Chapter 1: General Introduction

Australia and New Zealand contribute 33 and 38%, respectively, of all sheep meat exported around the world (Meat and Wool New Zealand (MWNZ) 2008a) but sheep numbers in these countries are declining rapidly, to the extent that current populations are at levels not seen since the early part of last century (85.7 million in Australia (Nossel *et al*. 2008) and 34 million in New Zealand (MWNZ 2008b)). As a result of this decline in numbers, the supply of lamb from Australia and New Zealand has decreased, pushing prices up to historically high levels (Nossel *et al*. 2008).

There are many varied reasons for the decline in sheep numbers in both Australia and New Zealand. In both countries there has been an increase in competition for land use from other farming practices like dairying, cropping and beef production, or from social usages like conservation, tourism, housing and recreation. Some of these changes in land use have occurred in response to climate change and/or droughts, and some have occurred as a result of the higher profitability of other farming systems in some environments. Other negative influences on sheep numbers include the intense competition in the market place from other meats, rising input costs and a preference for faster growing, leaner lambs (MWNZ 2008b; Nossel *et al*. 2008). Faster growing and leaner lambs are genetically correlated with increased mature size (Brash *et al.* 1994; Fischer *et al.* 2004b; Mousa *et al.* 1999, which leads to higher feed requirements and fewer, larger sheep that can be maintained on a given amount of resources (Taylor 1980).

Some authors like Dickerson (1970), Fitzhugh (1976), Lambe *et al.* (2006), and Robertson (1987) have advocated selection to maximise early growth whilst minimising any increase in mature size, also known as "(growth) curve bending", as an option for increasing the efficiency of the production system. The advantages of this approach include reducing the relative feed requirements of adults compared to sale progeny, the elimination of the requirement for difficult and expensive feed input measurements, and the ability to use this technique in conjunction with other methods of increasing efficiency like the use of terminal sires (Dickerson 1970; Large 1970; Thompson 1991) or increasing the fertility of the flock (Amer *et al.* 1999; Dickerson 1970). Because this approach does not involve the

crossing of breeds of divergent size, breeding stock can also be kept as replacements allowing any genetic improvements to be cumulative. However, the strong genetic correlations between early growth and mature size (Brash *et al.* 1994; Fischer *et al.* 2004b; Mousa *et al.* 1999) and between mature size and feed efficiency (Taylor 1980) prevents rapid genetic improvement in efficiency by this method.

This thesis investigates whether incorporating the variation known to exist in growth rate and mature size between rams and ewes (sexual dimorphism; Kirton *et al.* 1995a; Lee *et al.* 1990; Lewis *et al.* 2002; Mousa *et al.* 1999; Pattie 1965; Stanford *et al.* 2001; Thompson *et al.* 1985; Thonney *et al.* 1987; Young *et al.* 1965) into the "curve bending" approach could be used to increase the rate of genetic gain in efficiency of a self-replacing meat sheep production system. In a self-replacing production system, most young ewes are retained as flock replacements, while most rams are destined for sale (Figure 1.1). By combining the greater size and growth of rams with the sex-specific roles in a production system, there is potential to increase the response to selection in "curve bending" by selecting rams with fast early growth and smaller mature sized ewes. While this technique is also limited by the genetic correlation between growth to slaughter and mature weight, the limitation of each trait to the relevant sex (growth to sale in rams and mature weight in ewes) may reduce the genetic correlation between the traits sufficiently for this approach to be viable.

