Chapter 1: General Introduction

1.1 Introduction

Increased competition due to the globalisation of agriculture, greater quantities of available information and the need to adopt more sustainable farming practices have in part been responsible for an increase in the complexity of decision making associated with agricultural production (Newman et al. 2000). Meat production systems, in particular cattle and sheep production, have in recent times had to face the challenge of optimising their utilisation of inputs whilst maximising efficiency in contrast to past production goals of simply maximising output (Ball et al. 1997). Maximising efficiency is a function of the quantity of resources used to achieve a given production goal, making proper use of these resources, and having an appropriate production goal for the prevailing system. Consequently, not only does mismatching resources with desired outcomes have detrimental impacts on production but so does having desired outcomes that mismatch with the prevailing production environment (e.g. growing animals for inappropriate markets).

The vast number of decisions that could be made in beef cattle production systems all potentially have important impacts on production and thus efficiency. These decisions cover a large number of fields of expertise from genetics to nutrition through to management and marketing. The managers of beef enterprises are required to interpret and combine fragmented information coming from these disciplines in order to evaluate the risks that are associated with specific strategic decisions (Jenkins and Williams 1998). Optimising these decisions for a single enterprise to satisfy the desired outcomes of that enterprise with a high level of efficiency is not a simple logistical problem to solve. The problem becomes even more complex when these decisions are optimised across more than a single enterprise.

The outcomes of scientific research have combined the power of the human mind with computers to produce decision support systems (DSS) that assist the decision making process (Newman et al. 2000). The development of DSS such as GrazPlan (Freer et al. 1997), HOTCROSS (Newman et al. 1997) and the Feeding Standards for Australian Livestock (SCA 1990) have both increased the information available and facilitated

the use of this information for making animal production decisions. They do not however have the capacity to provide an indication of what decisions would be optimal and what decisions would not. In contrast, Total Genetic Resource Management (TGRM), a DSS developed in Australia for the purpose of optimising mate selection decisions, will optimally achieve the desired outcomes of a breeding program, that include genetic gain, maintaining genetic diversity, operational costs and logistical constraints (Kinghorn and Shepherd 1999).

Simulation models are used to describe the complex interactions that occur between environmental, digestive, physiological, genetic and metabolic elements that influence animal performance and cannot be feasibly analysed by either the human mind or traditional research methods (Baldwin 1976). Most animal production DSS are constructed around these types of models (Newman et al. 2000) and thus their success is dependent upon how indicative these models are of the system being modelled. Moving forward from TGRM and developing a DSS that optimises drafting, feeding, marketing, logistics and cost decisions rather than just simply breeding decisions would require a base model that was capable of modelling animal growth in a variety of prevailing production environments for a variety of different animal types. This DSS would help increase the efficiency of production by helping to utilise resources in the most appropriate manner and finding a production goal that is appropriate to the prevailing system. Such a DSS could also be used to help obtain some of the resources required to achieve a certain production goal, e.g. it could drive breeding decisions to obtain the genetic resources necessary for different market objectives.

1.2 Objectives

The objective of this thesis was to explore and contribute to solving issues that relate to the development of a DSS that is capable of optimising the types of decisions that are currently made during beef cattle production. The first issue explored is the type and availability of animal growth models that could potentially be used as the foundation for such a DSS. This included models that are capable of predicting whole body growth as well as body composition. Secondly, methods for estimating growth model input parameters appropriate for cohorts of animals were also investigated. Finally, a potential application of this DSS was explored to illustrate how it could be

used to allocate animals to different market endpoints in order to more appropriately use resources. These issues will be addressed in turn.

1.2.1 Available Growth and Composition Models

The development of mathematical equations for the purpose of describing animal growth is not a new science. The form such equations have taken has varied across the last two centuries with the earliest forms simply being single equations that were fitted directly to growth data as a function of time. The more recent modelling systems developed are an amalgamation of a series of equations that are capable of linking the animal to its surrounding environment and are capable of illustrating some of the complex interactions seen in production environments.

Perhaps the earliest, best known and most widely used growth function is that developed by Gompertz (1825). This equation simply draws an asymptotic relationship between live weight and time. It does not take any information concerning feeding, environmental stressors or physiological status into consideration and thus could be seen as representing potential rather than realised growth. Many other functions of this nature were developed in an effort to obtain a higher degree of fit to live weight data. The logistic function (Nelder 1961) uses a point of inflection at 0.5A (A =mature weight) compared to the 0.368A used by the Gompertz function. Brody (1945) developed a system that uses two equations rather than one and applies these either side of what other functions consider the point of inflection.

Attempts to increase the level of fit to realised growth data led to the development and application of functions known as multiphasic functions. These functions were developed on the premise that growth occurs in phases, cycles or spurts that are systematic departures from the smooth sigmoidal shape of growth assumed by the Gompertz function. Multiphasic growth has been attributed to environmental and nutritional changes at birth and weaning, hormonal stimuli of puberty, distinction between increases in cell number (hyperplasia) and increases in cell size (hypertrophy) and successive development of various tissues in a morphological and chemical sense (Koops 1989).

The realisation that factors other than time have important influences on growth and can be used to predict realised growth led to the development of growth simulation models. These models vary widely in how they represent growth and the type of information used to predict growth. The model developed by Parks (1982) uses a model similar to those discussed above but contains a parameter that represents feed intake, which is described by a separate function. It however does not give any consideration to the internal workings of animals or other environmental inputs.

It has long been recognised that the physiological processes that occur within an animal play an important role in growth. Systems were developed, such as the ARC (1965) and NRC (1970) nutrient requirement recommendations, to model these processes in an attempt to better understand how energy and protein are partitioned to most appropriately meet the maintenance and production requirements of animals. Although much research and development has occurred, these early efforts form the basis of many of the current day growth simulation models that are used for research purposes and by DSS.

The Parks (1982) model and those based on the ARC (1965) and NRC (1970) nutrient requirement recommendations use current body weight and some measure of mature weight as the basis from which a change in whole body weight is predicted. Estimates of chemical body composition can then be obtained by back-estimation from this weight change. Alternative methods use body composition as the basis for determining animal requirements as well as predicting growth when consuming a given diet, rather than back-estimating. This approach has taken two forms; one uses DNA content to make predictions while the other relies on chemical composition.

The model proposed by Baldwin and Black (1979) and further developed by Oltjen et al. (1985; 1986b) uses DNA accretion and energy intake to predict protein accretion as the difference between protein synthesis and degradation. Methods have been developed, which are both variations of this model and variations of the approach, to include digestion and metabolism components (Di Marco and Baldwin 1989), heat production (Oltjen et al. 2000) and partitioning into body components (Hoch and Agabriel 2004a; Soboleva et al. 1999). Alternatively, the body can be viewed from a chemical perspective, which is used as the basis for determining animal requirements

and the form growth takes. This approach has been successfully applied by Loewer et al. (1983b), Bridges et al. (1992a), Emmans (1997), Knap (1999) and Wellock et al. (2003a).

The characteristics of the system being optimised influence what form a model should take to be considered adequate for representing that system. The Australian beef industry supplies a variety of markets with different consumer needs in terms of carcass characteristics. Consequently, a model considered appropriate for this system would need to be capable of predicting physical composition. A relatively small number of models exist in the literature that are capable of partitioning the whole body into physical components. One approach combines a series of functions that were developed using multiple curvilinear regression analysis of various experimental datasets (Song and Dinkel 1978b). This system uses variables that included live weight, mature weight, degree of maturity and crude fibre percent (%) of diet amongst others. Another method, mentioned above, produced a model in a collaborative effort that partitions the body into viscera, muscle and fat pools in animals experiencing different nutritional conditions (Soboleva et al. 1999).

The models and functions briefly mentioned above are some of those available in the literature to describe animal growth. Each was developed and tested in its own environment and were generally shown to perform well in these circumstances. The overall usefulness of DSS and decisions made using information provided by DSS is dependent on the reliability of the animal growth models to give sensible results in any target production system. This requirement necessitates that the models available to describe animal feeding and growth be tested against both simulated and production data. Some of the models discussed above have not been tested outside their own development environment and would be expected to have a limited ability to predict performance outside such an environment.

The objective of chapter 3 was to test some of the growth models available in the literature against production data that included age and feed intake information, to assess their performance in circumstances foreign to their development environment. An attempt was made in chapter 4 to address the relatively small number of models available for predicting physical body composition. The objective was to develop a

number of approaches for predicting physical body composition and test these against those that are available.

1.2.2 Estimating Growth Model Input Parameters

The growth and composition models discussed above are only representative of what is perceived to be an 'average' animal and generally give little consideration to the between-animal variation that is inherently present in the world. Studies have found that the outputs from such models do not agree with the mean responses seen for cohorts of animals (Pomar et al. 2003). Thus, it has been argued that between-animal variation should be incorporated into growth models particularly when they are used for simulating production systems, predicting nutrient requirements or economic optimisation (Knap 1995; Pomar et al. 2003).

Incorporating such information into growth models is not an easy task given the difficulty associated with measuring the underlying physiological traits (Doeschl-Wilson et al. 2006) let alone measuring such traits repeatedly (e.g. mature protein content). However, methods termed "inverted modelling" (Knap et al. 2003) have been proposed as an alternative for estimating difficult to measure parameters. The form that such methods take is extremely important in terms of the accuracy of the parameter estimates obtained. The objective of chapter 5 was to test the speed and accuracy of different methods for estimating the mean and standard deviations of growth model input parameters along with testing the predictive accuracy of such parameters. The outcomes of this testing are very important because these parameterisations have direct impacts on the accuracy of model outputs which in turn influence the robustness of any production decisions made by a DSS.

1.2.3 Allocating Animals to Market Endpoints

The pressure coming from the globalisation of agriculture and the requirement for improved production practices to increase sustainability has resulted in the need for beef cattle production to increase efficiency in conjunction with more appropriate use of resources. The ability to predict what effect different management, nutritional and breeding decisions have on the growth and development of livestock within a

production system would greatly assist in the above outcomes being achieved. The growth and composition models tested in chapters 3 and 4 along with estimation of appropriate parameters (chapter 5) provide a means of predicting growth outcomes.

The optimal growth trajectory for any given animal in any given production system is a function of the available resources and management methods available for use. The ability to manipulate animal management has the capacity to greatly influence the production efficiency of any system. Drafting to (re)constitute different management cohorts is one mechanism that can be employed to meet the needs of the physical constraints of a production system (e.g. available pasture, number of paddocks and available feedlot places). The market end-point(s) being targeted also has an important influence on what is an optimal growth trajectory(ies). Drafting provides the opportunity to take advantage of variation in animal growth potential by allocating and growing animals to different end-points to meet different market specifications. In circumstances where the targeted markets are not appropriate for the prevailing production environment or the production ability of animals, the efficiency of production will be compromised.

The objective of chapter 6 was to present and use a method for drafting animals into different market cohorts based on their production ability. The decisions made by this method during the drafting process would be based on the predictions of animal growth made by a feeding and growth model, given a simulated production environment.

Chapter 2: Literature Review

2.1. Introduction

The push for modern agricultural enterprises to increase efficiency and profit while decreasing the impact they have on the environment has forced producers to shift their focus away from maximising production to meeting the requirements of the modern consumer. This literature review explores issues relating to the development of a system to aid in the forward planning and decision making associated with manipulating beef cattle growth trajectories to meet consumer demands in a sustainable manner. The characteristics of beef cattle growth in the Australian production environment are investigated in section 2.2 with some reference to other agricultural species. Section 2.3 describes how decision support systems have integrated information from specific research disciplines to help decision making and a system for solving complex problems using heuristics that can be applied to the manipulation of growth trajectories. Section 2.4 is dedicated to a description of the extensive number of functions and models that have been developed to describe both whole body growth and body composition. Chapter 3 tests the predictive capacity of five of the whole body growth models described and a polynomial model. Chapter 4 tests the capacity of the models developed by Song and Dinkel (1978b) to predict physical body composition in comparison to five alternate ways of using allometric equations. Section 2.5 describes attempts to arrive at optimal solutions for optimisation problems without the use of search methods (e.g. deriving algebraic solutions) and the success of one such attempt. Section 2.6 describes the issues associated with choosing a heuristic for solving complex problems while section 2.7 compares a number of deterministic and stochastic search methods. Section 2.8 gives numerous examples of where heuristics have been used in agricultural problem solving and their relative success. The conclusion is drawn that differential evolution (DE) is the most appropriate heuristic for optimising the manipulation of growth trajectories, and this is used in chapters 3, 5 and 6.

2.2. Characteristics of Animal Growth

Widdowson (1980) gives the simplest definition of growth as being an increase in size. In livestock this increase in size is associated with not only the production of

new cells (hyperplasia) but also the enlargement of existing cells (hypertrophy). Both processes are dependent upon the incorporation of components (nutrients and energy) from the environment. In circumstances where the environment is non-limiting an animal's observed growth pattern is often thought of as a consequence of its "genetic potential." This somewhat simplified description of growth provides a basic insight into the complex interactions that exist between the environment and an organism.

The process of growth is initiated at the time of conception and continues uninterrupted in an ideal environment until an equilibrium size (maturity) is reached where growth comes to a virtual standstill (Brody 1945). Such a pattern of growth follows a smooth uninterrupted path and is considered more of an exception than the rule in extensive Australian production environments. The growth patterns of most extensive livestock in Australia contain some form of interruption. These interruptions can be the result of nutritional restriction (eg. seasonal feed supply), environmental impacts (eg. extreme temperatures) and disease status (eg. tick infection in northern Australia).

In order to achieve their ultimate goal of reproducing, animals must grow to reach sexual maturity (Emmans and Kyriazakis 1999) by reacting in the appropriate manner to changes in their prevailing environment. The objective of this process is to react in a manner that allows the maintenance of a constant internal environment. In biological systems the term 'homeostasis' has been used to describe reactions that buffer against the changes that might be expected in non-living systems (Brody 1945). A change in environmental temperature is a good example as it does not always produce body temperature changes as thermo-regulatory systems are initiated to counter the external change. Cascades of physiological events are involved in such processes and help illustrate that animals do not operate in equilibrium conditions (Oddy et al. 1997a), in fact they are constantly attempting to adapt to a continually changing internal and external environment (Butterfield 1966).

These characteristics of growth and development are constantly at work influencing the form an animal takes at any particular time throughout its life. The success or failure of animal production is dependent on the form an animal takes at the point of sale and whether this meets consumer requirements. Thus the characteristics of growth, including body composition, are investigated primarily focusing on the impact nutrition has at different stages in an animal's life. Subsequent to this the discussion focuses on what modelling systems and search methods are available for locating the optimal use of nutrition and other resources when producing animals for numerous endpoints.

2.2.1. Pre-Natal Growth

The growth of an animal proceeds continuously from the formation of the zygote until birth. This process can be partitioned into three periods; these being the ovum, embryonic and foetal periods, depending upon the stage of development (Winters et al. 1942). The ovum period is the time between fertilisation and implantation where the embryo retains a spherical form. The following period is the embryonic period and in cattle it lasts until approximately day 45 of gestation. This period is the time during which cell differentiation occurs to form the major tissues and organs. The foetal period includes the time remaining from day 45 until the end of gestation. The primary function of the foetal period is the enlargement of the tissues and organs, which is a result of both hyperplasia and hypertrophy. Hyperplasia plays a more active role in the early gestation whilst hypertrophy becomes more apparent towards the end of gestation and in post-natal life (Robelin et al. 1991).

