole the superiority of the ActEBW model seen in Table 4.12 is due to this model making more accurate predictions of both viscera and remainder than the DOM model (Table 4.14). The ActEBW model predicts viscera with the highest accuracy and maintains its predictive superiority for bone and flesh seen in Table 4.13. The ChemDOM2 model predicts all traits with the lowest accuracy while the HDOM model predicts remainder with the highest accuracy. The DOM and HDOM models have similar predictive accuracies for bone and flesh while the HDOM model predicts viscera with higher accuracy. Inspection of the predictions made for individual traits reveals that the change in predictive ability of the DOM model is due to inaccuracies in predictions of viscera and remainder tending to cancel each other out when summed to produce whole non-carcass predictions in T1 (this can be seen in Figure 4.7). Inspection of predictions of individual traits reveal the change in predictive performance of the ActEBW model is attributable to inaccuracies in predictions of viscera and remainder not cancelling out when summed and in some cases producing larger predictive errors.

Table 4.14: The MSE, SD of MSE and R^2 values for each trait predicted in T2 averaged across animals for the ActEBW, DOM, HDOM and ChemDOM2 models.

Model	Bone		Flesh		Viscera		Remainder	
	Ave MSE	R^2	Ave MSE	R^2	Ave MSE	R^2	Ave MSE	R^2
ActEBW	25.58	0.987	88.92	0.999	50.74	0.991	291.94	0.966
DOM	47.67	0.977	106.5	0.999	107.45	0.981	314.55	0.963
HDOM	46.09	0.977	108	0.999	71.25	0.987	235.37	0.972
ChemDOM2	50.89	0.975	414.62	0.996	367.7	0.933	839.09	0.902

The results presented in Table 4.14 are reproduced in Figure 4.7 to illustrate any bias in model predictions. The higher accuracy that flesh is predicted with can be clearly seen in Figure 4.7a. All the models are evenly distributed around the data versus data line with the ChemDOM2 model having more variation in its predictions. All four models have a tendency to over predict at lower observed bone weights. The ActEBW, DOM and HDOM models tend to continue to over predict as observed bone weight increases whilst the ChemDOM2 model's predictions appear to be evenly distributed around the data versus data line but have a greater spread (Figure 4.7b). All the models tend to over predict viscera while under predicting remainder. The ChemDOM2 model tends to show these trends to the greatest extent with the HDOM model tending to do it the least for remainder (Figure 4.7c) and the ActEBW model the least for viscera (Figure 4.7d). Also illustrated in Figures Figure 4.7a and Figure 4.7b is the smaller amount of bias contained in the predictions of flesh and bone made by the DOM, HDOM and ChemDOM2 models compared to the ChemDOM1 and the two Song and Dinkel models in Figures Figure 4.6a and Figure 4.6b.