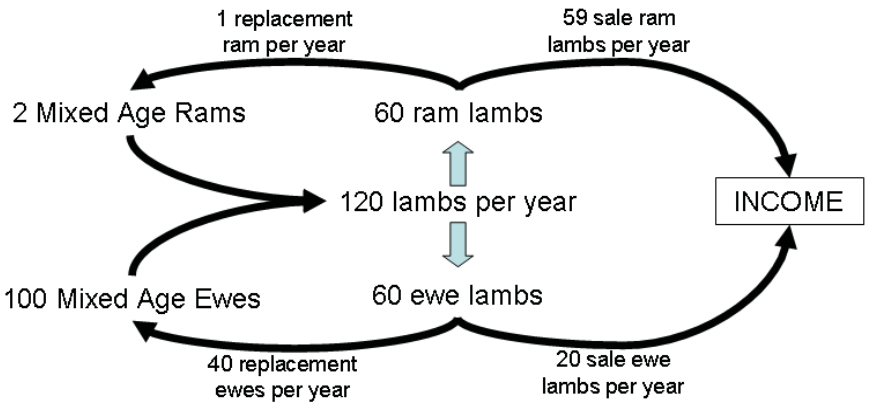

Figure 1.1: Model of a self-replacing sheep production system. The mating ratio and weaning rate used are those given by (NSW DPI 2009) for 1st cross ewes and may not be representative of all flocks and breeds. Zero mortality at all ages was assumed and the sale of cast for age adults is not shown.

Currently, most breeding programs assume that growth is inherited equally by both sexes and as such, no active selection is placed upon sexual dimorphism. This statement is reflected in the paucity of single sex or between sex genetic parameters published in scientific literature (for a review of genetic parameters in sheep see Safari & Fogarty 2003) and that sex specific selection indexes are uncommon in livestock production. If growth is not inherited equally in both sexes (i.e. the genetic correlation between ewes and rams for the same trait is less than 1.0), then genetic changes in sexual dimorphism are likely to occur (Robertson 1959). The reason for this likelihood is that in all livestock production systems, sires can be mated to many dams and, as a consequence, males have higher selection intensities and would be expected to have a higher response to selection than females. The magnitude of this sexually dimorphic response would also be influenced by any differences that exist between the sexes in phenotypic variation and heritability (Cheverud *et al.* 1983 & 1985; Eisen & Hanrahan 1972; Lande 1980; Reeve & Fairbairn 2001). Breeding programs seeking to utilise these differences could estimate separate breeding values for ewe and ram growth. This would allow the direct selection on ewe growth in rams and vice versa (similar to selecting for milk in dairy bulls).

The estimation of sex-specific genetic parameters is also important where new reproductive technologies (sexed semen, sexed embryo transfer, etc.) are used to influence the sex ratio in flocks, where the selective recording of traits according to sex occurs or where the differences in genetic parameters are sufficient to cause different selection responses in each sex. In these situations, knowledge of how the various genetic parameters vary between the sexes is important for the accurate prediction of the response to selection, genetic evaluation, the design of breeding programs, and can also give insight into the genetic mechanism(s) defining a trait (Lax & Jackson 1987; Safari *et al.* 2005 & 2007).

1.1 Objectives

The objective of this thesis was to investigate whether sexual dimorphism is a practical selection strategy for enhancing the meat production efficiency of sheep. Genetic parameters were estimated for and between traits expressed in rams and ewes. The economic benefit of increasing sexual dimorphism in pastoral maternal sheep production systems was also investigated. The aims and corresponding chapters of this thesis were:

Chapter 2: Present a review of the literature relevant to using sexual dimorphism to increase the efficiency of sheep production. This included discussions on the efficiency of pastoral sheep production and how it can be improved, the correlation between size and feed efficiency, the evolution and presence of sexual dimorphism in nature, variation between the sexes in the physiological processes influencing growth, possible genetic mechanisms influencing sexual dimorphism, methods used to estimate sex-specific genetic parameters, and the results of such studies in sheep and other livestock species.

Chapter 3: Estimation of the magnitude of sexual dimorphism in live weight at five ages, ranging from weaning (100 days) to adult (> 530 days) and in fat and eye muscle depths at 225 days of age. The phenotypic variation and heritability for each of these traits in each sex was estimated.

Chapter 4: Estimation of intersex genetic correlations between traits measured in opposite sexes. These estimates were then used to predict the response to phenotypic and EBV selection, which is comprised of the direct response to selection in each sex and the correlated response to selection in one sex due to selection in the other sex.