A normal pattern of foetal development is displayed in Figure 2.1. This pattern has a flattened sigmoidal shape that following mid-gestation progresses from an exponential phase to a rapid linear phase and then diminishes towards the end of gestation (Greenwood and Bell 2003). A developmental pattern similar to this is expected in the absence of genetic defects and environmental limitations with the exact shape being a function of both foetal and maternal potential. Also illustrated in Figure 2.1 is a retarded pattern of foetal growth. Nutritional restriction plays an important role during foetal development and has the capacity to cause these types of altered growth patterns depending upon the time of restriction. Severe nutritional restrictions during the last half to one-third of gestation are required for a reduction in foetal growth to occur (Holland and Odde 1992) as prior to this stage foetal growth in absolute terms is minor and the supply of nutrients is adequate (Widdowson 1980). It has been shown that nutritional restrictions of heifers until 140 days gestation (Cooper et al. 1998) and

of cows for the second trimester only (Freetly et al. 2000) had no effect on birth weight. In contrast, under-nutrition during both the second and third trimesters caused birth weight reductions of calves from heifers and mature cows (Freetly et al. 2000; Hennessy et al. 2002).

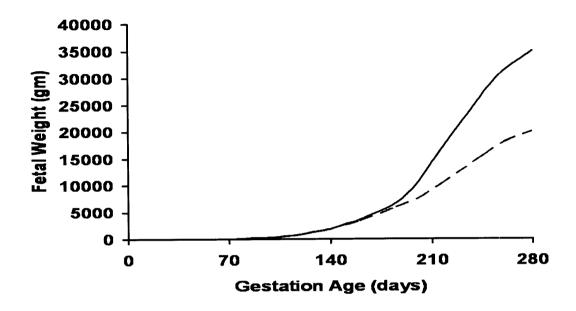


Figure 2.1: Normal (——) pattern of foetal growth in cattle adapted from the data of Winters et al. (1942) and a retarded (---) pattern of foetal growth.

The effects of nutritional restriction during prenatal development can influence both postnatal growth and mature size (Allden 1970; Widdowson 1977). Even though livestock have the ability to recover body mass postnatally given adequate nutrition, studies have illustrated that weight differences seen at birth remain at weaning (Hight 1968b) and post-weaning growth rates of prenatally restricted animals are lower than their unrestricted contemporaries (Greenwood et al. 2005). Pre-natal nutritional restriction has been shown to cause constrained appetite compared to non-restricted contemporaries and has been attributed to appetite centres in the hypothalamus being programmed during their development for small animal size and slow weight gain (Widdowson 1977). The detrimental consequences of pre-natal growth retardation on postnatal muscle growth capacity and visceral mass have been illustrated in sheep (Greenwood and Bell 2003). However, with adequate nutrition cattle have the capacity to overcome pre-natal growth retardation to attain equivalent body composition as non-restricted contemporaries at the same weight, although at older

ages (Greenwood et al. 2005). Small weaners can however become fatter at equivalent post-weaning weights if fed high concentrate diets. These potential consequences of nutritional restriction during gestation can have important influences on postnatal animal performance in terms of both absolute weight gain and body composition, as well as future milk production of females retained for breeding.

2.2.2. Post-Natal Growth

The new born calf undergoes the transition from a diet consisting primarily of glucose and amino acids to one that is consumed in greater quantities and contains proportionately more fat (Greenwood et al. 2005). During early postnatal life the diet gradually changes to include greater quantities of forage that result in volatile fatty acid and microbial protein production, which the animal becomes fully reliant upon after weaning. When these changes in diet and the available quantities pose no restriction on growth, an animal in a disease free, thermoneutral environment can be considered to be achieving its potential and in these circumstances growth is considered to follow a smooth S-shaped or sigmoid form as the animal ages (Emmans and Kyriazakis 1999; Koops 1989) (Figure 2.2).

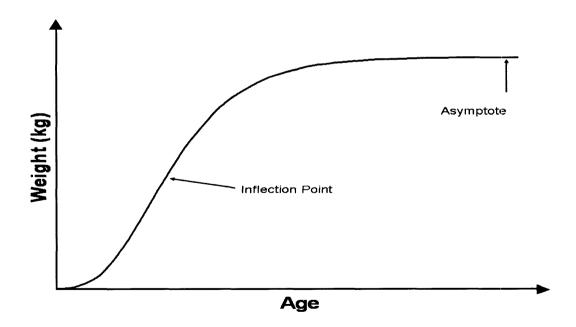


Figure 2.2: A sigmoidal curve representing growth beginning at conception when no restrictions are preventing potential from being reached.

Brody (1945) describes a growth pattern of this nature as being determined by two opposing forces and thus consisting of two segments; the first is termed the 'self-accelerating' phase where a growth-accelerating force is acting while the second is the 'self-inhibiting' phase where a growth-retarding force acts. The point where the two phases meet is termed the point of inflection (Figure 2.2). This represents the point where growth rate ceases to increase and begins to decrease; therefore the point where growth is most rapid and could be considered most economical (Brody 1945) in a simple system. The point of inflection is also when the change in acceleration of growth is zero representing the point where geometric and physiologic ages are equivalent and coincides with the interval that puberty has been shown to occur in numerous species (e.g. vaginal opening at 65 days of age in rats and between the ages of 12 to 15 years in humans (Brody 1945)). Following inflection the growth-retarding force becomes sufficient to overcome the growth accelerating force and exerts a counteracting influence on growth, limiting it and ultimately bringing it to a halt at an asymptotic weight (Figure 2.2).

Age or time is a convenient frame of reference to describe the changes that occur in an animal during development, but it is not the cause of these changes. It has been shown that body composition is influenced by bodyweight relative to mature weight (degree of maturity) to a greater extent, than by age (Berg and Butterfield 1976). The mass of the body is the sum of the organs and tissues which do not mature simultaneously (Owens et al. 1993). Rather, the growth rates of the various tissues and organs tend to peak in a regular sequence known as growth waves. These growth waves produce a general gradient that begins with the central nervous systems and finishes with adipose tissue. In terms of the whole body a gradient exists that moves from the head to the tail and from the extremities to the core (Batt 1980). Consequently the shape an animal's body takes changes continuously over time.

The changes of greatest interest to beef producers are those that occur in the quantity of saleable product as an animal matures. The order of maturation of body components as the whole body matures is bone, muscle and fat, respectively. Figure 2.3 illustrates that in cattle, muscle and bone decrease as a proportion of live weight with increasing maturity while fat increases. Patterns of component maturation similar to Figure 2.3 have been illustrated by Thompson et al. (1985a) for merino sheep and

by Butterfield et al. (1984b) for Dorset Horn sheep. Growth waves are not restricted to tissue groups; they exist within tissue groups, as tissues are not uniformly laid down throughout the whole body. For example, kidney fat is the first adipose depot to be established while the intramuscular fat depot is the last to mature (Batt 1980).

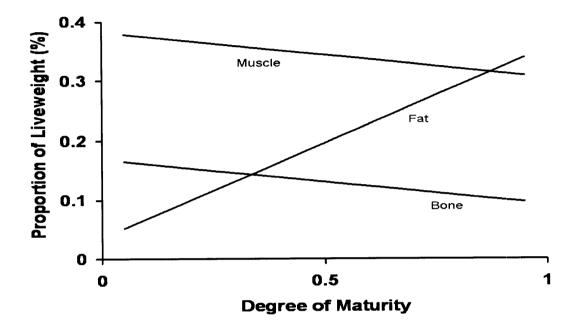


Figure 2.3: Changes in proportion of total body bone, muscle and fat with increasing maturity in body weight of British bred cattle (data taken from Moulton et al. (1922)).

2.2.3. Restricted Growth

Nutrition is the major non-genetic factor that influences both growth and mature body size of healthy, moderately active mammals in thermoneutral environments (Taylor and Murray 1987). The description of growth until this point has been focused on animals whose nutritional requirements are being fully met. Such a situation rarely exists as in most pastoral regions of the world animals encounter periods of undernutrition as a result of reductions in both quantity and quality of the available diet at some point during their life. It has long been recognised that nutritional restriction not only reduces growth rate, increasing the growing period (Berge et al. 1991; Crichton et al. 1959) but also influences body composition to differing degrees depending upon when and to what degree the restriction is imposed (Pálsson 1955).

The most direct and obvious effect of nutritional limitation on the productivity and efficiency of beef production is the extended time required for animals to attain marketable weights (Meadowcroft and Yule 1976). This has been clearly illustrated by Tudor and O'Rourke (1980), who grew two groups of Hereford calves to slaughter weights of 400 kg. Both groups were fed a diet consisting of reconstituted milk and a calf ration that allowed them to attain a daily weight gain of 0.7 kg/day up to 200 days of age. Following 200 days one group was fed a high energy diet containing a mixture of lucerne chaff and rolled sorghum while the other grazed Paspalum (Paspalum dilatatum) or Rhodes grass (Chloris gayana) pastures with supplementation from oat (Avena spp.) or wheat (Triticum spp.) crops, of a lower energy value. These diets produced dramatic differences in growth rates post 200 days with the intensively fed animals achieving 0.83 to 0.97 kg/day (depending on sex) while the pasture group achieved 0.36 kg/day (Tudor and O'Rourke 1980). The impact this had on finishing time was that the intensively fed group achieved a live weight of 400 kg in approximately 460 days while an additional 300 days was required by the pasture group.

The increasing pressure to meet quality specifications for beef markets means the impact nutritional restriction has on body composition has important implications for overall productivity. In the past there has been conjecture concerning the ultimate effect nutritional restriction has on body composition. The most commonly held view is that a decline in the rate of fat deposition occurs when restricted quantities of energy are supplied above maintenance whilst higher rates of lean deposition are maintained (Bass et al. 1990). The study of Murphy and Loerch (1994) supports this view where steers restricted to 80% of ad libitum feed intake maintained similar protein and water accretion rates as ad libitum feed animals but fat deposition rates were reduced. Consequently animals fed below ad libitum contain lower proportions of fat and higher proportions of lean and bone when compared to unrestricted animals at the same live weight (Bass et al. 1990; Wright and Russel 1991). This is also well illustrated by the data of Moulton et al. (1922) (Figure 2.4) who fed one group of animals to attain their ad libitum intake (a) while feeding a second group to attain a daily growth rate of ~0.25 kg (b) (Moulton et al. 1921).

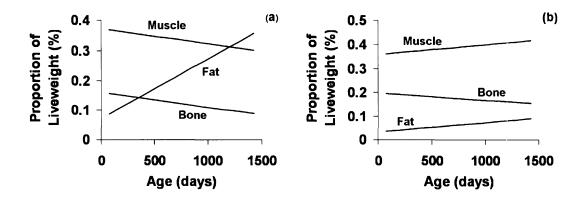


Figure 2.4: Changes in proportion of total body bone, muscle and fat with increasing age of British bred cattle when fed *ad libitum* (a) and restricted (b) quantities of the same diet (data taken from Moulton et al. (1922)).

An alternative view is that body composition is determined by body weight and is independent of nutritional history for animals of the same sex and breed (Black 1974). Kellaway (1973) found that body composition of sheep was not affected by their plane of nutrition when compared at similar body weights. In contrast other studies have found that nutritionally restricted animals contain higher proportions of fat but lower proportions of lean tissue (Baker et al. 1985). These differences in body composition are difficult to resolve but the ratio of protein to energy contained in the diets fed influence the rates of fat deposition relative to protein deposition (Black 1974). Biochemical studies have suggested that an inadequate supply of substrate (eg. amino acids) can limit protein synthesis (Bergen 1974). Studies in sheep have indicated that the quantity of available dietary protein may affect a growing animal's protein content, particularly during early growth (Ørskov et al. 1971). Wardrop (1966) has shown that the quality of the diet fed immediately post partum has important impacts on body composition. In this study calves suckled by their mothers contained higher proportions of fat and lower proportions of bone compared to those raised on two milk replacer diets. Grings et al. (2001) has shown animals that receive higher quantities of undegradable protein had higher weight gains from weaning to 386kg live weight. The stage of maturity when restrictions are applied as well as the duration and severity of the restrictions also contribute to differences seen in body composition (Carstens et al. 1991).

2.2.4. Weight Stasis

As the severity of a nutritional restriction increases an animal will reach a stage where it is unable to increase live weight and thus growth becomes stagnant. During such periods of restriction changes in body composition primarily involve a reduction in the proportion of visceral tissue, particularly those with high metabolic activity (e.g. digestive tract and liver) (Foot and Tulloh 1977). Changes of this nature have been linked to a reduction in maintenance requirements (Kellaway 1973) and consequently a decline in the quantity of feed required to maintain live weight in animals with positive growth rates prior to restriction (Foot and Tulloh 1977; Turner and Taylor 1983). The decline in visceral mass must equal the increase in carcass weight in order to allow body weight to be maintained. The carcass composition changes that occur are thought to primarily involve the fat depots with little effect on the lean or muscle mass of immature cattle and sheep (Murray and Slezacek 1988; Murray et al. 1974). However, it has been shown in the study of Afonso and Thompson (1996) that ewe and ram lambs increased both muscle and fat proportions while a reduction in visceral mass was occurring. This study also demonstrated that fat utilisation from the subcutaneous fat depot occurs relative to the intermuscular and internal depots during periods of weight stasis. Contrastingly, in steers fed maintenance rations the kidney and channel fat decreased in size while the carcass fat was not utilised (Murray et al. 1974). The general effect of weight stasis on animals is thought to be a reduction in viscera and internal fat with an increase in carcass fat whilst muscle mass remains relatively unaffected (Ball et al. 1997).

2.2.5. Weight Loss

When nutritional restrictions continue beyond the point where sufficient quantities of nutrients are not supplied to support maintenance needs animals are forced to mobilise their own tissue thus losing weight. The marked fluctuations in both pasture quantity and quality seen throughout the northern pastoral regions of Australia (Norman 1963) produce a 'saw-tooth' pattern of growth where animals gain weight during summer but lose weight in winter in order to maintain themselves (Norman 1965). Joubert (1954) has also demonstrated the seasonal fluctuations in pasture production and quality as well as the subsequent effect on animal growth in the Bankenveld region of South Africa.

The ultimate effect that weight loss has on body composition is dependent upon the rate that which weight loss occurs. Searle et al. (1972) illustrated higher rates of weight loss increase the level of lean tissue mobilisation whereas lower rates of weight loss increase fat mobilisation. During periods of severe nutritional restriction there appear to be two phases of tissue mobilisation that occur during weight loss. Initially, lean tissue from the visceral organs is mobilised, however as weight loss progresses this is partly replaced by lean tissue loss from the carcass (Searle et al. 1979; Thornton et al. 1979). The second stage of weight loss involves a reduction in the rate of lean tissue mobilisation from the viscera and carcass in conjunction with an increased rate of fat mobilisation from the body (Aziz et al. 1992). Some conjecture exists as to which fat depots are mobilised during this phase of weight loss. Seebeck (1967) has found in young steers that kidney and channel fat is mobilised at a faster rate than the other carcass depots. In contrast, others have found that depletion of the subcutaneous fat depot occurs whilst the visceral depots tend to remain unaffected (Butterfield 1966; Seebeck 1967).