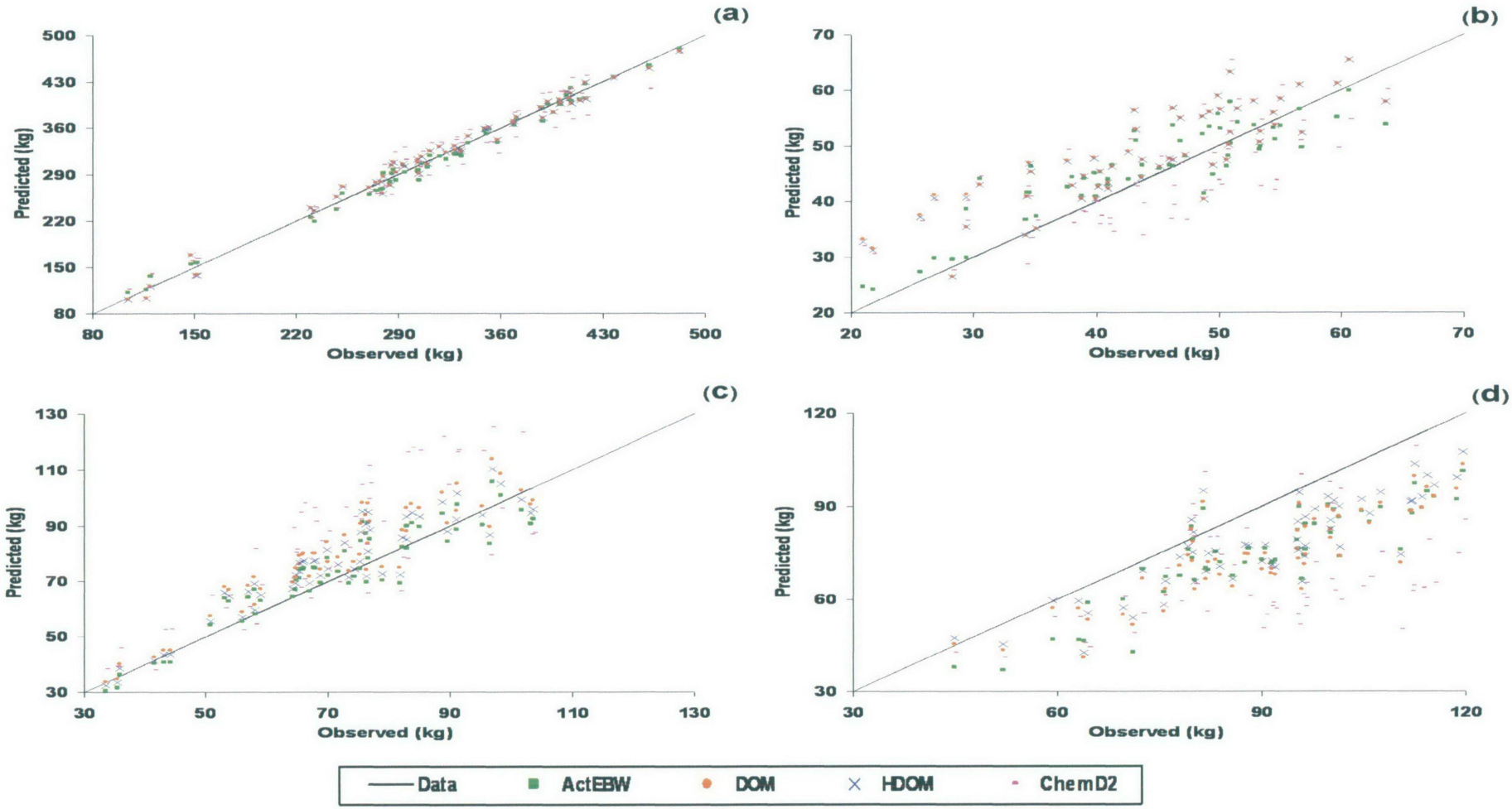

Figure 4.7: Observed vs predicted weight of flesh (a), bone (b), viscera (c) and remainder (d) for the ActEBW, DOM, HDOM and ChemDOM2 models tested during T2.

The results in Tables Table 4.11 and Table 4.12 indicate that the HDOM model predicted body composition with a higher accuracy regardless of how the body composition data was pooled for testing. The DOM model predicts body composition with similar accuracy to the HDOM model during T1 while the ActEBW model predicts body composition with similar accuracy to the HDOM model during T2. The results contained in Tables Table 4.13 and Table 4.14 help reveal why these changes in predictive accuracy occur. The ActEBW model consistently has higher predictive accuracy for bone and flesh but presenting the remaining components as non-carcass for testing (whole non-carcass vs viscera and remainder) influences its accuracy of prediction. When the data are presented as viscera and remainder the ActEBW model has greater capacity to predict viscera than the HDOM model. But when predicting remainder the opposite is the case. The reason for the DOM model's higher accuracy of prediction in Table 4.13 is revealed to some extent in Table 4.14 and also by Figures Figure 4.7c and Figure 4.7d where it has an inferior predictive capacity for both viscera and remainder compared to the ActEBW and HDOM models. Inspection of the actual predictions for the non-carcass traits shows that inaccuracies in these predictions cancel each other out when summed to produce whole non-carcass predictions. This is an attribute of the DOM model that is masked by the testing procedure and is not a desirable attribute of a body composition model.

4.4. Discussion

The current study developed and parameterised five models that use allometric equations in different ways to predict physical body composition. The study subsequently compared the predictive abilities of these models with two models developed by Song and Dinkel (1978b).