Chapter 5: Estimation of the sex-specific variance components for weight over a continuous trajectory of time using random regression. The analysis of weight as a continuous variable across time allowed greater resolution than possible with the analysis at five discrete time points as used in Chapter 3. This allows more insight into how genetic parameters in each sex vary with age.

Chapter 6: A bio-economic model was created to describe the potential feed efficiency and profit benefits of incorporating sexual dimorphism into a maternal sheep breeding program.

Chapter 7: Finally, in the general discussion, the main outcomes of the thesis are discussed and topics not covered in the previous chapters are highlighted. These topics include the benefits of increasing the efficiency of a maternal sheep production system, possible methods of identifying sexually dimorphic individuals and other potential benefits of estimating sex-specific genetic parameters.

Chapter 2: Literature Review

2.1 Introduction

High demand for lamb, yet falling sheep numbers have forced the sheep industry to consider how to increase the efficiency (ratio of lean tissue available for sale to the amount of feed consumed) of their production system. This literature review explores topics pertaining to the potential to increase the efficiency of pastoral sheep production systems via sexual dimorphism (variation in growth rate and mature size between rams and ewes). Section 2.2 introduces the concept of lamb production efficiency and discusses what traits influence it and how they may be improved. Particular emphasis is placed upon the correlation between size and feed efficiency, and the potential of sexual dimorphism to increase efficiency. The presence of sexual dimorphism in nature and how it may have evolved are discussed in section 2.3. The physiological regulation of sexual dimorphism is discussed in section 2.4. The genetic mechanisms by which sexual dimorphism may be inherited is discussed in section 2.5, which leads on to section 2.6, which discusses methods of how the inheritance of sexual dimorphism can be quantified, a summary of other researchers' results and how the results can be used to predict the sexually dimorphic response to selection. The results and techniques discussed in section 2.6 are directly applicable to those used in Chapters 3 to 5. The use of bio-economic models to simulate sheep production systems is discussed in section 2.7 and relates to Chapter 6 where a bio-economic model is used to test the economic value of sexual dimorphism as a trait.

2.2 Efficiency of Lamb Production Systems

The efficiency of a lamb production system depends on the balance between the value of the products (e.g. meat) produced and the cost and quantity of the inputs required. The inputs and outputs of the production system can be divided into two categories, the biological traits that directly influence the system and the economic forces that affect the weighting placed on these traits. By ignoring the economic forces, the efficiency of a lamb production system can be described in general terms by the following equation (Large 1970):

$$\text{Lamb Production Efficiency} = \frac{(\text{carcass weight per lamb} + \text{co-products}) \times \text{the number of lambs reared per ewe}}{\text{feed intake of lamb until slaughter} + \text{feed intake of the ewe} + \text{non food inputs}}$$

Equation 2.1

where the feed intake of the ewe includes that required for growth to mature size, for maintenance, for pregnancy and for lactation and the non-food inputs include the management and health inputs required to keep a ewe, her lamb(s) and her ram requirement productive (Dickerson 1970; Thompson 1991).

While the energy cost of pregnancy and lactation is small compared to the cost of growth to maturity and maintenance (Dickerson 1978), it is correlated with the number of lambs born and raised by each ewe (Large 1970). This type of interaction between the traits involved in determining the efficiency of a lamb production system is not uncommon, with the pasture feed intake by each lamb increasing with the number of siblings they have to share their mother with (Large 1970) and the correlation between size and feed requirements as discussed in the next section of this literature review.

It is important for a modern breeding program to account for these correlations in order to balance the benefits of positive selection on a trait and the possible correlated responses that may occur in related traits. The importance of considering correlated responses in breeding programs is best illustrated in livestock species intensively selected for extreme production values. Selection in these species have led to a number of behavioural, physiological and immunological problems like pale, soft, exudative muscle in pigs and ascites in chickens (Rauw *et al.* 1998; Roux 1992a). One reason suggested for this phenomena is that artificial selection can lead to all resources being used at maximum efficiency, leaving no buffer to respond to unexpected stresses and challenges like infections (Rauw *et al.* 1998).