Ultimately a gradient exists in the mobilisation of tissues during severe nutritional restriction. Initially during weight loss animals of similar weight will be comparatively fatter than continuously fed animals but as the nutritional restriction progresses mobilisation of tissue shifts to the adipose depots and these animals will become comparatively leaner. Another result of nutritional restriction is the proportionally higher quantity of bone contained in the carcass compared to continuously grown animals. Figure 2.5 illustrates the percentage changes that occur in muscle, carcass fat and bone weights relative to their respective weights prior to a grow-on period for merino wethers that were initially grown from 23 kg to 33 kg and then fed to lose 10 kg in 75 days (Aziz et al. 1992). These wethers were still in the initial phase of weight loss having lost proportionally more visceral mass than fat mass when this experiment ended. They are comparatively fatter than the animals slaughtered prior to the grow-on phase with similar proportions of muscle and higher proportions of bone.

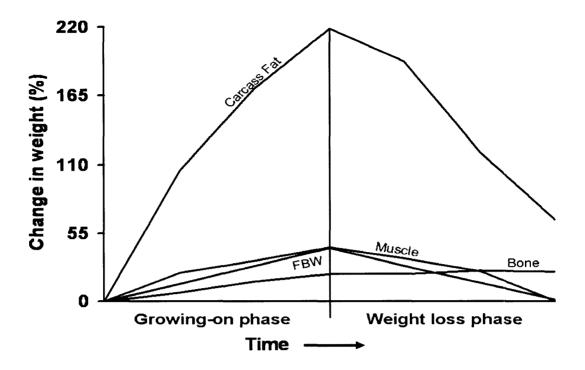


Figure 2.5: Percentage changes in weights of muscle, bone, carcass fat and full body weight (FBW) following grow-on (approximately 55 days) and weight loss phases (75 days) of merino wethers, relative to their weights immediately prior to the growing-on phase, modified from Aziz et al. (1992).

Figure 2.6 illustrates the percentage changes that occur in muscle, carcass fat and bone weights relative to their respective weights prior to a grow-on period for Angus steers that lost 13% of their full body weight at a rate of 0.5 kg/day that required a period in excess of 70 days to achieve (Seebeck and Tulloh 1968b). In comparison to the wethers in Figure 2.5 it can be seen that by the end of this experiment these steers had already moved through the first phase and into the second phase of weight loss. These steers had lower percentages of muscle and fat but a higher percentage of bone compared to continuously grown steers of the same weight that were slaughtered prior to the grow-on phase.

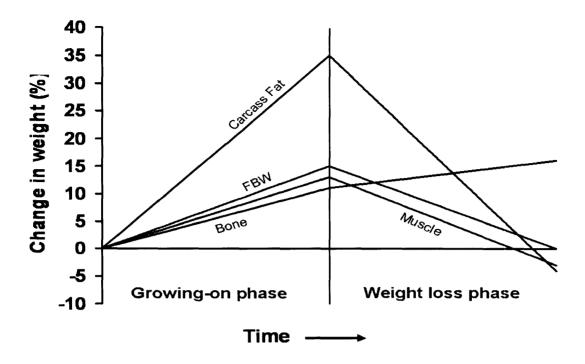


Figure 2.6: Percentage changes in weights of muscle, bone, carcass fat and full body weight (FBW) following grow-on (in excess of 40 days) and weight loss phases (in excess of 70 days) of Angus steers, relative to their weights immediately prior to the growing-on phase, modified from Seebeck and Tulloh (1968b).

2.2.6. Realimentation

An immediate increase in body weight is seen when the feed resources available to animals that have experienced nutritional restriction, weight stasis or weight loss are increased. The size of the increase in body weight is a direct consequence of the level of available feed resources. When a restriction is completely removed, animals that have experienced retarded growth exhibit growth rates that are greater than those of unrestricted animals with the same chronological age (Wilson and Osbourn 1960) (Figure 2.7 and Figure 2.8). This growth phenomenon has long been recognised in higher order animals and was given the name of 'compensatory growth' (Bohman 1955). The seasonal variations in pasture growth and quality in northern Australia makes compensatory growth economically important because it allows animals in such areas to grow and fatten. During spring in the southern pastoral areas of Australia it has been shown that compensatory growth is more economically efficient than supplementary winter feeding (Bennett et al. 1970).

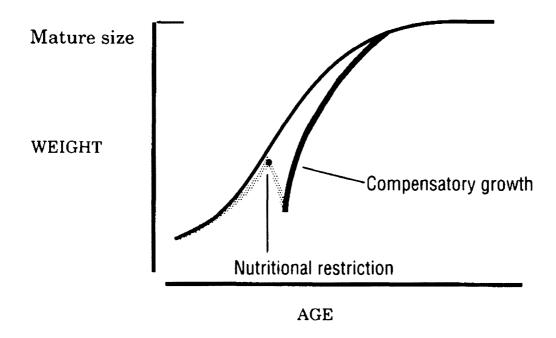


Figure 2.7: An example of compensatory growth where an animal has recovered its weight-for-age and subsequently followed an *ad libitum* curve (modified from Hogg (1991)).

The importance of compensatory growth to beef cattle production has attracted much interest from the scientific community. In their reviews of compensatory growth, Wilson and Osbourn (1960) and Hogg (1991) have highlighted a number of factors that influence the degree to which compensatory growth occurs. These factors include animal age when the restriction begins; the severity, duration and nature of the restriction as well as the diet used for realimentation and the quantity of time that is available (Owens et al. 1993). Nutritional restrictions for short periods of time, such as that depicted in Figure 2.7, or restrictions at a high degree of maturity may not have large detrimental effects on growth or composition. Limited reports have indicated that animals are able to recover their weight-for-age following restriction and then follow *ad libitum* growth paths (Thornton et al. 1979) with it being evident that compensatory growth alters composition during the growth period with little effect remaining at maturity (Owens et al. 1993; Widdowson 1977). However, the commonly held view is that even though animals may express compensatory growth, they prolong their growth period (Wilson and Osbourn 1960) and continue to grow

after unrestricted contemporaries have ceased growing (Allden 1970; Berge et al. 1991; Crichton et al. 1959) (Figure 2.8).

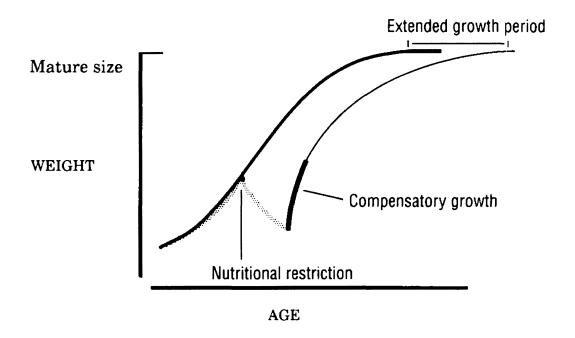


Figure 2.8: An example of compensatory growth most commonly seen where the growth period of the animal is extended (modified from Hogg (1991)).

Even though compensatory growth may occur upon realimentation, when feed requirements are not met at critical times of an animal's development then carryover effects on production can be extremely important (Hight 1968a). A commonly seen consequence of very severe, prolonged nutritional restriction is that an animal is not able to catch up growth and the longer the restriction lasts the less complete any catch up is (Widdowson 1980). The ultimate consequence of a restriction of this magnitude is an animal will attain a mature body weight lower than would otherwise be expected (Figure 2.9), which has consequences for both the animal's potential to meet market requirements if it is a slaughter animal and the reproductive capacity of the animal if it is a heifer retained for breeding purposes. Wardrop (1966) and Hennessy and Morris (2003) have suggested that nutritional deprivation in the first few weeks of life can have permanent detrimental effects on the occurrence of compensatory growth.

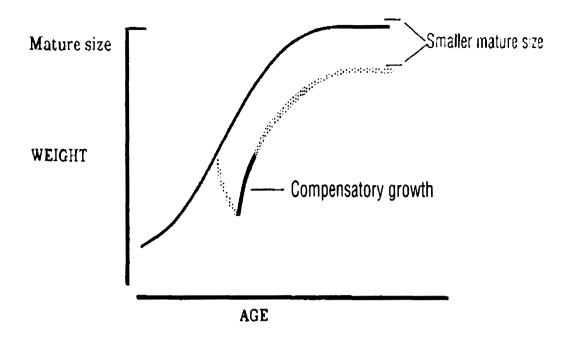


Figure 2.9: Permanent stunting as a result of nutritional restriction where the animal does not reach the expected mature weight (modified from Hogg (1991)).

Realimentation of restricted animals has been associated with an increase in feed intake in comparison to unrestricted animals (Bohman 1955; Graham and Searle 1979) which has been identified as one factor contributing to the increased growth rates seen during compensatory growth (Allden 1970). There are some reports however where no differences in feed intake upon realimentation have been seen between restricted and unrestricted animals (Foot and Tulloh 1977). The extent to which an elevated feed intake persists partially controls how long and to what extent compensatory growth is expressed. Compensatory growth is in turn related to the level of the previous stress and to how quickly an animal is able to adapt to a new feed environment (Hogg 1991). The physical form feed takes has been shown to play an important role in the time animals require to achieve normal feed intakes (Wright et al. 1986, 1989).

An additional benefit associated with restricted growth when animals are returned to *ad libitum* feeding is the reduced maintenance cost and fasting heat production (Graham and Searle 1975, 1979). This decrease is influenced by the severity of the nutritional restriction with greater nutritional restrictions producing greater decreases

in the maintenance requirement (Hogg 1991), which in turn has been linked to an increase in growth efficiency. Carstens et al. (1988) gave a maintenance requirement of 140 kcal/EBW^{0.75} for cattle exhibiting positive growth whilst reporting cattle at the point of realimentation have a maintenance requirement of 123 kcal/EBW^{0.75}. However, this improved efficiency is only transient due to maintenance requirements and heat production both increasing rapidly as compensatory growth progresses. This is a predictable response given that protein deposition occurs rapidly in the metabolically active visceral organs during early compensatory growth (Webster 1980). It has been suggested that this period of improved efficiency can last as little as one month in lambs (Graham and Searle 1979).

The increase in growth efficiency is not the only consequence of compensatory growth; there are also important outcomes in terms of body composition. Both the increased feed intake and higher rates of growth during the compensatory period have been associated with an increase in the percentage of body fat (Widdowson 1980). Widdowson (1980) has also found this is more prevalent in animals that have experienced longer periods of nutritional restrictions and when catch-up growth is less complete as a result of severe restriction. Allden (1970) also indicated fat is the quickest tissue to respond to high nutrient intakes immediately following realimentation but that this effect is only transient and is lost in later life.

A contrasting view of compensatory growth has been reviewed by Ball et al. (1997). This view proposes that several discrete stages of compensatory growth exist (Wright and Russel 1991) where the initial stage is primarily associated with a high rate of protein deposition in the visceral organs, including the digestive tract (Drouillard et al. 1991a; Drouillard et al. 1991b; Williams et al. 1992b). Other studies have also shown that protein deposition occurs at higher rates during early compensation (Searle and Graham 1975; Wright and Russel 1991), which therefore produces leaner animals at this stage of compensation. The proposed second stage of compensation involves a higher level of fat deposition following visceral organ replenishment and has been shown to allow animals to achieve similar body compositions to unrestricted animals (Wright and Russel 1991). However, it has also been shown that compensatory growth produces differential fat partitioning in compensating animals. Hayden et al. (1993) suggested that feed restriction had a greater effect on internal fat depots

compared to later maturing depots (subcutaneous and intramuscular) which accumulate lipid during the later stages of compensatory growth.

The disparity between the view held by Widdowson (1980) and that reviewed by Ball et al. (1997) can be attributed to a number of factors; these include the nature and length of the restriction, the time allowed for the feed restriction to be overcome i.e. the amount of time the animal spends in the second stage of compensatory growth and the tissues most affected by the restriction. Ball et al. (1997) ultimately draw the conclusion that when given adequate periods of time to recover no difference exists between the body composition of restricted and continuously grown animals (Everitt and Jury 1977; Reardon and Everitt 1972). They also point out special cases primarily associated with severe restriction where attainment of normal body composition is not possible and attribute it to the viscera, particularly the liver, not fully compensating, altering endocrine control and substrate supply for tissue deposition.

The nature of the restrictive diet and the realimentation diet also play an important role in the extent of compensatory growth and final body composition. In both lambs and steers, Drouillard et al. (1991a; 1991b) have indicated that compensatory growth occurs to a greater extent when it follows energy restriction rather than protein restriction. The ratio of protein to energy contained in the realimentation diet would be expected to influence protein and fat deposition rates during compensatory growth in a similar manner to the effect they have during restricted growth. Protein deposition rates in muscle and skin have been increased when amino acid supply is high relative to energy at low energy intakes (Hegarty et al. 1994; Oddy et al. 1994), which would facilitate protein deposition in these depots during compensatory growth at the expense of fat deposition. This effect is however lost as energy supply is increased and, due to amino acid oxidation, can result in increased fat deposition (Oddy et al. 1997b), producing excessively fat animals if a high protein diet is used for realimentation.

2.2.7. Other Environmental Factors

Although available nutrition has an important influence on the growth and development of animals, Batt (1980) suggests that environmental temperatures have

just as important an impact. The endothermic nature of livestock means they are constantly reacting to their external environment in an attempt at maintaining homeostasis. Only a narrow temperature range exists in which animals are able to survive and within this an even narrower range exists where growth and development are able to occur optimally (Batt 1980). This zone is the ambient temperature range where body temperature is maintained by sensible heat loss only (The Commission for Thermal Physiology of the International Union of Physiological Sciences 2001) and has been termed the thermoneutral zone.

The lower boundary of the thermoneutral zone is termed the lower critical temperature which is the ambient temperature below which an increase in heat production using processes such as shivering is required to maintain body temperature (Yousef 1985). This increases the activity level and thus nutritional requirements of an animal which to some degree can be met by increased feed intake (Batt 1980). The upper end of the thermoneutral zone is termed the upper critical temperature. Above this ambient temperature evaporative heat loss processes such as sweating and panting are employed to maintain body temperature (Yousef 1985). Temperatures above this level result in reductions in feed intake which decrease the amount of feed related heat production and thus total heat production. This is commonly seen throughout Australia where the decreased feed intakes and growth rates of growing animals are a result of increased summer temperatures. Thompson et al. (1985b) have attempted to model feed intake and growth rates by superimposing a sine curve over Parks's (1982) feed intake function to account for annual temperature oscillations in western New South Wales.

Many other environmental stresses exist that animals are required to cope with in order to maintain homeostasis and continue to grow. Micro-organisms and parasites are one other important environmental factor for grazing livestock. These organisms have the capacity to slow growth and increase the quantity of feed required to attain a given body weight in comparison to animals raised in sterile environments. In some cases growth rates of birds raised in sterile environments have been increased by 10% (Batt 1980). Other environmental factors have also been implicated in the growth and development of animals from conception to maturity; including light, social stress, atmospheric pressure and seasonal influences (Batt 1980; Holland and Odde 1992).

All environmental factors have important impacts not only on growth but also body composition. It has been shown that calf birth weights were increased by 3.1kg when Holstein cows in Florida are provided with shade (Collier et al. 1982). Andreoli et al. (1988) showed that severe cold stress reduced birth weights of calves from heifers by approximately 5.5kg compared to heifers maintained in thermoneutral temperatures. As discussed earlier, restrictions in birth weight of this nature can have detrimental effects on the growth period of cattle and thus overall production efficiency. Permanent growth retardation, comparable to nutritional restriction, can result from exposure to severe cold temperatures early in post-natal life (Batt 1980). In response to decreased temperatures heat production is initially increased by catabolism of triglycerides in adipose tissue with muscle becoming a considerable energy source as the temperatures become more severe or sustained (Batt 1980). The natural growth patterns of animals can also be altered by rearing in cold climates. The large subcutaneous fat quantity of species living in cold climates used for both insulation and energy storage is a good example.