4.4.1. Development and Parameterisation of Body Composition Models

The allometric coefficients (b) estimated for the ActEBW (Table 4.1) and DOM (Table 4.2) models are identical because both models use the frame work displayed in Figure 4.1 to predict body composition but use the a constants in different ways. The ActEBW model uses the a constant for prediction but the DOM model transforms this constant to calculate the ratio between body components and EBW at maturity (Z_i).

The allometric coefficients estimated for the ActEBW and DOM models represent sensible patterns of development for the body components relative to EBW. Flesh would be expected to be late maturing given it is the sum of lean and fatty tissue in the carcass. In sheep, total and carcass fat have both been shown to be late maturing in comparison to EBW (Butterfield and Thompson 1983; Butterfield et al. 1985; Butterfield et al. 1984b) while lean tissue has been shown to be slightly earlier maturing (Butterfield et al. 1983a; Butterfield et al. 1984b). Similar developmental patterns have also been shown to exist in cattle (Perry and Arthur 2000). The allometric coefficient for viscera indicates it matures at a similar rate to the whole EBW which is a consequence of viscera including visceral fat. Studies have shown that visceral organs are earlier maturing than EBW while visceral fat is later maturing (Butterfield et al. 1985; Butterfield et al. 1984b; Perry and Arthur 2000). The developmental patterns of blood and hide are in agreement with patterns presented in the literature (Butterfield et al. 1983b; Butterfield et al. 1984b; Thonney et al. 1987b), as are those for bone (Butterfield and Thompson 1983). At maturity the proportions of blood and skin in the empty body (Table 4.2) are similar to the proportions of live weight estimated for Dorset Horn rams and wethers (Butterfield et al. 1984b). The proportions of flesh and bone are higher while the proportion of viscera is lower in comparison to estimates for Dorset Horn sheep (Butterfield et al. 1984b). This could be attributable to species or diet differences even though the cattle in Haecker's (1920) experiment and the sheep in the experiment of Butterfield et al. (1983a) received similar diets.

The allometric coefficients estimated for the HDOM model also follow sensible patterns of body component development. The later maturing pattern of CHTF, similar to the pattern found for carcass weight in goats (Thonney et al. 1987b), is due to the later maturing of fat depots while the earlier maturing pattern of BSV is due to the early maturing patterns of vital organs and tissues (e.g. heart, skin, blood, central nervous system, etc). The maturing patterns of flesh and bone relative to CHTF can be explained with similar rationale. The fat depots in flesh slow rate of development while the necessity of bone for animal movement and support demand it matures earlier. Similar rational can again be used to explain the maturing patterns of viscera, blood and skin. The fat depots in viscera slow its rate of development while the vital

nature of skin and blood to an animal's survival necessitate their early maturation. When the ratios between components at maturity (Z_i) presented in Table 4.3 are multiplied out to relate the weight of a body component to EBW the values obtained are similar to those presented in Table 4.2. This is a desired result as the relationships between body components and EBW do not change relative to how an animal is broken up and described upon slaughter. Using the HDOM approach to describe these relationships increases the accuracy with which the parameters can be estimated.

The trends seen in the allometric coefficients presented in Table 4.2 are reflected to a certain degree in the allometric coefficients estimated for the body component/empty body protein relationships used in the ChemDOM models. Relative to empty body protein content, the protein in flesh matures later while the protein in the other four body components matures earlier. The allometric coefficient estimated for flesh protein (Table 4.4) and flesh (Table 4.2) are similar in magnitude indicating they follow similar maturation pathways. The coefficients for the remaining body components change in comparison to those in Table 4.2. The protein contained in bone, blood and skin mature slower relative to empty body protein than the whole body components mature relative to EBW. The protein contained in viscera matures earlier than viscera as a whole due to the adipose cells developing early in life but not storing lipid, which is responsible for most of the weight of fat depots, until later in life. The ratios of body component protein content to empty body protein content at maturity reveal that the majority of protein is partitioned into flesh similar to the majority of EBW being contained in flesh. The percentage of protein in blood at maturity is similar to the percentage blood is of EBW. An interesting comparison is the percentage viscera, bone and skin are of EBW versus the percentage of protein contained in these body components is of total empty body protein. A higher percentage of protein is contained in bone and skin while a reduced percentage is contained in viscera in comparison to whole weight percentages of these body components.