A further example of a correlated response which could adversely affect the advocated breeding program in the correlations between birth weight and later growth and between Most of the biological traits important in determining the efficiency of a lamb production system are subject to economic considerations, including the influence of market forces like supply and demand on the cost of various inputs and outputs. Examples that influence the value of the outputs from the production system include variation in the value of the outputs with age (e.g. lamb vs. mutton), with quality, with cut type (e.g. chops vs. loin) and/or seasonal variations in prices received (Amer *et al.* 1999; Archer & Amer 2009;

Dickerson 1978; Large 1970). Variation in the costs of production appear to be less pronounced (Roux 1992a), though feed costs do vary between the seasons and non-feed costs like management and health supplies are also subject to market forces. These fluctuations can complicate genetic selection which is generally a long-term strategy that requires stable goals (Kinghorn 1985).

2.2.1 The Correlation Between Size and Feed Efficiency

Fast growth to slaughter weight is desirable because it allows lambs to reach market weight before the dry weather in summer inhibits pasture growth and assists with the targeting of the higher prices available at certain times of the year (Archer & Amer 2009). The feed requirement of faster growing lambs is also reduced due to their younger age at slaughter contributing to lower overall individual maintenance requirements. However, the feed requirements of the parents is increased due their greater size (Brody 1945; Taylor 1980) which occurs as a result of a strong genetic correlation between mature size and early growth (Brash *et al*. 1994; Fischer *et al.* 2004b; Mousa *et al.* 1999). The increase in mature size of the parental stock is considered beneficial by many farmers because larger ewes are more fertile (Morel & Kenyon 2006), have a higher salvage value, are more economical as regards to the per head costs of shearing, crutching, shipping and sale (Robertson 1987; Thompson 1991) and have leaner progeny at the same weight (Taylor 1980). However, larger ewe weights are thought to be correlated with a greater incidence of injuries to shearers which cost Australia $11.7 million in 2005-06 (including income compensation, medical and related expenses; Michael Lawerence and Associates Pty Limited 2007).

Studies have shown that the ewe is responsible for over 80% of the total food costs in a self-replacing lamb production system (Amer *et al.* 1999; Thompson 1991). This is due to the larger size of the ewe compared with its slaughter progeny and its consequently higher maintenance requirements, and the need to maintain ewes year round, including during the winter months when more feed is required to maintain body heat and feed is typically limited. As a consequence, studies conducted by Thompson (1991), Snowder and van Vleck (2003), and Morel and Kenyon (2006) have shown that there are no gains in efficiency (the ratio of lean tissue produced to feed consumed) to be made via larger sheep in lamb production systems.

Despite its importance, the relative costs of feed for progeny and parental stock are typically ignored in most breeding programs because its direct measurement requires specialist apparatus which is expensive in both economic terms and in management/growth terms. It is also difficult to use accurately (Amer & Emmans 1998; Snowder & van Vleck 2003). By comparison, the relevant outputs in a lamb production system (lamb weight and carcass quality, number of lambs weaned per ewe, surplus ewe value) can be easily counted, measured or weighed. These issues result in few animals being tested and those that are, are only tested in a single environment over a short subset of their life, reducing the accuracy of the measurement (Amer & Emmans 1998). As a consequence, accurate estimates of an individual's genetic value and genetic parameters for feed efficiency are rare, adversely affecting the design and success of breeding programs incorporating this trait.