2.2.8. Practical Implications

The characteristics of growth and their interaction with nutritional and other environmental influences discussed above are issues that are dealt with by animal producers on a daily basis. In order to meet customer requirements at the point of sale producers must correctly interpret what the consequences of nutritional and environmental influences will be on growth and body composition. If these consequences are detrimental to the production system then decisions need to be made concerning both whether a correction is required or can be made and if so, what form the correction needs to take. The review of Allden (1970) focuses on the consequences of nutritional deprivation to productivity. The reviews of Owens et al. (1993), Murphy and Loerch (1994), Sainz et al. (1995) and Ball et al. (1997), the later of which describes how market requirements can be met using nutrition to manipulate body composition, are testament to the importance of these types of decisions to livestock production as a whole and beef cattle production in particular.

2.3. Decision Support Systems

The decisions made in agricultural production require producers to convert and integrate information developed in specific, fragmented agricultural research disciplines (Jenkins and Williams 1998). Rarely is research directly integrated into whole farm systems but when implemented, producers need to determine what changes are required to achieve the greatest benefit (Olney and Kirk 1989) and evaluate the risks associated with such decisions (Jenkins and Williams 1998). The strategic decisions made in beef enterprises concerning mating systems, feeding programs, genetic resource use and market endpoints are all influenced by animal growth. The influence nutritional and environmental factors have on animal growth are complex and difficult to comprehend when studied in isolation. This complexity is further increased in a production environment where these factors act in unison.

Dealing with the levels of complexity seen in beef enterprises when attempting to make decisions is a challenging task. Intelligent support systems are computer based systems that have been developed in an attempt at assisting problem solving (Lynch et al. 2000) and decision-making (Newman et al. 2000) of this nature. Intelligent support systems include expert systems and decision support systems (DSS) that contain different levels of complexity. Expert systems are used to solve problems at levels considered equivalent to human experts or specialists in a field and are capable of giving an explanation of the reasoning process. In contrast, decision support systems use quantitative rules rather than qualitative reasoning and place more responsibility on the user for solving the problem (Lynch et al. 2000).

Numerous decision support systems have been developed for assisting in agricultural production with varying success rates. One DSS that has had some success in Australia is the GrazPlan DSS (Donnelly et al. 1997) targeted at the grazing industry to allow more effective transfer of research findings. GrazPlan contains modules such as GrassGro (Moore et al. 1997) and GrazFeed (Freer et al. 1997) that can be used as independent DSS for aiding pasture production and animal growth/feed formulation decisions, respectively. Other DSS developed within Australia include Total Genetic Resource Management (TGRM) (Kinghorn and Shepherd 1999) for optimising mate selection and HOTCROSS (Newman et al. 1997) for combining selection and

crossbreeding to meet an array of potential markets. Numerous other DSS have been developed but are not discussed here.

All problem solving processes, including DSS, involve two separate general steps: the first is the creation of a model of the problem and the second is generation of a solution with this model:

Problem
$$\rightarrow$$
 Model \rightarrow Solution (2.1)

(Michalewicz and Fogel 2000). Models are required as a simplification of the real world, otherwise the natural setting's complex and unwieldy nature make problem solving untenable. Sanders and Cartwright (1979a) recognised this fact during development of the Texas A&M University model (TAMU) and indicated that wiser decisions will be made with the aid of models than are otherwise possible. This also highlights the fact that every time a problem is solved in reality the solution is only the solution in terms of the model. If a model has a high degree of fidelity then more confidence can be placed in the solution being meaningful in real world terms (Michalewicz and Fogel 2000). Models containing many unfulfilled assumptions and rough approximations may produce solutions that are sub-optimal and possibly even worse than simple intuitive decisions. The transportability of a model is an important attribute that is intricately linked to its successful application in the real world. Models that have been developed using a statistical data fit could be considered naïve because they have no knowledge of the system being represented. These models may contain implied assumptions that were part of the fitting data set and are inappropriate when the model is used outside this context. In contrast, a systems or biology model that may not have as greater statistical fit but has been biologically inspired is more desirable due to the higher likelihood that it and any intrinsic assumptions it contains are valid in scenarios that are outside the original developmental dataset(s), but inside the nature or scope of the model.

Even when models are used as simplifications of the real world, the problems they are used to solve may not become any simpler. To solve more complex problems many heuristics have been developed ranging from algorithms that search every possible solution (exhaustive search) to those that mimic the processes of evolution

(evolutionary algorithms) to only search the more appropriate areas of the solution space. Michalewicz and Fogel (2000) outline three concepts that every algorithmic approach for problem solving should follow. These include: 1) the representation, 2) the objective and 3) the evaluation function. The evaluation function is effectively the model representing the problem to be solved that is able to indicate the quality of a solution or at least allow comparisons of multiple solutions. The representation and objective are characteristics of the heuristic. The representation is how alternative solutions are encoded to allow manipulation during the search procedure while the objective is simply the purpose of the search contingent on any constraints. This can involve maximisation (e.g. maximising production) or minimisation (e.g. reducing costs) or both (e.g. TGRM maximises a function that among other things increases genetic gain whilst decreasing inbreeding).

Manipulation of animal growth trajectories via nutritional manipulation is a highly complex task that is not easily performed without some sort of decision aid. The available decision aids, which range from basic feed nutrition tables through to the more complex GrazPlan DSS, can aid the decision making process associated with nutritional manipulation but they do not have the capacity to perform manipulations in an optimal manner to maintain and/or improve both biological and economic efficiency. The concepts outlined by Michalewicz and Fogel (2000) above are pertinent to this problem. A model is required that is capable of accurately representing animal growth under nutritional conditions present throughout the Australian production environment, and a means of determining the most appropriate growth trajectories using this model is also required. In order to obtain realistic outcomes from an optimisation process such as this, the model selected is required to operate sensibly in all given circumstances, which may require the presence of internal constraints (eg. maximum physical feed intake). The following sections of this literature review will be focused on these two questions, what growth models are available and what heuristics are capable of performing the task of growth trajectory optimisation.

2.4. Growth Functions

Using mathematical equations to represent the growth of animals is not a new concept, with many different forms having been developed and tested in the last two centuries. These mathematical formulations can be categorised into two distinct groups: functions and simulation models. Functions generally describe growth with a single equation whilst simulation models use a series of equations that can include a base function to model the interactions between growth, nutrition and the environment.

2.4.1. Empirical Functions

A plethora of functions is available for predicting potential animal growth with each using different approaches to draw an asymptotic relationship between weight and time. The Gompertz (1825) function is perhaps one of the best known and widely used functions for predicting potential growth (Richards 1959). The function relies on a growth rate parameter and transformed degree of maturity at time, t = 0 (may not be age = 0) to predict the relationship between weight and time. Another characteristic of the Gompertz function is the location of its point of inflection at 0.368*A* (*A* = mature weight) to increase flexibility compared to the logistic function (Robertson 1908), whose point of inflection occurs at 0.5*A*. The logistic function uses a linear decline of the relative growth rate, similar to the Gompertz (1825) function to predict the relationship between weight and time.

The von Bertalanffy (1957) function predicts weight given time by using the allometric relation that exists between weight and an animal's metabolic rate during growth. The function achieves this by making anabolism proportional to the m^{th} power of weight, catabolism proportional to weight and estimating the slope (m) of the allometric line between anabolism and catabolism somewhere between 2/3 and unity. Richards (1959) argues the assumption of m being restricted between 2/3 and unity is incorrect as values exceeding unity are needed if the function is to have wide empirical applications. Richards (1959) states the growth rate becomes that of the Gompertz function as $m \rightarrow 1$ and the logistic (Robertson 1908) function when m > 1. Consequently, the point of inflection is also determined by the value assigned to m.

The function developed by Brody (1945) however does not contain a point of inflection but instead divides the growth trajectory into two stages at the point other functions would consider the point of inflection, t. Brody (1945) concluded t was sufficiently near to the age of puberty that the discontinuous growth rate was an animal's physiological change from being vegetative to being procreative. The portion of growth prior to t was subsequently termed self accelerating and the portion following self decelerating. However, there is not necessarily any biological significance about the point of inflection of the growth curve, as it is a mathematical inevitability that such a point should exist because animals do not continue to grow indefinitely.

For a wide range of domestic species, Brody (1945) has presented a table that contains estimates of mature weight (A), maturing index (k) and time origin (t^*) of the fitted curve. Brody (1945) also indicated that the age when animals reach different degrees of maturity was related to their maturing interval (τ , also $\frac{1}{k}$). Although it is evident that Brody was aware of the interspecific relationship between mature size and age to maturity, this aspect of his work was never fully developed (Taylor 1965). Günter and Guerra (1955), using their theory of biological similarities concluded all time factors in biology are dependent on weight to a power that lies between the values of 0.16 and 0.33, with 0.31 being the most applicable. Their regressions for weight (kg) on age (months):

$$t_{0.98} = 14.7A^{0.255}$$
 and $t_{0.5} = 4.3A^{0.245}$ (2.2)

where A is mature weight and t_x is age at degree of maturity x, produced power coefficients that fall within this interval but are significantly less than the suggested 0.31. Not satisfied with this suggestion having general applicability for the time taken to mature and these regressions being insufficient to substantiate a general empirical relation, Taylor (1965) referred back to Brody's original data table in an attempt at substantiating an empirical relationship between mature weight and time to maturity.

Taylor (1965) using the mean of $\log \tau$ and $\log A$ for the 11 species in Brody's table obtained the regression coefficient, 0.286 ± 0.047 as illustrated in Figure 2.10. Upon inspection of the data Taylor identified the human species (highlighted in Figure 2.10) as a "noticeable deviant". The regression coefficient became 0.265 ± 0.035 , subsequent to the human data being excluded and 0.259 ± 0.028 subsequent to pigeon data also being removed. The value of 0.27 ± 0.04 was adopted by Taylor (1965) as the most satisfactory representation of the relation between mature weight and time to mature from the information he had available. Further analysis using Brody's time origin parameter (t^*) revealed it is also proportional to approximately the same power of weight, i.e. both t^* and τ vary with the 0.27^{th} power of mature weight.

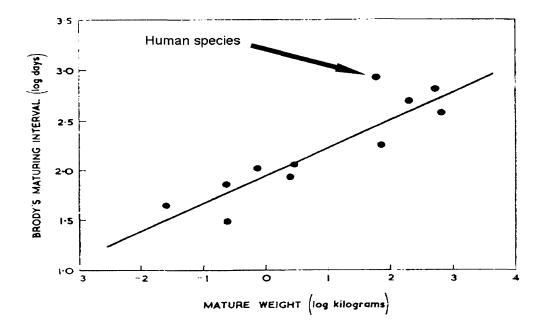


Figure 2.10: Interspecific relationship of Brody's maturing interval to mature weight, modified from Taylor (1965).

The relationship between degree of maturity and metabolic age (calculated as $\theta = \frac{[t-3.5]}{A^{0.27}}$) forms the basis upon which the function developed by Moore (1985) predicts potential growth. The relationship was determined using body weight data from embryo to adulthood of eight domesticated mammalian species collected by

Taylor (1980). The function has added flexibility in that it can have a single flexible point of inflection or multiple points of inflection that can allow negative growth, depending on the values of $p_n(\log_n \theta)$ used, where p_n is the n^{th} order polynomial.

As previously stated, the growth models described above draw an asymptotic relationship between weight and time using various means. Rather than using weight, Kinghorn (1985) uses body length (L) as an alternative measure of size, based on the relationship formulated in the 1800's by Sarrus and Rammeaux (as quoted by Brody (1945)), between heat production and the square of linear size (L^2). Following Maynard Smith (1968) who relates rate of oxygen supply and muscle power output to body length, Kinghorn (1985) relates various animal and production characteristics to body length, including weight gain. Assuming no changes in animal shape occur over time, this simple argument leads to a prediction of 0.33 (or $\frac{1}{3}$) for the size-scaling coefficient, which accommodates the idea that the cube of length (L^3) is proportional to weight. The difference between this value and Taylor's (1965) value of 0.27 could be attributed to the shape of animals actually changing as they grow.

2.4.2. Multiphasic Functions

The multiphasic property of growth, which is based on the existence of growth phases, cycles or spurts, is an aspect of Robertson's (1923) work that has received little attention. Multiphasic growth can be described as systematic departures from the smooth sigmoidal shape of the growth functions mentioned above. A number of suggestions have been made regarding the causes of multiphasic growth, including:

- 1) environmental and nutritional changes at birth and weaning
- 2) hormonal stimuli of puberty
- 3) temporary predominance of some internal secretion glands
- 4) relative activity of hormonal glands (activity of individual glands is not constant across life)
- 5) distinction between increases in cell number (hyperplasia) and increases in cell size (hypertrophy)
- 6) successive development of various tissues in a morphological and chemical sense (Koops 1989).

It has become widely accepted that the human growth curve occurs in three phases (Cheek 1968; Marshall 1977; Tanner 1962). These three phases are described in terms of height gain; the first peak occurs within 1 year, the second (mid-growth spurt) occurs at about 7 years and the third (pubertal) occurs at 12 and 14 for girls and boys respectively. Upon comparison to other species Tanner (1962) concluded the third phase was an evolutionary step taken by primates, whilst other studies in other species have found up to three phases occur, in terms of the growth represented by weight gain (Brody 1921; Eisen 1976; Koops 1986; Koops et al. 1987; Sørensen et al. 2003a).

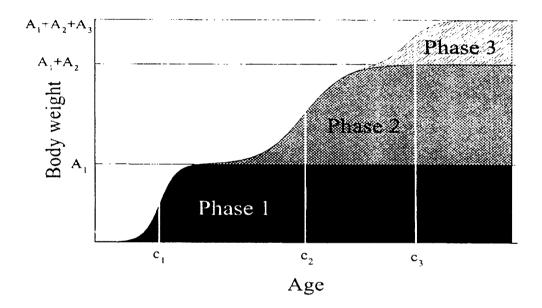


Figure 2.11: Idealised schematic of a three phase growth curve taken from Sørensen et al. (2003a). For phase, i (i = 1, 2, 3), A_i is the upper asymptotic body weight of the phase, c_i is the time of maximum increase of the phase and b_i (not shown) is a measure of the duration of the phase.

Using the terminology presented by Koops (1989) a multiphasic growth function with n phases, can be represented by:

$$Y_{t} = y_{1t} + y_{2t} + \dots + y_{it} + \dots + y_{nt}$$
 (2.3)

where Y_t is total growth at age, t and y_{it} is the amount of growth at age, t in phase i. Brody (1921) used a logarithmic form of the logistic growth function when analysing the postnatal growth of dairy cows. Tanner (1962) proposed separate functions for the growth of human height from birth to 10 years of age and then from ten years of age to maturity. Koops et al. (1987) and Grossman and Koops (1988) also applied the logistic function to their analyses of mice and chickens. The form of the logistic function applied by Koops (1987) and Grossman and Koops (1988) has also been applied to the growth of mink by Sørensen et al. (2003a), as illustrated in Figure 2.11. In this example of multiphasic growth three distinct growth phases are being represented. Each phase, i, is described by the three parameters, A_i which is the asymptotic body weight for that phase, b_i , although not shown in Figure 2.11, is the duration of the phase and c_i is the point of maximum increase in that phase.

The common thread amongst all the above functions is that age (time) is the only information source used for prediction of growth. These functions can be considered as making predictions of potential growth, with the exception of the multiphasic functions that can be considered to describe realised growth, but it is only in the absence of any nutritional and other environmental constraints that actual growth will be potential growth (Emmans and Kyriazakis 1999). For this reason, growth functions have been extended in the form of animal growth simulation models to use information from numerous sources for predicting growth.