The quantity of ash contained in blood and viscera at maturity as well as the quantity contained in skin and flesh throughout development is less than 6% of the protein weight of all these body components. This reveals the small contribution that ash makes to the overall weight of these components. In contrast, the ash to protein ratio

at maturity for bone is close to 1, highlighting the contribution ash makes to bone weight. The estimated allometric coefficients indicate ash matures faster than protein in viscera but slower in bone and blood. The slower maturation of ash in bone can be attributed to the hardening of bone that occurs as animal's age. The faster maturation of ash in viscera could be explained by the requirement vital organs and tissues have for micro and macro minerals to allow them to produce enzymes, hormones, etc that are essential for normal body function. However, it would also be expected that this would apply to blood because of its requirement for micro and macro minerals e.g. iron to form haemoglobin.

The allometric coefficients estimated for water contained in the body components indicate that water matures earlier than protein in all body components. This pattern of maturation agrees with that found for the empty body in a number of species where water matures earlier than protein (Emmans and Kyriazakis 1995; McPhee and Trappett 1987; Moughan et al. 1990). The low allometric coefficient for bone indicates that initially a higher proportion of bone is made up of water but this reduces over time and supports the concept that hardening of bone occurs as animal's age. The other allometric coefficients also indicate that as an animal ages the percentage of water contained in these body components decreases. A similar pattern has been found to exist for the empty body and has been linked to the percentage increase in lipid that occurs with increasing age (Burton et al. 1974). The ratios of water to protein in the body components indicate that those body components with high metabolic activity contain higher proportions of water relative to their protein contents (e.g. flesh, viscera and blood) whilst those with lower metabolic activity contain lower proportions of water relative to their protein contents (e.g. bone and skin). These ratios also show that the contribution water makes to bone at maturity is similar to that made by both protein and ash.

The allometric coefficients estimated for lipid contained in the body components indicate that lipid matures later than protein in all body components. This pattern of maturation agrees with that found for the empty body in a number of species where lipid also matures later than protein (Emmans 1988; McPhee and Trappett 1987; Moughan et al. 1990; Thompson et al. 1985a). These findings also support the relationship between water and lipid content of the empty body illustrated by Burton

et al. (1974). The ratios of lipid to protein in the body components indicate the majority of lipid is being partitioned to viscera and flesh while smaller quantities are partitioned to bone and skin. This outcome is not surprising given that the major fat depots in the body are contained in flesh and viscera. Another interesting result, that is a consequence of the structure of the ChemDOM1 model, is that even though there is a large difference in lipid to protein ratios between viscera and flesh, the small quantity of protein in viscera limits total lipid in viscera to 45 kg if mature empty body protein content is 100 kg while approximately 160 kg of lipid would be present in flesh. This lack of flexibility seen when partitioning lipid between body components is the primarily the cause of the poor predictive performance of the ChemDOM1 model. The ratios of body component lipid to empty body lipid content at maturity used in the ChemDOM2 model, partition lipid in a similar manner to the allometric coefficients estimated in Table 4.7 and used in the ChemDOM1 model but contain more flexibility due to the interaction allowed between the mature protein and mature lipid:protein ratio parameters of the Amer and Emmans (1998) model. This approach allocates over 90% of the lipid contained in the empty body to flesh and viscera depots with the remaining lipid split between skin and bone.

The partitioning of flesh and bone between carcass and non-carcass depots was undertaken in somewhat of an arbitrary manner. The linear regression analysis revealed that 71% of bone contained in the empty body was contained in the carcass with the remaining 29% contained in the non-carcass regardless of the degree of maturity of empty body protein. This could be perceived as an inadequate simplification given that if animals were feed restricted then differential bone growth may occur (e.g. continued growth of the skull and spinal column while reduced growth may occur in other bones). However, for *ad libitum* fed animals this appears to be an adequate approach. The linear regression analysis of flesh in carcass and non-carcass produced results that indicate that the vast majority of flesh is contained in the carcass and changes little as protein matures in the empty body (Table 4.9). These linear regressions could also be perceived as inadequate simplifications given that lean tissue in the legs form part of an essential body component for movement. In animals that are under fed less tissue maybe lost from these depots than from other depots that are less essential for animal survival. Again for *ad libitum* fed animals these linear regressions appear to be adequate for this testing process. In

circumstances where animals are underfed, models similar to the ChemDOM approach may prove to be more appropriate for predicting how chemical body components are partitioned.