Dickerson (1970), Fitzhugh (1976), Robertson (1987), and Lambe *et al.* (2006) have advocated selection to maximise early growth whilst minimising any increase in mature size. This is also known as "(growth) curve bending" and can be used to increase the efficiency of a lamb production system. The main advantage of curve bending is that the feed requirements of adults is reduced relative to those of the sale progeny, but the strong genetic correlations between early growth and mature size (Brash *et al.* 1994; Fischer *et al.* 2004b; Mousa *et al.* 1999) means that any improvement in lamb production efficiency by this method is slow.

The use of terminal sires is a crossbred version of "feeder breeder dimorphism" which is where large offspring for slaughter is obtained from small breeding animals (Roux 1992b). In this situation, a large terminal sire breed is mated to a smaller ewe breed to take advantage of the lower feed requirements of the smaller ewe while half of the large mature sized sire benefits (faster growing and leaner) are conferred to the progeny (Dickerson 1970; Large 1970; Thompson 1991). While it is undesirable to keep replacements from this type of production system (hence the 'terminal' name), there are large benefits in the amount of lean meat marketed per feed consumed. Thompson (1991) found that a 30% larger male resulted in a 7% increase in efficiency, while Large (1970) found that the gain

in efficiency from the use of a terminal sire was equal to increasing fertility by 300% in a large ewe.

2.2.2 Sexual Dimorphism in Livestock Production

Increasing the sexual dimorphism (sex-specific variation in growth rate and terminal size) of dual purpose breeds is an alternative to the use of terminal sires and does not have the disadvantage of having to maintain independent purebred lines or the crosses not being suitable for further breeding (Roux 1992b). This technique is an extension of the curve bending approach described in the previous section where selection is applied in a sexually dimorphic manner to maximise early growth in rams whilst minimising any increase in the mature size of ewes. There are two assumptions that are required for this approach to work. The first is that most ewe offspring are destined to be retained as flock replacements, whereas the majority of rams are destined for slaughter. This is true in a self-replacing production system but could lead to issues in a terminal sire production system if the extra ram growth resulting from sex-specific selection does not compensate for the restricted ewe growth. The second assumption is that there is variation between the sexes in how growth is inherited. This variation will reduce the genetic correlation between early growth and mature size which otherwise limits the potential of the curve bending approach to improve the efficiency of lamb production (Fitzhugh 1976; Robertson 1987). This assumption is tested in Chapter 4 of this thesis and the results obtained by other researchers are presented in a section 2.6 of this literature review.

The use of sexual dimorphism in breeding programs that are designed to reduce the feed requirements of a production system was first published for chickens by Jaap (1969). The approach suggested for use by Jaap (1969) was to use a recessive, sex-linked dwarf gene discovered by Hutt (1959) to reduce the size and feed requirements of female (hen) parents. The dw gene reduced adult hen body size by 30% (from 5kg to 3.5kg) and feed intake by 33%, and increased the housing density by 40%, yet their progeny retained normal growth rates (Hutt 1959; Merat 1984).

It is surprising, given the large number of papers that have been published on the topic of sexual dimorphism reducing the feed requirements of chicken production systems, that beef cattle are the only other livestock species in which this concept has been investigated (Roux

1992b; Schoeman 1996). Part of the reason for the lack of research interest is that there are no known major genes responsible for sex-linked dwarfism or gigantism, without negative effects on the viability of individuals or progeny, in either sheep or cattle. It is possible that dwarfism genes exist in these species but typical selection rapidly eliminates smaller individuals, preventing their detection. The biological modelling used by Roux (1992b) and Schoeman (1996) to test the viability of using sexual dimorphism in South African beef production systems assumed that any genetic changes in the degree of sexual dimorphism would be the result of polygenic inheritance. These experiments revealed that the gain in efficiency from utilising sexual dimorphism was dependent upon the degree of sexual dimorphism and the proportion of females marketed/kept as replacements (Table 2.1; Roux 1992b) and that the most efficient breeds were those that exhibited the highest degree of sexual dimorphism (Schoeman 1996).