2.4.3. Animal Growth Simulation Models

The series of growth simulation models discussed below use information concerning age, feed quantity and quality, and other environmental factors in different ways. They all however simulate animal requirements and subsequent growth based on whole body weight and some measure or internal prediction of mature weight. The growth simulation models discussed subsequent to this take the alternative approach of determining requirements and predicting growth as a consequence of body composition (i.e. use chemical composition or DNA content).

Growth simulation models based on whole body weight:

A systems analogy was used by Parks (1982) to illustrate how growth is described by empirical and multiphasic functions, including some of those discussed above. In this analogy an animal is represented by a single or series of interconnected "black boxes" that describe growth as an output only. The boxes are considered to be "black" as these models do not give any consideration to the internal workings (e.g. biological processes, catabolism and anabolism of protein and lipid) of an animal. Parks (1982) also used the black box analogy when describing an electrical analogue of animal growth, but recognised, despite the apparent success of the analogue, that "the lack of explicit expression of food or energy input to growing animals" was a serious defect of this and other such approaches. In attempting to address this defect, Parks (1970a) extended the black box analogy to consider input in the form of feed intake.

As described by Spillman, the law of diminishing returns has long been recognised as applying to circumstances where a decrease in the per unit effect of a casual factor occurs as the acting factor's magnitude increases (cited by Brody (1945)). Brody (1945) (chapter 5) and Henricks et al. (1931) applied the law of diminishing returns across various species and found it described the relationship between animal biomass and their cumulative feed consumption. Parks (1970a) found that the law of diminishing return could also be applied to the relationship between an animal's age and ad libitum feed intake. Combining these functions describing the two relationships allowed Parks (1970a) to convert the black box analogy into an inputoutput system that considered information concerning feed intake as well as age. Attempts have also been made to illustrate the effect that diet composition, feeding level and temperature have on growth function parameters (Parks 1970b, 1970c, 1971, 1982), with it being shown that some parameters, particularly those related to efficiency, are affected. Although it has been illustrated how adjustments to these parameters can be made (Parks 1970c, 1982) the model continues to give little consideration to the internal workings of animals.

All growth simulation models can be seen to fit the box analogy used by Parks (1982). Each growth simulation model uses information from at least two sources (in many cases more) as inputs whilst potentially producing a number of outputs (eg. weight gain, milk production, conception rates). However a difference between the Parks

(1970a) model and other growth simulation models is that the latter give more consideration to the internal workings of animals thus, whitening the box to some degree.

Energy Partitioning

The objective during development of the Texas A&M University (TAMU) Cattle Production Systems Model was to create a model that simulated performance using specified feed resources and cattle production potentials from equations describing the biological processes involved (Sanders and Cartwright 1979a, 1979b). This model simulates on a whole herd basis (except sires) by dividing the herd up into a series of classes (eg. weaners, replacement heifers, pregnant cows, dry cows) and using average characteristics of each class to simulate animals within that class. The model contains three subroutines that simulate, where applicable, growth (GRO, including lactation), fertility (FERT) and death (DIE) for each animal class. Within these routines the model estimates the maintenance, pregnancy, lactation and reproductive (oestrus) needs of animals. These requirements are determined from measures of current skeletal size, current body weight and parameters describing mature skeletal size at 25% body fat, maturing rate, milking and reproductive potentials plus a series of correction factors for lactation and reproduction.

A further step taken by Sanders and Cartwright (1979a; 1979b) to whiten the box is to consider the impact dietary characteristics, such as dry matter digestibility (DMD), crude protein (CP) content and total availability, along with physiological limits have on actual feed intake. Nutrient partitioning within animals is modelled to allow digested nutrients to meet maintenance and reproductive requirements at the expense of growth and milk production where necessary, or to allow excess fat deposition to occur when intake is in excess of all other requirements. To allow this partitioning to occur the simplifying assumption that digestible dry matter is equivalent to total digestible nutrient (TDN) (Sanders and Cartwright 1979b) is made. This model, with modifications, has been used to examine various characteristics of beef production relating primarily to economic and biological efficiency (Bourdon and Brinks 1987; Notter et al. 1979).

Somewhat similar approaches are taken by other growth simulation models where the maintenance, pregnancy, lactation and reproductive requirements are modelled. However in many cases the models simulate on an average animal basis rather than on a whole herd basis. The United States National Research Council (NRC) system for estimating beef cattle nutritional requirements is one such model and until 1970 this also used TDN for estimating the available energy of feeds (Tedeschi et al. 2005). Following 1970, the development of the California net energy (NE) system, from the experiment of Lofgreen and Garrett (1968), along with the experiment conducted by Moe et al. (1972) provided adequate information for the net energy system to be implemented in the NRC nutrient requirement recommendations (NRC 1970). This system forms the basis for the NE system used in subsequent revisions of the NRC (1996) nutrient requirement recommendations and The Cornell Net Carbohydrate and Protein System Model (CNCPS) (Fox et al. 2004).

The Agricultural Research Council (ARC) recognising the deficiencies in the TDN system and starch equivalents system (used in Britain since about 1912) proposed an alternative system following the calorimetric approach for predicting production attainable from a given ration (ARC 1965). This approach had three main stages, the first being estimation of ration metabolisable energy after accounting for feeding level; the second estimated maintenance energy expenditure expressed as metabolisable energy and lastly leaving the metabolisable energy available for production that is used to estimate production using conversion efficiency estimates (ARC 1965). This system provided the basis for the ME systems used in ARC (1980), AFRC (1993) and The Standing Committee on Agriculture (SCA) (1990) nutrient requirement recommendations and the animal biology model used in the GrazPlan DSS (Freer et al. 1997).

Protein Partitioning

The preceding discussion has focused primarily on how different growth simulation models estimate available feed energy. The manner in which protein requirements are dealt with is a major difference between the models developed by Parks (1970a) and Sanders and Cartwright (1979a; 1979b) and the growth simulation models. Tedeschi et al. (2005) describes the development of the ruminant nitrogen and metabolisable

protein (MP) systems by ARC (1980) and NRC (1985) as a major advancement in accounting for a greater portion of the variation associated with protein requirements. Each system is based on the prediction of microbial protein production (MCP) from a single microbial pool using estimated fermentable organic matter (Tedeschi et al. 2005). These systems also partition feed protein into two pools; the first estimates ruminally degradable protein (RDP) that predicts available nitrogen for microbial growth and the second estimates ruminally undegradable protein (RUP) that escapes rumen degradation (Tedeschi et al. 2005). A similar approach is taken in the SCA (1990) nutrient requirement recommendations and the animal biology model in the GrazPlan DSS (Freer et al. 1997).

The NRC (1996) and AFRC (1993) nutrient requirement recommendations take different approaches to dealing with amino acid utilisation. Amino acids derived from the diet and absorbed from the small intestine are utilised for the synthesis of tissue protein. The efficiency with which this occurs is dependent upon the amino acid mix of the absorbed protein relative to that of the tissue to be synthesised. This efficiency is best represented by the biological value of the dietary protein mix. In ruminants biological value depends upon the biological values of the digested protein obtained from both microbial and undegraded dietary sources and it varies with the primary function for which it is used (McDonald et al. 2002). The biological value of microbial protein is thought to be relatively constant at approximately 0.8, but that of dietary origin is dependent upon the characteristics of the diet and is difficult to predict as the values of individual dietary proteins give little guidance as to their value when digested in combination (McDonald et al. 2002). The AFRC (1993) uses the term relative value (RV) (equivalent to biological value in non-ruminants), to correct for these effects. The efficiency of utilisation of truly digested protein is described by AFRC (1992) in terms of the efficiency of use of an ideally balanced amino acid mixture (k_{aai}) . Using information from a range of circumstances k_{aai} was estimated as 1.0 for maintenance and 0.85 for most other conditions (AFRC 1992). Different RV were adopted for growth, pregnancy, lactation and wool growth allowing estimates for the net efficiency of utilisation of absorbed amino acids (k_n) to be produced when combined with k_{aai} .

An alternative approach is to estimate the essential amino acids available to the tissues following absorption from the small intestine and relate this to animal amino acid requirements (McDonald et al. 2002). This is the approach used by NRC (1996) and requires information on the truly digestible amino acid content of microbial and undegraded dietary protein. Although it has frequently been claimed that the essential amino acid content of ruminal microbial protein is constant, large differences have been shown to exist in amino acid composition of microbial protein samples (McDonald et al. (2002), Table 13.11). McDonald et al. (2002) also illustrated the challenges of attempting to estimate amino acid contribution by undegradable dietary protein. In their Table 13.12, McDonald et al. (2002) demonstrate that significant differences exist between the amino acid profiles of undegraded dietary protein and protein of the original feedstuff. Consequently, the suggestion is made that the amino acid contribution of feed to amino acid supply should be based on the insoluble fraction of the dietary protein. The CNCPS model (Fox et al. 2004) and NRC (1996) nutrient requirement recommendations use the soluble protein fraction to estimate amino acid supply. When modelling cattle growth the SCA (1990) nutrient requirement recommendations and the model in GrazPlan (Freer et al. 1997) however do not give any consideration to amino acid supply or animal amino acid requirements.

The various growth simulation models and nutrient requirement recommendations briefly described above vary in the manner they deal with the requirements of animals, nutrients supplied by the diet and utilisation of these nutrients by animals. These systems also use information from sources relating to environmental conditions, primarily wind, maximum and minimum temperatures (Fox et al. 2004; Freer et al. 1997; NRC 1996; SCA 1990). The SCA (1990) nutrient requirement recommendations and model in GrazPlan (Freer et al. 1997) also take rainfall events into consideration when dealing with new born lambs and cold stress. The conditions in which animals are maintained, in terms of grazing energy expenditure when estimating animal maintenance needs, are also taken into consideration in most cases. The exact details of the NRC, ARC, AFRC, SCA nutrient requirement recommendations as well as the CNCPS model and the model in the GrazPlan DSS can be found in NRC (1996), ARC (1980), AFRC (1993), SCA (1990), Fox et al. (2004) and Freer et al. (1997), respectively.

Growth simulation models based on body composition:

Besides the similarities discussed above, all those growth simulation models predict animal requirements as a function of current body weight and some prediction of mature weight with growth being output as a change in whole body weight that chemical composition (i.e. protein and fat content) can then be back-estimated from. Alternative approaches exist that use body composition (e.g. DNA content or chemical composition) for both determining animal requirements and predicting what form growth takes when consuming a given diet.

Using DNA Content to Predict Requirements

In the mid 1980's, Oltjen et al. (1986b) and Oltjen et al. (1986a) stated that although widely accepted within the cattle industry, the NRC and ARC systems omitted a number of important factors affecting performance, including genetic background, nutritional history and body condition. Oltjen et al. (1986b) also indicate that although the simulation models of Sanders and Cartwright (1979a; 1979b) and Loewer et al. (1983b) (see below for details) consider a greater number of factors that affect growth, these systems are not representative of the underlying processes regulating growth. Models such as those proposed by Baldwin and Black (1979) and Burleigh (1980) represent fundamental processes regulating growth. These models are based on biological principles, they operate at tissue or sub-tissue levels and the components and relationships contained in them associated with hyperplasia and hypertrophy apply across species. Oltjen et al. (1985) hypothesised that development of such causal models would allow identification of critical determinants of whole animal growth and aggregation to the whole animal level would increase predictive accuracy and application to a wider range of conditions in comparison to empirical models. However, it is also evident that the complexity and operating costs of these models preclude their use in routine management applications as growth predictors and restrict their use to research purposes (Oltjen et al. 1985).

The model for DNA accretion, protein synthesis and degradation in organs and tissues proposed by Baldwin and Black (1979) was applied to whole body protein as a single entity for rats (Oltjen et al. 1985) and cattle (Oltjen et al. 1986b). This approach predicts protein accretion as the difference between protein synthesis and degradation

which are both functions of DNA accretion and a measure of energy intake relative to 'normal growth'. Partitioning of energy follows the net energy format used in the NRC (1976) system, where energy is partitioned, according to requirements, initially to maintenance (predicted from EBW) then predicted protein accretion and then finally fat synthesis. In an effort to increase accuracy of prediction with diets of extreme energy content, Di Marco et al. (1989) extended the Oltjen et al. (1986b) model to contain two protein pools (body and viscera) and their associated DNA pools as well as a body fat pool. These changes were made in an effort to account for variable maintenance requirements and differing efficiencies of using absorbed energy. In a subsequent paper, Di Marco and Baldwin (1989) extended this model to include digestion and metabolism components that are represented by six nutrient fluxes and nine state variables, respectively. The nutrient fluxes are inputs to the metabolism component whilst some of the state variables are from the growth model and some are model inputs. The complexity of this model makes it useful for studies of complex interactions between diet, age, feed intake, physiological status, nutrient partitioning, body composition and energy costs of maintenance and growth (Oltjen et al. 2000).

The inability to accurately characterise feed chemical composition is a shortcoming of implementing the model developed by Di Marco et al. (1989) and Di Marco and Baldwin (1989). A collaborative effort developed a dynamic model of the development of viscera, muscle and fat pools in sheep (Soboleva et al. 1999) that simplifies the DNA size concept presented by Baldwin and Black (1979) and uses maximum protein content of muscle and viscera rather than DNA content. This model represents an intermediate step to that of Di Marco et al. (1989) and Di Marco and Baldwin (1989) where energy is partitioned between metabolically active (viscera) and less active (muscle and fat) protein pools. The model partitions energy following the format used in the NRC (1976) system but also contains a function that accounts for the lag effect of maintenance requirements associated with changes in energy intake. This model was extended by Oltjen et al. (2000) to include heat production.

The models developed by Hoch and Agabriel (2000; 2004a; 2004b) were constructed on the basis of variations in body protein and fat content, similar to the model developed by Oltjen et al. (1986b). Following Di Marco et al. (1989), they also

partition body protein between viscera and muscle pools but do not base protein predictions on body DNA content. However, rather than treating total body lipid as one entity, Hoch and Agabriel (2000) partition body lipid into carcass and non-carcass lipid pools. The accretion of lipid and protein in each chemical pool follows the same formulation, being the difference between synthesis and degradation, which are in turn influenced by ME intake. Estimation of lipid-free mass and full body weight is performed using allometric relationships with total body protein and EBW, respectively. The effect of changing energy intake on maintenance requirement is also modelled using a lag effect in Hoch and Agabriel (2000) and extended to include gut fill effects (Hoch and Agabriel 2004a).

The models using DNA and protein pools discussed above represent one alternative for predicting what form growth follows when consuming a given diet. In addition, the more recent versions of these models have been shown to perform in a manner consistent with compensatory growth following feed restriction (Soboleva et al. 1999), which is a desired characteristic when predicting growth in the Australian production environment. These models in their presented form do not however provide a means for predicting the growth potentials of animals and thus their dietary requirements. This would be a highly desirable attribute as it allows an optimisation procedure to determine firstly whether a given animal can achieve the desired production level (in terms of both weight and composition) and if so whether the production environment can support this production level.

Using Chemical Body Composition to Predict Requirements

An alternative to predicting animal nutrient requirements as a function of current body weight and a measure of mature weight (ARC 1980; NRC 1996) is to use changes in body composition to estimate requirements. This is the approach taken by Loewer et al. (1983b), who consider an animal's body to be composed of fat, protein, water and minerals. A Gaussian relationship is used in the model to describe the sigmoidal growth pattern of each body component, independently. The protein or water content of the whole body is used to determine physiological age of animals and growth in each component is taken as the difference in mass of the component at subsequent physiological ages. Changes in protein and fat content are used to determine the

energy requirements above maintenance using the assumption that water and mineral changes require no energy (Loewer et al. 1983b).