4.4.2. Validation of Body Composition Models

The R^2 values presented throughout the results section indicate that all the models have a high degree of fit to the body composition data. This is a consequence of two factors. The first is the maturity range over which animals were slaughtered in the NSW agriculture experiment. This produces as much or greater variation in any given trait due to changes in maturity as there is in that trait at a single degree of maturity. The second factor is the models base their predictions of body composition on estimated or measured EBWs. These weights remove any large scale error that maybe present in their predictions (e.g. difference between actual EBW and that that could be predicted by the models), leaving only the error associated with how the models partition body composition between depots. Thus the R^2 values presented above give an indication of the models abilities to predict body composition relative to each other.

The results from the initial testing process reveal that using actual measurements made prior to slaughter resulted in substantially higher accuracy. This result was expected and can be attributed to the error associated with estimating EBW with the growth model being passed onto the body composition models and consequently biasing their predictions. The EBW estimates made with the growth model were greater for every animal than the EBW measured prior to slaughter which is illustrated by the frame shift down seen between Figures Figure 4.5 and Figure 4.6. This result also highlights a shortcoming of the method used for obtaining body weight estimates from EBW predictions made by the growth model during the model fitting. The model uses the simple modification presented in equation (4.17) to estimate live weight from EBW. This is a simplistic approach to estimating total gut fill and has limitations particularly when dealing with non-uniform diets, such as pastures whose composition can change over space and time. The obvious step forward from this point is to employ modelling systems that take account of characteristics of the diet to predict gut fill, such as the models presented by Williams

et al. (1992b) and Song and Dinkel (1978a) that account for the percent crude fibre of the diet.

The initial testing process also compared the predictive abilities of the body composition models under both circumstances. The models maintained similar orders of predictive ability when either actual or model estimated EBW were used for predicting body composition. The results indicated that the models developed by Song and Dinkel (1978b) and the ChemDOM1 model perform at comparatively poor levels and were subsequently considered to be inadequate for predicting physical body composition.

The poor performance of the ChemDOM1 model can be partly attributed to its use of the mature lipid to protein ratio in each body component to predict lipid content of that component. This ratio relies on the relationship between lipid and protein content of the mature empty body ($\frac{L_m}{P_m}$) remaining constant, however this relationship has been shown to be independent of mature size (Emmans 1988) and is modelled as being independent by Emmans (1997). Thus when this ratio changes between genotypes these parameters no longer accurately describe the lipid-protein relationships within body components. For this reason ChemDOM2 was developed using the relationship between lipid and protein at maturity in each body component to the lipid and protein ratio of the mature empty body. This relationship is based on the premise that the relationship between mature empty body protein and the lipid content of a particular body component at maturity is constant regardless of the path followed to achieve it. Following the approach used in the ChemDOM1 model, at maturity, the lipid content of body component, i is modelled as:

$$L_{mi} = P_{mi}.Q_1 \quad (\text{kg}) \tag{4.22}$$

where Q_1 is the ratio of lipid to protein and P_{mi} is the mature protein content of component, i at maturity. P_{mi} is modelled by:

$$P_{mi} = P_m.Q_2 \quad (\text{kg}) \tag{4.23}$$

where Q_2 is the ratio of protein in the mature body component to mature empty body protein and P_m is mature empty body protein. An alternative method of relating mature component lipid content to mature empty body protein content is using:

$$L_{mi} = L_m.Q_3 \quad (\text{kg}) \tag{4.24}$$

where Q_3 is the ratio of lipid in the mature body component to mature empty body lipid and L_m is mature empty body lipid. L_m is modelled as:

$$L_m = P_m.Q_4 \quad (\text{kg}) \tag{4.25}$$

where Q_4 is the ratio of lipid to protein and P_m is the protein content of the empty body at maturity. As stated above the relationship between mature empty body protein and lipid content of a mature body component are constant regardless of the path followed making these approaches equivalent and upon simplification produce the relationship:

$$Q_1 = \frac{Q_3.Q_4}{Q_2} \tag{4.26}$$

where Q_1 represents the approach taken in the ChemDOM1 model but expressing it in the above manner allows it to become a function of the lipid to protein ratio of the mature empty body (Q_4) and thus, as this ratio changes, appropriate changes will occur in the ratio of lipid to protein of each body component (Q_1). The improved predictive ability shown by the ChemDOM2 model supports this development made to the ChemDOM1 model. The poor performance of the ChemDOM1 model is the result of the groupings in its predictions. In Figures Figure 4.5 and Figure 4.6 it can be clearly seen that the predictions made for flesh and non-carcass by this model form two distinct groups; over and under predictions. This grouping is linked to the mature protein (P_m) parameter in the Amer and Emmans (1998) model that is used in equation (4.9). This equation relies on a fixed relationship between protein and lipid content in the body and body components. This assumed relationship results the ChemDOM1 model predicting extremely large lipid contents of the body components for animals that have high estimated mature protein contents (P_m) (e.g. above a value

of approximately 90 kg). The opposite occurred for animals that had estimated mature protein contents below approximately 90 kg. This effect is not seen in the ChemDOM2 model's predictions due to the flexibility added by equation (4.10) which allows the estimated mature protein (P_m) and mature lipid:protein ratio (Q) parameters in the Amer and Emmans (1998) model to interact, diluting the effect that the mature protein parameter has on the prediction of body composition.

The poor performance of the models developed by Song and Dinkel (1978b) displayed above in Tables Table 4.10 and Table 4.11 is due to several factors. The regression coefficients used for predictions were those estimated by Song and Dinkel (1978b) and presented in their Tables 2, 3 and 4. Given these models are quadratic regressions then it is not a great surprise that extrapolation outside of their original datasets did not produce accurate predictions. The structure of the models, primarily the non-carcass model, could explain the downward bias seen in non-carcass predictions. Separable fat is used as one of the variables for predicting non-carcass and given there was an upward bias in flesh prediction then a bias in non-carcass predictions would be expected. In this case the bias is downward because the regression coefficients for separable fat are negative. Also, but possibly of minor importance, is the simplistic approach used for estimating gut fill in the growth model that could account for some small portion of their inaccuracy.

Following the removal of the ChemDOM1 model and the two Song and Dinkel models the remaining models were tested against four body components rather than three. Results from this comparison reveal that the manner in which body composition data was presented to test the models influenced the predictive ability of the ActEBW and DOM models (Table 4.11 vs Table 4.12, Table 4.13 vs Table 4.14 and Figure 4.5 vs Figure 4.6). However, the HDOM model performed comparably in both cases. To quantify this, the predictive ability of the ActEBW model improves when tested against four body composition traits where as the predictive abilities of the DOM and ChemDOM2 models decrease. In an attempt to explain this occurrence the abilities of the models to predict each trait used in the comparisons were tested (Tables Table 4.13 and Table 4.14).

When testing three traits (Table 4.13), the DOM and HDOM models have comparable predictive abilities across all traits. The predictive differences seen between Tables Table 4.11 and Table 4.12 are due to differences in predictive ability for remainder where the ActEBW model performs at an inferior level and the ChemDOM2 model's performance is slightly inferior again. Testing four traits (Table 4.14) reveals that the predictive abilities of both the DOM and ChemDOM2 models are inferior for both viscera and remainder to the abilities of either of the other two models. Inspection of the predictions for viscera and remainder made by these models indicate that when the traits are combined to form non-carcass, errors in predictions made by the DOM and ChemDOM2 models cancel out (i.e. errors are in opposite directions) where as errors in predictions made by the ActEBW model are additive in some cases (i.e. occur in the same direction). Both the DOM and ChemDOM2 models tend to consistently over predict viscera whilst under predicting remainder. The behaviour of these models could be explained by an autocorrelation between body components that is attributable to error associated with the division of the animals upon slaughter. However, if this were the case then it would be expected that the HDOM model would also behave in a manner similar to the other three models. The results in Tables Table 4.11 and Table 4.12 indicate that this model performs comparably irrespective of how the body composition data was presented for testing, thus suggesting such an error does not exist or does not have a large effect.