Table 2.1: Predicted gain in feed efficiency through sexual dimorphism (Roux 1992b)

	Male/female weight			
% females marketed	1.0	1.2	1.6	2.0
50	0%	6%	16%	25%
67	0%	5%	14%	22%
75	0%	5%	13%	21%

The level of sexual dimorphism reported in different breeds of sheep at different ages and under different nutritional regimes is highly variable. From literature that reported ewe and ram weights from the same flock, it was found that sexual dimorphism varied between 1.0 (ram/ewe weight; Stanford *et al.* 2001) and 1.5 (Thompson *et al.* 1985; see Appendix 1 for full listing). By comparison, Taylor *et al.* (1985) reported that the average sexual dimorphism in beef cattle was 1.4 and Roux (1992b) found it varied between 1.2 and 1.6 in all South Africa cattle breeds. To achieve greater levels of sexual dimorphism, Roux (1992b) advocated a combination of genetic selection and restricted feeding for females. However, some authors have suggested that there are biological limits to what degree of sexual dimorphism is practical. For example, large size differences may prevent mating, or small mothers might be incapable of giving birth to, or producing enough milk to feed large progeny (Merat 1984; Roux & Scholtz 1992).

2.3 Sexual Dimorphism in Nature

Evolutionary biologists have paid considerable attention to the presence of sexual dimorphism in nature, appearing to be intrigued by the evolution of dimorphic sizes and shapes in each sex. One also cannot discount Charles Darwin's interest in sexual dimorphism, expressed as the theory of sexual selection in "The descent of man, and selection in response to sex" (Darwin 1875) as a stimulus for future generations of researchers (Smith 1999). Body size is the most obvious example of sexual dimorphism, as it is exhibited in our own species and also in common pastoral livestock species like sheep, cattle, deer and goats (Glucksmann 1974). Other examples of sexual dimorphism include the size of various mammalian internal organs (Glucksmann 1974) and the horn or antler size of bighorn sheep and some deer species (e.g. Clutton-Brock *et al.* 1982; LeBlanc *et al.* 2001; Poissant *et al.* 2008).

The presence of sexual dimorphism throughout the animal kingdom suggests that there is a wide variety of reasons for its occurrence (Slatkin 1984). However, the proposed mechanisms can be summarised into two categories: sexual selection or intersex niche divergence. Of the two hypotheses, sexual selection is the most widely accepted. Sexual selection was suggested by Darwin (1875) to occur because of the sex-specific factors that influence reproductive success. For example, the reproductive success of polygynous males (as found in all livestock species) is limited by access to females. This places emphasis upon selecting males with good growth, mobility and fighting traits that enhance an individual male's ability to find, build and maintain a harem. The reproductive success of females, by comparison, is not as dependent upon body size but upon investment in condition, early maturity at expense of size and reproductive lifespan (Clutton-Brock *et al.* 1982; Lawler 2009; LeBlanc *et al.* 2001; Post *et al.* 1999; Shine 1989). This is illustrated in various deer species in Figure 2.1 where the number of hinds mated by each stag (also known as polygyny or breeding party size) increases with sexual dimorphism. Ultimately, sexual selection occurs when there is variation between males and females in the optimal value of individual traits, which leads to divergent selection (Reeve & Fairbairn 2001). This is valuable for the overall survival of the species, as it promotes genetic diversity by mating individuals who are dissimilar genetically (Foerster *et al.* 2007; Kruuk *et al.* 2008).

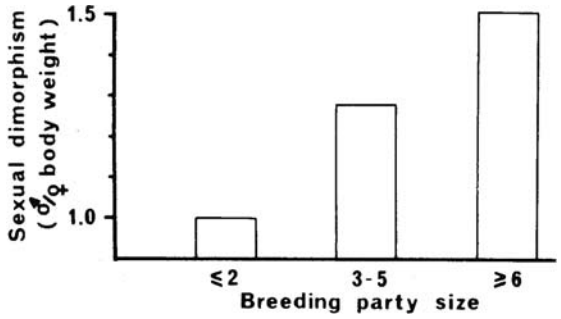

Figure 2.2: Sexual dimorphism in response to variation in polygyny in various species of deer. The variation in sexual dimorphism in each group is illustrated by the error bars (Clutton-Brock *et al.* 1982).