The Guassian relationship used above forms part of the extended growth simulation model described by Loewer et al. (1983a). This relationship is used as a measure of skeletal size whilst determining physiological limits to dry matter intake. Thermodynamic limits on intake are also determined in the model by estimation of heat loss potential (both from skin surface and respiratory heat loss) and heat production potential as influenced by environmental temperatures and humidity levels. Once dry matter intake has been determined then available nutrients are partitioned between body functions with the following priority; basal metabolism, maintenance, foetal growth, lactation and growth (Loewer et al. 1983a). The functions used for partitioning the available nutrients follow NRC (1976) and the California net energy (Lofgreen and Garrett 1968) systems.

This model also includes the concept of body stores which the animal is able to draw upon when nutrients are not provided at adequate levels. Water being the exception, each body component has two weight classifications, physiological and excess (Loewer et al. 1987). The maximum quantity an excess component can achieve is a fixed proportion of the physiological component whose maximum is determined by physiological age. The excess portions of components are utilised completely prior to those contained in the physiological portions when dietary nutrients are limiting. In the case where neither body stores nor the diet can provide adequate nutrients, body functions are altered in the order of reduced milk production, aborting a pregnancy, reducing activity and finally, death (Loewer et al. 1983a). Model behaviour in this situation and various others including those dealing with adequate and inadequate nutrient and energy supplies are illustrated by Loewer et al. (1987). This model provides the basis for a pig growth simulation model (Bridges et al. 1992a; Bridges et al. 1992b) that includes the effects of heat production and environment (Usry et al. 1992) but uses the function developed by Bridges et al. (1986) for describing the growth patterns of each body component.

The pig growth simulation model presented by Wellock et al. (2003a) uses a similar approach to that of Loewer et al. (1983a; 1983b). This model considers the effects

environmental variables (temperature, humidity) have on animal requirements and performance. The model takes a further step by accounting for the effects of social stressors using factors such as space allowance, group size and feeder space allowance (Wellock et al. 2003c). In a similar manner to the models of Loewer et al. (1983a; 1983b) and Bridges et al. (1992a; 1992b) it considers an animal's body to be made of lipid (fat), protein, water and ash (minerals). However, rather than treating the potential growth pattern of components as independent, allometric relationships are used to relate water, lipid and ash content to protein content (Emmans and Fischer 1986). The potential growth of protein is modelled using a Gompertz function which has been shown to be suitable (Emmans 1988; Emmans and Kyriazakis 1997, 1999) and perform adequately in comparison to other empirical models (Wellock et al. 2004a).

The model presented by Wellock et al. (2003a), again similar to Loewer et al. (1983a; 1983b) and Bridges et al. (1992a; 1992b), uses the changes in protein and lipid content of the body to predict nutrient requirements. However, the functions used to predict these requirements are quite different to those used in other models. The maintenance requirements of animals are based on body protein content (Emmans and Fischer 1986) rather than body weight and the system used for estimating energy needs is the effective energy system (Emmans 1994). Once feed intake is known after considering limits to intake then consumed nutrients are partitioned according to maintenance, protein deposition and finally, fat deposition, similar to Soboleva et al. (1999). To achieve this partitioning the ideal digestible crude protein (IDCP) content of a diet is used in conjunction with the efficiency (e_p) of IDCP use proposed by Kyriazakis and Emmans (1992a; 1992b). A diet's IDCP content is the product of the crude protein content and this protein's digestibility and biological value. The model gives no consideration to lactation or pregnancy in its present form, it has however been shown how potential milk production can be incorporated into estimates of animal requirements (Emmans and Kyriazakis 2001).

Although this model has been developed primarily for simulating pig production, the approach to modelling growth potential has been shown to apply across species (Emmans 1988, 1997). During development of this model it has been demonstrated that under ideal production conditions the genetic variation seen in growth is

explained by three parameters. These include mature protein content (P_m) , mature lipid to protein ratio (Q) and a general rate parameter (B^*) . Based on these characteristics the model has also been used in presenting a method for incorporating feed intake into breeding objectives through prediction of needs, rather than analysing large datasets containing feed intake to obtain empirical estimates (Amer and Emmans 1998).

The growth simulation models discussed above in comparison to empirical functions all consider a greater number of information sources than just age (time). The quantity of information considered varies from age and quantity of feed intake in the case of Parks (1970a) to age, feed quality (ME, CP, RDP) and environmental conditions in the case of AFRC (1993), NRC (1996), SCA (1990), Fox et al. (2004) and Freer et al. (1997). Wellock et al. (2003c) take it further to consider social stressors (space allowance, group size and feeder space allowance) in addition to these other information sources. The form used to represent the animal and its growth also varies from simply whole body or empty body weight (AFRC 1993; NRC 1996) to partitioning the body into its chemical components; lipid (fat), protein, water and ash (minerals) (Bridges et al. 1992a; Loewer et al. 1983b; Wellock et al. 2003a) as well as partitioning the body into its physical components; muscle, viscera and fat (Soboleva et al. 1999).

2.4.4. Body Composition Models

As mentioned above there are two methods for describing body composition; these being physical and chemical composition. Physical composition models partition the body on the basis of biological function. In the study of de Lange et al. (2003) the EBW of pigs was partitioned into six components, including muscle, fat, visceral organs, bones, blood and skin. Few models exist in the literature that partition the body in this manner, and those that do use quite different approaches.

Song and Dinkel (1978b) developed a series of functions for predicting both chemical and physical body composition using multiple curvilinear regression analysis of data from various experiments. The live weight of an animal was partitioned initially into hot carcass (HC), gut fill (GF) and remainder (RMD) with HC and RMD being further

separated into subcomponents. Water loss, separable muscle (SM), separable bone (SB) and separable fat (SF) were deemed to constitute HC whilst RMD was divided between hide/hair (%Hide), blood/organs (%BO), offal fat (%OF), bone (%Bone) and soft tissue (%Scrape) from head/tail/legs.

Two models were investigated for predicting SM, SF and SB. The independent variables used in model I were live weight (LW), mature weight (MW), degree of maturity (DOM), crude fibre percent (%) of diet (CF) and "biological type-I" (BT1), where the latter is referred to as "the energy in therms (1 therm = 105.4804 MJ) produced from the average annual milk production of a breed". The regression analysis also included quadratics of LW, DOM, BT1 and interactions between LW/MW, LW/CF, LW/BT1 as well as quadratic interactions between LW/DOM and LW/BT1. The same independent variables were used in model II with the addition of "biological type-II" which is referred to as "breed differences in physiological demand for energy expressed as a ratio of each breed to the average of the Hereford and Angus breeds". The quadratic of biological type-II and interactions with live weight were also included. The model used for predicting the subcomponents of RMD included percent separable fat of the dissected cold carcass and degree of maturity along with their quadratics as independent variables. The estimated coefficients for each of the models are located in Tables 2, 3 and 4 of Song and Dinkel (1978b). GF is estimated using the model developed in Song and Dinkel (1978a).

A collaborative effort between scientists from a number of countries produced a model for the development of viscera, muscle and fat pools in growing animals experiencing different nutritional conditions, which also has the capability of describing compensatory growth (Soboleva et al. 1999). This effort predicts physical body components from the chemical components based on the principles of energy and mass conservation. The quantities of muscle and viscera in the empty body are constrained by upper limits, m^* and v^* , respectively. The upper limit for muscle has a fixed value and the possibility of reaching this limit is dependent upon current and previous nutritional conditions. Current and previous nutritional conditions also have an impact on the upper limit of viscera. Following on from other growth models (Oltjen et al. 1986b), the net energy available after taking maintenance needs into

account is partitioned between viscera and muscle growth before fat deposition is considered.

Maintenance requirements are modelled using the approach developed by Corbett et al. (1987), which partitions maintenance energy between that associated with metabolism and that associated with feed digestion. As reviewed by Turner and Taylor (1983), changes in energy intake are associated with a lag in animal metabolism and consequently maintenance energy needs. Soboleva et al. (1999) modelled this lag effect and added it to the maintenance function. For the equations and a full explanation of the development of this model see Soboleva et al. (1999) and for the additions concerning heat production see Oltjen et al. (2000).

Sainz and Hasting (2000) developed a simulation model for partitioning body fat between different adipose depots, namely the visceral, intermuscular, intramuscular and subcutaneous depots. The model developed by Oltjen et al. (1986b) forms the basis, to which functions were added that predict the development and growth of each fat depot based on the accumulation of DNA. The quantity of fat (triacylglycerol) partitioned into each depot is controlled by the ratio of $\frac{FAT_i}{DNA_i}$ to $\frac{FAT_{MAX}}{DNA_{MAX}}$, where

$$\frac{FAT_i}{DNA_i}$$
 is the current ratio of fat to DNA in the *ith* depot and $\frac{FAT_{MAX}}{DNA_{MAX}}$ is the

maximum fat to DNA ratio of the *ith* depot, i.e. the maximum adipocyte size. Full details concerning model equations and testing can be found in Sainz and Hasting (2000).

Chemical composition partitions the body into its chemical components, namely lipid, protein, water and ash. Chemical composition can be predicted either as a consequence of nutritional intake in relation to animal requirements or as a function of body weight or body weight changes. The first approach is taken by Loewer et al. (1983b), Bridges et al. (1992a) and Wellock et al. (2003a), which has been discussed above. In these models, growth of protein, lipid, water and ash are predicted from nutrient intake and summed to produce changes in body weight.

The alternative approach is to use body weight or changes in body weight as the basis from which to predict chemical body composition or composition of body weight changes. Separable fat predicted by the physical composition functions developed by Song and Dinkel (1978b) using body weight as an independent variable, as discussed previously, forms the basis from which chemical composition of the body is predicted. The percent chemical water and chemical fat in separable muscle is determined via multiple curvilinear regression analysis with percent separable fat as the independent variable (Song and Dinkel 1978b). The percent chemical protein and ash are taken as 95 and 5 percent of the remaining mass of separable muscle, respectively. Multiple curvilinear regression analysis is used again to predict the percent chemical fat in separable fat with the logarithm of separable fat (log₁₀PSF) used as the independent variable. The percent chemical water, protein and ash are taken as 77, 20.7 and 2.3 percent of the remaining mass of separable fat, respectively.

The model developed by Keele et al. (1992) predicts the chemical composition of changes in body weight of growing animals and has been shown to work with a reasonable degree of accuracy (Williams et al. 1992a). This model partitions the empty body into fat (ether extractable lipid) and fat-free matter (FFM), which includes water, protein and ash. The quantity of FFM in body weight change is modelled as a function of current FFM content of the body, the expected FFM content when body composition is at equilibrium on a given quantity of a diet, current body weight and body weight change. A lag factor is also included in the model to account for the time required for changes in nutrition to have their full effect on body composition. Following a different formulation Williams and Jenkins (1997) developed a model that predicts chemical composition of changes in body weight of mature cattle. During their evaluations of this approach it was recognised that the model did not model compositional changes in lactating cows with great success. In response the model was further developed to account for the greater quantities of fat in weight lost during early lactation and regained in later lactation. Although developed using different formulations both of these models can be represented by a single equation (Williams and Jenkins 1998). As a result Williams and Jenkins (1998) developed a transition function to combine these two models to form a single model capable of predicting body composition for all degrees of maturity. These models have been extended to include the effects of feeding level and previous plane of nutrition (Williams and

Jenkins 2003a) and the consequences on body composition (Williams and Jenkins 2003b).

The characteristics of the system being optimised also influences the type of model that would be considered adequate for representing that system. The Australian beef industry supplies a variety of different markets and given consumer preferences vary between markets and within markets, meat quality can thus be viewed as not being an absolute (Egan et al. 2001). For this reason from a production perspective models capable of predicting physical composition would be of greater benefit than those capable of predicting chemical composition.

The models and functions discussed above are a sample of those available in the literature to describe animal growth whether it be on a whole body or composition basis. Each model has been developed for use in certain circumstances and has generally been shown to perform well in these circumstances. However, when attempting to optimise growth trajectories of animals in a number of different production environments, the model used for predicting animal performance is required to perform adequately under all circumstances. Some of the models discussed above would have a limited ability to predict performance outside their development environment.

2.5. Deriving optimal solutions

Obtaining optimal solutions for complex problems is not a new challenge and has been undertaken in a number of different ways throughout history. Perhaps the earliest and most commonly used method is mathematical derivation, which can be used to efficiently solve numerous problems (see examples presented by Michalewicz and Fogel (2004)). In this approach model equations are algebraically derived to give "closed form" solutions with the desired outcomes on the left-hand side and remaining components of the problem on the right-hand side. An important advantage of this approach is it produces a unique solution without the requirement for numerical iteration (Knap et al. 2003). As a result it has been used throughout a wide variety of scientific and engineering disciplines. However, most real-world problems and the models derived to represent them have several attributes that make it difficult

to use such approaches to solve them. These attributes include the possibility that numerous feasible solutions exist at a single point in time for any given problem, they may have constraints that make it difficult to construct a single feasible answer and the conditions of the problem may change over time, which may result in a series of solutions rather than a single solution being appropriate (Michalewicz and Fogel 2004). However, these attributes have not stopped such avenues being explored to solve real-world optimisation problems.

Algebraic inversion of growth models has been explored as a means of estimating genotypic model parameters in pigs (Doeschl-Wilson et al. 2006). The results of this model inversion process found it was not an accurate means of describing pig genotypes. It was also highlighted that the process of algebraic inversion resulted in various sources of error being integrated, which is a consequence of the serious difficulties associated with inverting differential equations. Successful inversion of differential equations results in problems that are ill-posed that may have no solution, a series of non-unique solutions (as highlighted above) or solutions that are unstable relative to the derived input (Tikhonov and Arsenin 1977).

In the current context, when manipulating growth trajectories potentially one or more of the models and functions described in previous sections could be used for representing animal growth and body composition. These models contain differential equations and thresholds that could prove difficult to invert and result in models that behave inconsistently with reality. Therefore, to be able to optimise growth trajectories in an efficient manner given the complexity of the task some sort of search heuristic is required to search for the optimal levels of inputs, rather than deriving them.

2.6. Search Methods for Optimisation

There is a plethora of algorithms available that have been designed to search solution spaces for optimal solutions. These algorithms can be essentially divided into two categories, deterministic and stochastic, based on the rules they use to explore the solution space. A problem found with deterministic methods is that they are generally not adaptable to structural variations of the prevailing problem. Whenever the

problem changes the algorithm also needs to change, which represents one of the shortcomings of these types of algorithms (Michalewicz and Fogel 2000). However, when used for the appropriate task these methods can be very effective, even more so than more modern stochastic methods. This situation is explained by the no-free-lunch theorem (Wolpert and Macready 1996) which states no optimal method exists for solving every type of optimisation problem. Mayer et al. (1998a) explain this situation by stating that each search method has features that make it superior for solving certain classes of problems but generally result in poorer performance on other classes of problems. Some of the algorithms that fit into both the deterministic and stochastic categories will be discussed in the following section.