Tables Table 4.13 and Table 4.14 also illustrate the ability of each model to predict bone and flesh. Across all models flesh is predicted with the highest accuracy whilst bone tends to be predicted with the lowest accuracy. This is not unexpected given that the R^2 values generated during parameter estimation tended to be lower for skin and bone than the other traits. The explanation for this lies in the dissection data for skin and bone used to parameterise the models where the animal considered as mature in the experiment actually contained lower quantities of bone and substantially greater quantities of skin than animals of lower weight thus reducing the accuracy of parameter estimates. The rarity of datasets that contain such information for cattle is the ultimate limitation and development of datasets containing larger numbers of animals, particularly animals grown to maturity, would reduce the error seen in the parameter estimates made for skin and bone. However, the same quantity of data

produced higher R^2 values for flesh and viscera during the fitting process which were reflected in the higher accuracies of prediction for these traits.

4.4.3. General Discussion

The approaches taken in the DOM and HDOM models use the same basic allometric relationship. The HDOM model puts this relationship into a hierarchical structure where the empty body is sequentially partitioned until the body components at the lowest level of the hierarchy are reached. In contrast, the DOM model simply draws this relationship between the final body components and EBW. There is some degree of extrapolation occurring in the DOM approach and it was perceived that this could cause inaccuracies in the estimated allometric parameters. The allometry (*b* coefficients) between to two components of an animal is considered to be constant regardless of how it is estimated. This is illustrated in Figure 4.8 for bone and viscera using the allometric coefficients estimated for the HDOM and DOM models.

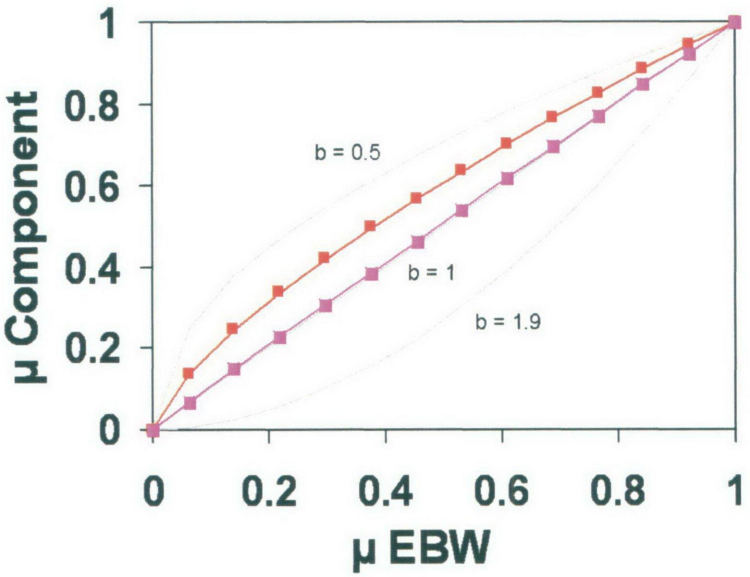

Figure 4.8: Comparison of the allometry of bone (red) and viscera (mauve) relative to EBW predicted from the DOM (squares) and HDOM (line) models with allometric coefficients (*b*) of 1.9, 1 and 0.5 (grey lines) also illustrated.

The greater predictive ability of the HDOM model in comparison to the DOM model shown in Tables Table 4.12 and Table 4.14 is thus not attributable to more accurate estimation of the allometric coefficients (b) as path to maturity for both body components for each model are identical (Figure 4.8). The improvement in accuracy of the HDOM model is due to less extrapolation when estimating the proportion each component is of the component above it in the hierarchy at maturity (e.g. Z_i in Table 4.2 vs Z_i in Table 4.3).

A perceived weakness of the current study could be the experimental data (Haecker 1920) used to develop and parameterise the body composition models. Firstly, the experiments were conducted using animals bred in the 1920's and it would be expected that body composition would have changed in the time up to 1986 when the first animals in the Trangie experiment were born. Given this possible limitation the models developed using this data, with the exception of the ChemDOM1 model, produced accurate predictions. However, this can not be taken to mean that the composition of animals has not changed over this period of time. Rather, the inferior performance of the ChemDOM2 model in comparison to the ActEBW, DOM and HDOM models could be taken to indicate that the composition of animals has changed, particularly chemical composition (lower lipid, higher protein) but any change has not greatly altered physical composition at higher levels in the hierarchy (carcass, flesh, total viscera). Identification of changes of this sort would require data where the empty body was sampled to a lower level (eg. flesh was sampled as lean and fat).