The presence of sexual selection can also be counter-productive. In order to grow to greater sizes or develop superior weaponry like horns or antlers, the males of some species directly utilise a greater proportion of the energy they obtain from feed than females and consequently, have less fat reserves which make them susceptible in times of feed shortages or ill health (Clutton-Brock *et al.* 1982; Post *et al.* 1999). Larger males are also more likely to fight to establish their dominance, thus risking injury which can reduce their ability to survive and/or breed. In fact in some species, it has been noted that smaller males wait for the larger males to be distracted by dominance competitions before sneaking in to breed with receptive females (Weckley 1998). The increased risk of male death in sexual selection is not important in the overall survival of polygynous species as it forms part of the natural selection and reduces the number of males competing for females (Clutton-Brock *et al.* 1982).

Differences between the niches occupied by each sex (intersex niche divergence) was also suggested by Darwin (1875) as a method by which sexual dimorphism may have evolved. However, Darwin doubted its validity as it implies that there is sufficient variation between the environments occupied by males and females to cause divergence in ideal trait values for each sex. This is unlikely to occur in domesticated livestock species, but there are examples of wild animals (e.g. lions and deer) where males and females live separately after weaning or reaching sexual maturity. For these species, there are often differences between the sexes in population density, climate, habitat use and diet selection which could lead to unequal selection pressures between the sexes (Clutton-Brock *et al.* 1982; LeBlanc *et al.* 2001; Post *et al.* 1999).

Lande (1980) proposed that sexual dimorphism evolved in two distinct phases, as shown in Figure 2.2. The first phase involves both sexes evolving in parallel towards an equilibrium point where the selective forces operating on each sex due to sexual selection and/or intersex niche divergence is equal in magnitude but opposite in direction. The similarity in response observed in each sex during this phase is due to the similarity in their genetic makeup and subsequent high intersex genetic correlation. Once the equilibrium point is reached, the second phase begins and the two sexes slowly diverge as mutations present in one sex and not the other weaken the intersex genetic correlation. This allows a divergent response between the sexes as they evolve independently towards their optimal genetic values.

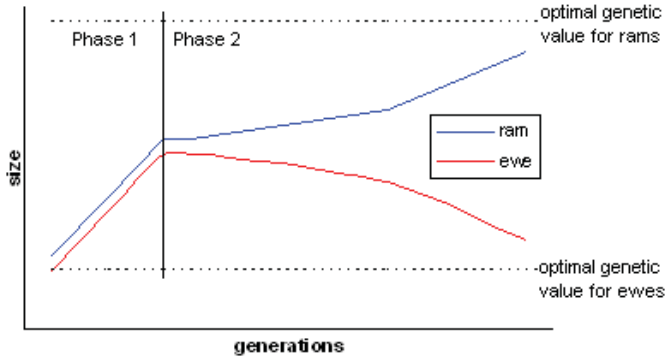

Figure 2.2: Graphical depiction of Lande's (1980) theory on how sexual dimorphism could have evolved.

2.4 The Physiological Regulation of Sexual Dimorphism

In 355 BC, Aristotle postulated that sexual dimorphism arose from differences in the heat of semen at the time of copulation. In his scheme, hot semen generated males, whereas cold semen created females (Haqq & Donahoe 1998). Today we know that the sex of most mammals is determined by the action of SRY (sex-determining region Y gene) on the short arm of the Y chromosome. The presence of SRY initiates testis formation resulting in male differentiation and its absence results in ovary formation/female differentiation (Haqq & Donahoe 1998; McClive *et al.* 2003; Williams & Carroll 2009). The resulting sexual differentiation is detectable as early as six hours after fertilisation at the 32 cell stage in large mammals, when male embryos grow up to five times faster than do female embryos in order to achieve early gonadal differentiation and the corresponding production of gonadal testosterone necessary to sustain their normal sex-specific development (Badyaev 2002).