2.7. Deterministic vs Stochastic Search Methods

2.7.1. Deterministic Search Methods

Exhaustive Search:

Holding true to its name, this search method checks every solution contained in a search space arising from all combinations of parameter values until the global solution is found (Michalewicz and Fogel 2000). This means that if the best solution is unknown every possible solution must be tested to ensure the best solution is actually found. An advantage of this search method is its simplicity. The only requirement being each possible solution to the problem is generated systematically with the order being of little relevance as the objective is to search each solution. However, exhaustive search is of little practical value for many real-world problems. Firstly, the size of the search space usually makes the time required to navigate it prohibitive, secondly, a convenient way to enumerate the search space may not exist (Burke et al. 2003) and lastly the search variables are often continuous in nature such that there are infinite locations.

Greedy Algorithms:

This type of algorithm solves complete problems by simplifying them down into a series of steps. Decision variables are assigned values one by one with the algorithm using a heuristic for decision making that presumably provides the best available solution at each step. This can be interpreted as being analogous to best "profit", thus

the name greedy (Michalewicz and Fogel 2000). The simplicity of the algorithms is an obvious advantage. However, the stepwise approach can also be interpreted as short-sighted as the optimum for each step will not necessarily produce the overall optimal solution, representing a disadvantage of the algorithm.

- Hill-Climbing:

Hill-climbing fits in the greedy algorithm class and uses the iterative improvement technique that presupposes the definition of solutions, a cost function and a generation mechanism (Aarts and Korst 1989), which allows transition between solutions by a small perturbation. Using the current solution as the starting point, a new solution is selected from the immediate neighbourhood at each iteration, consequently other names given to hill-climbing include neighbourhood search and local search (van Laarhoven and Aarts 1987). If the selected point provides a better value of the cost function it becomes the current point, whilst if the point proves to be inferior another neighbouring point is chosen and tested. If no further improvement is achievable then the process is terminated or the process can be stopped after a given time interval. An appealing advantage of hill-climbing is the ease with which it can be applied. When applied to real-world problems Hill-climbing methods often culminate in local optima that are dependent on the starting point, provide no information on the relative error (with respect to the global optimum) of the solution (Michalewicz 1996) and can not provide an upper bound on computation time (van Laarhoven and Aarts 1987).

Linear Programming:

Linear programming was first introduced by Dantzig (1963) with the objective of locating the extremum (maximum or minimum) of a linear function subject to constraints. These constraints are also of a linear nature being either linear equations or non-negativity bounds (Fletcher 1987). All vectors of variables that do not break constraints are considered feasible and the ultimate goal of linear programming is to locate the feasible vector that yields the best value from the evaluation function. If the problem is indeed linear then the optimal solution will be converged upon by linear programming. However, once evaluation functions become nonlinear other means need to be used to compensate for this such as trying to approximate the problem as if it were linear or perhaps quadratic or restricted to integer values. However, if this is

done it will generate the right answer to the wrong problem and no rule exists for just how bad that answer might be (Michalewicz and Fogel 2000). Once evaluation functions become multimodal or discontinuous linear programming breaks down. Many extensions of linear programming have been developed to overcome these situations including quadratic, integer and nonlinear programming, where a series of equations represent the system (Mayer et al. 1998b).

Dynamic Programming:

The basic idea behind dynamic programming rests on the principle of optimality coined by Bellman and Dreyfus (1962). This principle essentially states an optimal sequence of decisions can be constructed in a piecewise manner and has the property that regardless of the initial conditions all remaining decisions must constitute the optimal decision sequence for the remaining problem. The key to this concept is that decisions cannot be viewed in isolation since a balance must be achieved between the desire for low present cost and the undesirability of high future costs (Bertsekas 1995). Dynamic programming is able to capture this by ranking decisions (states) at each stage on the sum of present and expected future costs relying on the assumption that optimal decisions are made at subsequent stages. Dynamic programming also makes the assumptions that a well-defined cost function exists for traversing from state to state between stages and a recursive relationship, in that each next intermediate point is a function of the previous points visited, exists for making best decisions.

A weakness of dynamic programming is it can become computationally intensive as requirements are proportional to the number of operations, eg. where N represents both the number of stages and states per stage then the required number of operations is proportional to N^3 , therefore the computational burden of complex problems may be excessive (Bertsekas 1995). An additional shortcoming of the approach is it can become difficult to understand, which is due to the construction of the algorithm being dependent upon the problem under consideration. The construction process can be considered sort of an "artistic intellectual activity depending in part on the specific structure of the sequential decision problem" (Shapiro 1979).

Branch and Bound Algorithms:

Branch and bound algorithms work on the premise that portions of the search space are of limited value in finding an optimal solution. The search space is repeatedly partitioned into smaller and smaller subsets with successive iterations, analogous to a tree. Analogous to an unattended tree, the total number of partitions made as the algorithm progresses may become unmanageably large (Balakrishnan et al. 1991). To prevent this unruliness from occurring, a lower bound (upper bound in the case of maximising the solution) is calculated for the cost of solutions in each subset at the time of partitioning. Following each partitioning, subsets that have a lower bound exceeding the cost of a known feasible solution are excluded (pruned) from future partitioning (Lawler and Wood 1966). Put simply, if a current solution has a cost of z, any subsequent solutions tested that have lower bounds greater than z can be discarded and the algorithm can move onto the next possible solution without fully exploring that solution. A problem associated with this method is the means by which the lower bound is calculated. The more appropriate the lower bound the quicker the algorithm is able to explore the search space due to more solutions being eliminated. However, a cost exists for computing these lower bounds and for the method to be of use the cost of producing the lower bounds needs to be recuperated by the time saved in pruning branches. Preventing less desirable solutions from being explored could result in the algorithm being constrained to local optima.

Tabu Search:

Tabu search, was introduced by Glover (1989; 1990) with the objective of escaping local optima. The algorithm explores the solution space in a similar manner to the more traditional search methods by moving from one solution to the best performed solution in its neighbourhood. In contrast to the traditional methods the current solution may deteriorate between iterations (Cordeau et al. 1997) and does not always investigate every combination of input parameters. To prevent the algorithm from cycling over a series of solutions a tabu mechanism is implemented, where solutions are temporarily forbidden. In its naivest form the tabu mechanism would simply prevent the search from re-exploring previously encountered solutions, forcing the algorithm to explore new areas of the search space. However, in order to escape local minima a declared aspiration level, analogous to the probability used in simulated

annealing (see below), is used to allow previously visited solutions whose performance is less than this level to remain off the tabu list.

Implementing such a rigorous tabu mechanism typically results in excessive quantities of memory being used to store previously-visited solutions and can have an impact on the functioning of the algorithm. Numerous methods exist for altering the size of stored memory subsequently preventing it from becoming too restrictive. Short term memory involves storing some attributes of past solutions thus preventing any solutions that possess these attributes from being evaluated for a designated number of iterations, θ (Cordeau and Laporte 2002). Another implementation, often called long term memory, involves penalising frequently performed moves in an effort to ensure the search process will not be restricted to a limited section of the solution space. An aspiration criterion is a further effort to overcome memory restricting the algorithm. In certain circumstances the aspiration criterion allows an outstanding solution contained in the tabu list to be accepted and taken as the next point (Michalewicz and Fogel 2000).

The different uses of memory described above draw attention to the importance of this parameter in tabu search. Memory size is a problem-dependent parameter, as large memory may impact upon the time needed to scan the tabu list, while memory that is too small may result in cycling over previously visited solutions. This is a critical issue because in many cases the performance of tabu search is sensitive to the size of the tabu list and no algorithm exists for determining the optimal tabu list size other than experimental results, and, finally, a large tabu list requires large quantities of time and memory to run (Amein 2000).

2.7.2. Stochastic Search Methods

Simulated Annealing:

Simulated annealing is based on an analogy taken from condensed matter physics and has also been referred to as Monte Carlo annealing, stochastic relaxation, statistical cooling amongst other things. Kirkpatrick et al. (1983) first introduced concepts used in physical annealing to combinatorial optimisation. In condensed matter physics, physical annealing is a process that obtains low energy states of solids. This is

achieved by increasing the temperature of a heat bath to a maximum at which point a solid enters the liquid phase. The temperature is subsequently carefully lowered to allow particles to arrange themselves in the low energy ground state of the solid (Aarts and Korst 1989). In this ground state the particles form a highly structured lattice with the energy of the system being minimal, provided the maximum temperature is sufficiently high and cooling is performed sufficiently slowly (van Laarhoven and Aarts 1987).

In the early 1950's Metropolis et al. (1953) developed a simple algorithm for simulating the evolution of a solid to thermal equilibrium in a heat bath, based on Monte Carlo techniques. This algorithm generates a small random displacement for an atom at each step and the resulting energy change (ΔE) of the system is calculated. When $\Delta E \leq 0$ this energy change is accepted and the arrangement with this displaced atom becomes the new starting point (Kirkpatrick et al. 1983) but if $\Delta E > 0$ then this arrangement is accepted with a certain probability, analogous to the aspiration level used in Tabu search. This probability is given by:

$$P(\Delta E) = \exp\left(\frac{-\Delta E}{k_B T}\right) \tag{2.4}$$

where k_B is a physical constant known as the Boltzmann constant and T represents the temperature of the heat bath. The Metropolis algorithm can be applied to generate sequences of solutions of an optimisation problem based on the equivalences, 1) solutions in the optimisation problem are equivalent to states in a physical system, 2) a solution's cost (C) is equivalent to the energy of a state and 3) a parameter, termed the control parameter (c), plays the role of temperature. Following these substitutions simulated annealing can be viewed as an iteration of the Metropolis algorithm evaluated at a sequence of decreasing control parameter values (Aarts and Korst 1989).

Similar to hill-climbing algorithms a neighbourhood structure is established and a generation mechanism defined to allow generation of other solutions in the neighbourhood surrounding the starting solution. Following the Metropolis algorithm, when the cost of a selected new solution is lower than the current solution it is

accepted and becomes the new starting solution, however when the cost of the new solution is greater it is accepted with a certain probability, described by:

$$P(\Delta C) = \exp\left(\frac{-\Delta C}{c}\right) \tag{2.5}$$

If the new solution is not accepted, other solutions from the neighbourhood are subsequently tested. Using this type of probabilistic approach to selecting solutions offers the algorithm the flexibility to move in a backward direction to escape local minima. Initially, the control parameter is allocated a high value, making the search some what analogous to random search. The control parameter is lowered in a stepwise manner following convergence at each level until the algorithm is terminated at a small value of c when virtually no inferior solutions are accepted (van Laarhoven and Aarts 1987). During the final stages of a search, when control parameter values are small, simulated annealing resembles ordinary hill-climbing (Michalewicz and Fogel 2000). It should also be noted that simulated annealing only tracks a single "head" or current solution, which is in contrast to the evolutionary algorithms (described below) who maintain multiple different heads.

In comparison to the more traditional search methods outlined previously, simulated annealing has more parameters to handle such as the control parameter and its rate of reduction. Other questions also need to be answered including whether a termination criterion is needed to halt each step in the search process and how it is defined as well as what final criterion is used to halt the entire search. Consequently, thought has to be put into whether this algorithm makes sense for the particular problem and how parameters and criterions are chosen for the algorithm to operate optimally (Michalewicz and Fogel 2000). Other issues that have been highlighted as a cause for concern are the rates of convergence that result in excessive run times being required to achieve optimum solutions (Mayer et al. 2001) and that the solutions are dependent upon the starting values thus requiring many runs to be certain of achieving the global solution.

Evolutionary Algorithms:

The term evolutionary algorithm refers to a family of search algorithms that includes genetic algorithm (GA), evolutionary strategy (ES) and evolutionary programming (EP) which attempt to mimic the process of evolution by using selection, mutation and reproduction. The basic structure shared by each of these evolutionary algorithms includes the maintenance of a population of D-dimensional structures, "genotypes", each representing one of the potential solutions, "phenotypes", contained in the search space of a problem (Bäck and Schwefel 1993). These individuals receive a fitness value from the objective function or "environment" (aim of the search) in which they are contained and are evolved toward better performing regions of the search space with selection favouring individuals of higher fitness (Bäck 1992). Evolution of the population is dependent upon the production of offspring from individuals in the current generation using genetic operators such as recombination and mutation. Following reproduction, depending on the number of offspring produced, a selection operator is used to cull the population back to a desired size in preparation for the next iteration. Selection operators used to select parents and create the new populations can take many different forms and some of those used by each algorithm, along with the characteristics of the algorithms are discussed below.

- Genetic Algorithm (GA):

The traditional GA, also referred to as the canonical GA, is considered to be of a binary nature with each bitstring representing an allele or parameter, either as a real-value or discrete state. Depending upon the problem at hand these alleles can also represent a gene and thus the genotype is a direct representation of the phenotype. In this case, phenotype is a candidate solution to the problem at hand.

The recent blurring of the division between ES and GA has aided the development of real-valued GA, where the genotype is also a direct representation of the phenotype. On other occasions genes are a combination of alleles that have a phenotypic representation, i.e. parameters for optimisation (Eshelman 2000). GAs are distinctive amongst evolutionary algorithms for their reliance on recombination that operates at the genotypic level, for producing offspring. The original GA (Holland 1975), used Roulette wheel selection where individuals were chosen for mating based on their

observed performance (fitness of the phenotype) by assigning probabilities proportional to this performance, allowing better individuals greater opportunity to reproduce.

Once selection of superior parents has taken place, the GA mimics the process of sexual reproduction between individuals where genetic code sequences are mutated, crossed and mixed to produce offspring (Mayer et al. 1999). This process of reproduction, combines successful traits (i.e. parameter values) that improve population fitness and exploits low-level random mutation that parallels nature allowing novel genes to be generated, aiding exploration of the search space and lost genes of value to be rediscovered.

Following production of offspring, the parent and offspring populations must be combined into a single population for the algorithm to progress. Generally, GAs maintain a constant population size (M) meaning the parent and offspring populations need to be combined and reduced back to this desired size (Eshelman 2000). This objective can be achieved in a number of different ways depending on the number of offspring produced and whether bias is used. One option is to replace the entire parent population when the parent and offspring populations are of equal size, M. An option when < M offspring are produced is to randomly select individuals from the parent population to be replaced (Eshelman 2000). Incorporating bias during replacement of parents with offspring can be performed in numerous ways. Tournament selection with a tournament size of two individuals competing for each place in the population was shown by Mayer et al. (2001) to perform well across a number of problem types. In circumstances where higher selection pressure is required increased tournament sizes or truncation selection can be used. Another possibility is Roulette wheel selection used in the canonical GA (Holland 1975) but this tends to be more computationally demanding (Mayer et al. 2001). Other mechanisms for including bias also exist such as elitism where the best individual in the population is maintained between iterations (Michalewicz 1996).

Another type of search method is learning classifier systems (LCS) (Goldberg 1989) that contain GA as part of their internal workings. LCSs are more of a concept in many ways than an actual algorithm and thus will not be discussed further.

- Evolutionary Strategies (ES):

ES use real-number representations of the input values, so each parameter to be optimised is represented by one gene (Mayer et al. 1999). In contrast to GA, ES uses mutation rather than recombination as the key evolutionary operator. A mutation of each gene occurs according to a vector of mutation variances which evolves over time (Bäck and Schwefel 1993). This follows recombination of two randomly selected parents to create an un-mutated version of the solution. Although many symbolic notations exist, two notations are generally used for describing ES. The first, $(\mu + \lambda)$ ES represents an ES that spawns λ offspring from μ parents and selects the μ best individuals from the $\mu + \lambda$ individuals (Rudolph 2000). When parameterising this type of ES the convention $1 \le \mu \le \lambda < \infty$ is adopted. The original simple ES is represented by a (1 + 1) ES that is somewhat analogous to a random search with elitism. The second, (μ, λ) ES represents an ES that spawns λ offspring from μ parents but selects the μ best individuals from λ offspring only. Thus λ must be larger than μ and when parameterising this type of ES the convention $1 \le \mu < \lambda < \infty$ is adopted. Truncation selection is the main selection operator used in ES for reduction of population sizes back to μ .