A second perceived weakness relates to the limitation discussed above, where the composition data limited how carcass and non-carcass components within each model were partitioned and subsequently parameterised. The experiment conducted by Haecker (1920) partitioned the EBW of animals into inedible offal, edible offal, skin, blood, flesh, bone, cartilage and tendon. The models were subsequently developed to partition the empty body into viscera, skin, blood, flesh and bone where viscera included inedible and edible offal, while bone included bone plus cartilage and tendon. An approach that would be of greater benefit for predicting physical body composition would be to partition flesh into lean and fat as well as partitioning viscera between organs and visceral fat. One possibility for developing models with greater

depth (i.e. models predicting more traits) would be analysis of information rich data sets (e.g. information on a large number of traits) that would allow allocation of an allometric network. Partitioning on this basis would result in body components being grouped on a developmental basis rather than on a physiological or functional basis, as undertaken here. An approach such as this presents the problem, as experienced in this study, of requiring equally rich data sets to validate all the components of any models developed.

The different approaches to using allometric equations that were tested in this study can be used as the basis for developing more comprehensive models for predicting physical body composition. The limitation exists that they have been developed and tested using data for animals that are considered to be fed *ad libitum* and thus were assumed to be expressing their full growth potential. As discussed by Thonney et al. (1987b), in conditions where animals are not able to display their growth potential some conjecture exists concerning the effect this has on allometric coefficients. Seebeck and Tulloh (1968a) found most allometric coefficients were similar in growing and fasted cattle with the exception of bone and kidney and channel fat, which were higher. Other studies have found significant differences in allometric coefficients for subcutaneous, intramuscular and kidney and channel fat between different feeding systems (Kempster et al. 1976). Thus it is expected that allometric coefficients vary with feeding level and thus the predictive abilities of the models developed above would be reduced if used to predict body composition of animals with restricted intakes.

This scenario was one of the drivers behind the development of the ChemDOM models, because animals not expressing their growth potential would have reduced protein or lipid deposition and perhaps even both. Partitioning protein in the empty body into protein contained in different body components and subsequently predicting the remaining chemical composition of the component was hoped to provide the first step in partitioning chemical components during constrained growth. The poor performance of the ChemDOM2 model relative to the ActEBW, DOM and HDOM models could be due to the chemical components within the empty body not being partitioned appropriately between body components as no consideration is given to diet quality. Models such as that developed by Soboleva et al. (1999) are able to

perform such a task, however this model is limited in that it only partitions the empty body into muscle, fat and viscera as well as only functioning sensibly at body weights above 150 kg. This model does however contain attributes that would be desirable to incorporate when developing models for predicting physical body composition using protein partitioning among body components. These attributes include taking account of the effect that feeding level has on visceral mass (Oltjen et al. 2000), the lag effect that occurs in animal metabolism following a period of restricted energy intake, that different tissues (viscera vs muscle) have different sensitivities to changes in energy supply and the growth of the tissues is driven by available energy/protein (Soboleva et al. 1999) not simply by its relationship to mature body weight or mature protein content.

4.5. Conclusion

The models presented for testing during this study use the allometric equation developed by Huxley (1932) in different ways to describe physical body composition. The aim of the testing procedure used was to compare the abilities of these models and the two models developed by Song and Dinkel (1978b) for predicting physical body composition. The HDOM model consistently produced accurate predictions and will consequently be used in chapter 6 for modelling physical body composition. The DOM and ActEBW models predictive abilities were not as consistent as the HDOM model, but were superior to the other models tested. The two models developed by Song and Dinkel (1978b) were considered inadequate for predicting body composition.

4.6. Recommendations

The major limitation of this study is all models tested ignore the impact that nutrition has on body composition as discussed in chapter 2. The allometric models developed in this study, particularly the HDOM model provides a mechanistic base from which a more comprehensive body composition model could be developed. The inclusion of how nutritional elements affect metabolic pathways would be paramount to developing a model with high predictive ability. Refinement of the HDOM model could follow a system similar to that explored in the ChemDOM models that partition body protein and other chemical components between physical body components.