Individuals within the population constitute solutions within the search space and sometimes also include several parameters that control the individual mutation distribution (Rudolph 2000). Alternatively, the mutation distribution is controlled by separate parameters, with the possibility that population values impact on mutations, as in differential evolution (described below). The mutation distributions are usually described by a multivariate normal distribution with a mean of zero and a positive definite, symmetric covariance matrix. Angles (ω) and standard deviations (σ) are two of the mutation operators used to define the covariance matrix. These variances are initially larger to facilitate searching and over time narrow down to near zero as the genes converge to their optimal value (Michalewicz 1996), effectively fine-tuning the solution.

- Evolutionary Programming (EP):

Similar to ES and in contrast to the canonical GA, EP uses continuous variables and generates a predefined number of offspring, λ , from μ parents. In contrast to both GA and ES these offspring are exact duplicates of their parents as recombination is not used by EP. The offspring are subsequently modified by a mutation operator only, which is commonly a Gaussian distribution with a mean of zero and unit variance. More recent versions of EP are termed self-adaptive, in that the mutation operators adapt to the current state of the population. The evaluated fitness of each offspring and the evaluated fitness of their parents are used to cull the population size back to μ in preparation for the next iteration. Similar to ES truncation selection is the main selection operator used in ES for reduction of population sizes back to μ .

- Computational Representation:

• Recombination

Recombination produces extra variation among solutions, perturbing the population by mixing parental information to explore new combinations in offspring (Bäck and Schwefel 1993). The simplest form of recombination is that used in a binary GA which uses linear bitstrings where each position is a gene and the value at that position is an allele (0 or 1). Figure 2.12 depicts how recombination can be used to achieve the objective of maximising the number of 1's in the array. Two parents are selected from the population and a breakpoint is selected at random. Beyond this point the parental vectors exchange the remainder of their bit strings creating a new offspring. Depending upon the evolutionary algorithm being used there are many different forms of recombination that can be used including n-point, uniform and punctuated crossover, as discussed by Booker et al. (2000) and Spears (2000).

One-point crossover breakpoint

Parent A	1	0	0	1	1	1	1	0	0	1	1
Parent B	0	1	0	1	0	1	1	1	1	0	0
Offspring	0	1	0	1	0	1	1	1	1	1	1

Figure 2.12: Schematic of single point crossover used by a binary GA modified from Gondro (2005).

Mutation

In contrast to recombination, mutation introduces variability at individual loci (Bäck and Schwefel 1993), by making random changes to individuals. The simplest way of demonstrating how mutation introduces new variation into a population is to again use a binary GA example. Each position within an individual, in this case a bitstring, is tested using a uniform probability. On the occasion when the mutation operator returns true the bit located at that position is flipped (Figure 2.13). When real-valued vectors are being used mutation uses one of many mechanisms to create a new value then subsequently replaces the old value. These types of mutation along with many other forms have been discussed by Bäck et al. (2000c) and Bäck (2000). The role that mutation plays in the success of evolutionary algorithms should not be underestimated as it introduces new sources of variability into a population exposing new areas of the search space where recombination is only capable of shuffling the available variability (Gondro 2005).

One-point bit-flip mutation

1	1	0	0	1	1	1	1	0	0	1	Parent
			Ţ								
1	1	0	1	1	1	1	1	0	0	1	Offspring

Figure 2.13: Single point bit-flip mutation used by a binary GA modified from Gondro (2005).

Even though the processes of evolution as adopted in evolutionary algorithms appear to have been some what simplified, they are complex enough to produce robust and powerful search algorithms that have been used to solve a wide range of real-world problems (Banzhaf et al. 1998). For a complete description of evolutionary algorithms and issues associated with the implementation and design of evolutionary algorithms see Bäck et al. (2000a; 2000b). Applications for evolutionary algorithms also extend beyond solving numeric problems. They can be used to construct a representation of a problem in the manner demonstrated by Koza (1992), using Genetic Programming, and Ferreira (2001), using Gene Expression Programming.

Differential Evolution (DE):

DE can be considered somewhat of a hybrid between real-valued GA and ES that uses the self-adapting mutation of ES with the conventional vector structure of GA. In some senses it can be viewed as analogous to a population-based "multi-headed" simulated annealing where the mutation rate decreases as the population of solutions approaches convergence (Gondro 2005), corresponding to the temperature decrease in simulated annealing. DE is further advantaged in that information from each "head" or path-of-solutions is used to assist all other heads. The 20 lines of pseudo-C code required to implement DE is an obvious advantage of this algorithm and can be found in Price and Storn (1997) and Storn and Price (1997).

The structure of DE is relatively simple, it utilises *NP* D-dimensional real-valued vectors as the population for each generation, *G*. Within a single iteration mutation and recombination are integral operations that DE uses to produce *NP* offspring vectors that compete for positions in the new population. Each offspring vector is the product of a mutation operation, which entails the weighted difference between two population vectors being added to a third vector, and a crossover operation between this new trial vector and the target vector (Storn and Price 1997).

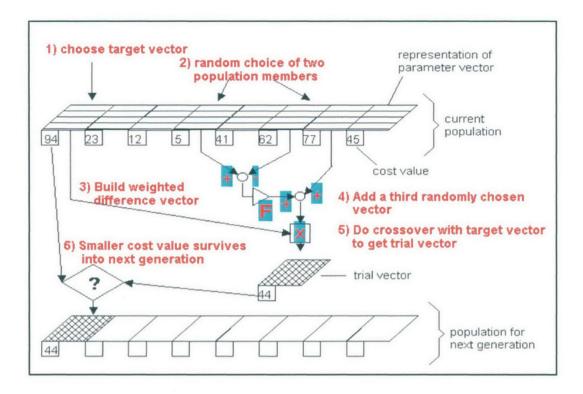


Figure 2.14: The basic mechanisms that operate within DE taken from Price and Storn (1997).

DE uses a greedy criterion to compare the value of the offspring vector to that of the target vector in contrast to the canonical GA, that uses ranking and proportional selection, and in the case of other GAs, an annealing criterion (Price and Storn 1997). For each position in the population the vector that possesses the greater fitness is maintained in the population for the next generation, as illustrated in Figure 2.14.

2.8. Optimisation in Agriculture

The search methods outlined above are only some of those available for optimising complex systems. Many of these have been applied in optimisation of agricultural systems with good results. Mayer et al. (1998a) have categorised the manner in which these methods are applied to agricultural systems modelling, into two main groups. This division is based on the level of interaction between the system model and the optimising method. The first group contains the deterministic search methods where systems are represented by a framework of mathematical equations and constraints (i.e. the optimising method has intricate knowledge of the modelled system). The

second group use the stochastic search methods by separating the system model from the optimisation method by considering the system model a "black-box" to be optimised.

In circumstances where the assumptions of deterministic search methods such as linear programming and its many extensions have been satisfied by the solution space, they have managed to locate global optima of large, complex problems with high efficiency (Mayer et al. 1998a). One key property required is convexity, where if two solutions are legal then the average of these two solutions is also legal. Forestry systems have had optimal harvesting schedules developed using linear and mixedinteger programming methods (Roise 1990). Dynamic programming has been used to optimally schedule irrigation in homogenous cropping areas (Botes et al. 1996). The Nelder-Mead simplex algorithm has also been used in this context, with it proving to be more flexible and realistic than dynamic programming (Botes et al. 1996). For animal production purposes, the quasi-Newton and Nelder-Mead simplex algorithms have been applied to a Queensland dairy farm model, with mixed results (Mayer et al. 1991). Linear programming has been used to create optimal ration mixtures for dairy cattle (Hulme et al. 1986), with this application being extended to a whole-farm system that includes pasture and fodder conservation feeds (Olney and Kirk 1989). Linear programming has also been used to compare nutritional and management strategies in Venezuelan dual-purpose cattle systems (Nicholson et al. 1994). When maximising the genetic merit of progeny is the objective, mate selection has been performed using linear programming (Jansen and Wilton 1985). Multiple-objective programming has been offered as an alternative to linear programming for reducing nutrient variation in poultry diets (Zhang and Roush 2002).

Circumstances also exist where these types of optimisation methods have been shown to be ineffective. In a horticultural example, linear and dynamic programming were considered too computationally intensive for practical purposes when optimising a space and labour allocation problem for greenhouses (Annevelink 1992). Gradient and direct search methods have been found to be ineffective for calibration of a catchment runoff model (Wang 1991). Linear programming has also been used in conjunction with the Cornell Net Carbohydrate and Protein system (CNCPS) to optimise diet composition (Tedeschi et al. 2000) and allocate home grown feed (Wang et al. 2000b)

across a dairy production system with the objective of reducing nutrient excretion from the system as a whole (Wang et al. 2000a). However, in achieving these outcomes non-linear components contained within CNCPS had to be linearised and subsequently iterated to produce sensible outcomes. Interrupting the integrity of a non-linear system such as this is potentially hazardous.

A more desirable option would be to maintain the integrity of such systems by using non-linear search methods for optimising them and is the type of approach taken by the second group defined by Mayer et al. (1998a). This approach separates the system model and the optimisation method allowing the system model to be developed, tested and refined independently from the optimisation method, thus maintaining the integrity of the model. It can be considered a 'plug-out and plug-in' approach that for many systems provides a more flexible and realistic approach (Botes et al. 1996). For simpler system models, exhaustive search methods where every possible combination of the input options is considered have been used to locate economic optimum combinations. Beef properties in central Queensland have had pasture management strategies explored across time using a two-by-two factorial design (with or without tree clearing or oversewing improved pastures) while all other management options remained at default values (McIvor and Monypenny 1995). The genetic gain associated with using different artificial breeding options in dairy herds has been explored using a complete factorial to optimise seven management options (Mayer et al. 1994). Investigations of whole-farm management options made across lengthy time periods have used a one-at-a-time approach so each is considered separately at fixed values of the other options (Buxton and Stafford-Smith 1996).

Although these approaches have performed adequately on smaller problems, their use becomes infeasible when presented with moderately-sized problems (Mayer et al. 1998a). For example, if the seven management options in the dairy system presented by Mayer et al. (1994) are allocated at the nearest 5% of their full range then 20⁷ combinations would need to be searched (Mayer et al. 1998a). Optimisation with the one-at-a-time approach prevents the combined and interacting effects of management options from being explored. Stochastic search methods are of interest in this respect as they do not interrupt the integrity of models, can be highly efficient and can accommodate epistatic effects (interactions between input variables) often found in

agricultural systems models (Mayer et al. 2005). The superior performance of GAs has been demonstrated in comparison to linear and dynamic programming when optimising space and labour allocation problems in greenhouses (Annevelink 1992) as well as in comparison to gradient and direct search methods when calibrating a catchment runoff model (Wang 1991).

GAs have also been applied to the formulation of silage additives (Davies et al. 2000), optimising the structure of the Australian sheep breeding industry (Horton 1996), selecting mating pairs (Hayes et al. 1997), designing crossbreeding programs (Hayes et al. 1998; Shepherd and Kinghorn 1998), optimising age structures in breeding populations (Meszaros et al. 1999) and a method of mapping multiple interacting QTL (Carlborg et al. 2000). The metropolis algorithm has been used to create spatial configurations on forestry landscape whilst dealing with constraints associated with timber harvesting (van Deusen 2001). A spatial decision support system used to support the design and evaluation of alternatives for resource allocation has used simulated annealing for supporting restoration of a ex-mining area (Aerts and Heuvelink 2002).

The nature of agricultural enterprises necessitates that the systems models used to represent them are of high complexity, usually resulting in no closed form solution to optimisation. These types of models consequently often suffer from the 'curse of dimensionality' (Mayer et al. 2005) which produces extremely large and highly complex non-smooth search spaces containing many local optima (Mayer et al. 1998b) as well as interactions between input variables creating epistatic effects in the solution space that further complicate optimisation (Mayer et al. 2005). During testing with a 16-dimension dairy farm model Mayer et al. (1996) have found that simulated annealing and a GA perform comparatively better than the simplex method or quasi-Newton methods. Using the same 16-dimension dairy model it has been shown that tabu search is not suitable for optimisation of models this level of complexity (Mayer et al. 1998b). In studies using a beef cattle herd dynamics model that has increased dimensionality in comparison to the 16-dimension dairy model, Mayer et al. (2001) have shown that both real and binary GAs have superior efficiency and reliability than simulated annealing.

When comparing the performance of GAs and evolutionary strategies it has been suggested that their merger into a single broader class of optimisation methods (Bäck and Schwefel 1993) offers the potential to create evolutionary algorithms superior to either methods (Mayer et al. 1999). DE fits this into this category as it can be viewed as somewhat of a hybrid between real-valued GA and ES using ES's self-adapting mutation along with GAs conventional vector structure. It has been shown that DE converges faster, is more repeatable and produces solutions closer to the global optimum when optimising continuous value parameter models for the lac operon compared to heuristics such as simulated annealing, GAs, ES and hill climbing (Gondro 2005).

DE has been successfully used in conjunction with linear programming for making mate selection decisions given operational and cost constraints (Kinghorn 1998). This approach has since been expanded to full mate selection used in the animal breeding decision support program Total Genetic Resource Management (TGRM) (Kinghorn and Shepherd 1999) that has been commercialised for use by Australian sheep breeders under LAMBPLAN (Banks et al. 1999) and many other industries (see www.xprime.com.au). DE has also been applied to the estimation of soil physical parameters (Johnson et al. 2002). Mayer et al. (2005) have demonstrated the simplicity of DE in terms of the level of coding and the number of operational parameters required in comparison to simulated annealing, GAs and ES. They have also illustrated the efficiency and robustness of DE in comparison to these other evolutionary algorithms when dealing with a beef cattle herd dynamics model. DE has been applied successfully in a wide range of optimisation problems outside of agricultural applications; frequently outperforming other heuristics. For a bibliography on DE applications see www.icsi.berkeley.edu/~storn/code.html.

The non-linear, complex nature of growth and the models used to represent it in production environments, necessitates that non-linear search methods be used to optimise the growth trajectories of beef cattle. The successful application of DE to large and complex animal breeding decision scenarios gives weight to it being able to handle highly non-linear optimisation problems. These factors, plus the ease of implementation of DE lead to it being chosen as the search algorithm to be used throughout the studies conducted in this thesis.

2.9. Summary

This literature review introduces the complexity of animal growth and development that is dealt with on a daily basis by producers when attempting to grow animals that meet consumer requirements. Section 2.3 presented a structure that can be applied to optimising the manipulation of growth, which requires a representation of the problem and a heuristic for solving the problem. Section 2.4 reviewed many of the models and functions that have been developed in the past to describe whole body growth and composition. Each of the models discussed have been developed in given circumstances and subsequently been shown to perform well in similar circumstances. However, the nature of the Australian production environment makes it a necessity that any model(s) used to represent animal growth are capable of performing in a wide range of circumstances. Chapter 3 will test the predictive ability of five growth models and a polynomial in two different production environments. Chapter 4 will attempt to address the general lack of models available for predicting body composition by proposing five ways to use allometric equations and comparing their predictive abilities to one other body composition model. The remainder of the literature review is dedicated to a discussion of the available methods for solving complex problems with the conclusion being drawn that Differential Evolution is currently the most appropriate method for manipulating growth trajectories and is subsequently used in chapters 3, 5 and 6.