Sexual dimorphism in sheep is the result of higher growth rates and a longer growing period in males (Badyaev 2002). The regulation of these growth patterns are thought to be under genetic control and arise mainly from the activation and repression of structural and regulatory genes which vary the metabolic activity and chemical composition of differentiated cells. At the cellular level, this results in a greater number of larger cells in males than females, variation in hormone secretion (particularly growth hormone) and in enzyme levels which leads to sex-specific protein and fat accretion and skeletal growth (Atchley 1984; Borski *et al.* 2000). The resultant variation in size and body composition between the sexes is detectable before puberty. Figure 2.3 summarises the process of the differentiation of males from females.

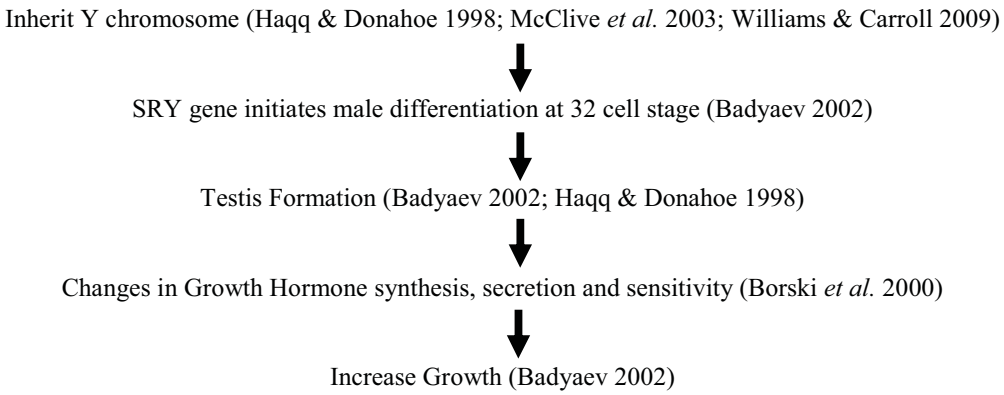

Figure 2.3: Summary of male differentiation

The sex-specific secretion and roles of growth hormone (GH) are well understood in sheep because it is one of the few species where the level of hormones (GH release factor and the GH inhibiting factor/somatostatin) that control the release of GH can be monitored separately to the levels of GH (Veldhuis *et al.* 2002). There are four processes that regulate sex-specific expression of GH induced growth. First, prenatal exposure to steroids (including those of maternal origin) determines the sex-specific sensitivity of the pituitary gland to GH controlling hormones (Gatford *et al.* 1998). Subsequent exposure to steroids (e.g. during puberty) produces strongly sex-specific GH release and thus sexually dimorphic growth (Badyaev 2002). Secondly, gonadal steroids, whose levels vary markedly between the sexes, can influence the hypothalamic secretion of GH controlling hormones directly and thus produce sex-specific concentrations of GH. Thirdly, sex steroids can

produce a sex-specific density and distribution of hormone receptors and hormone secreting cells in early development. This ultimately results in long-term variation in sensitivity to hormones across tissues (Badyaev 2002). The fourth process is GH stimulation of insulin like growth factors 1 and 2 (IGF1 & IGF2), which are believed to mediate many of the effects of GH on tissue growth and metabolism (Gatford *et al.* 1997).

2.5 The Inheritance of Sexual Dimorphism

The sex of all mammals is determined by the inheritance of either two X chromosomes (females) or an X and a Y chromosome (males). The presence of the Y chromosome in males and not in females makes the Y chromosome an ideal vehicle to carry the genes responsible for the greater growth of males leading to sexual dimorphism. However, both Reinsch *et al.* (1999) and Engellandt and Tier (2002) found little or no evidence of the genetic variation in growth being caused by variation on the Y chromosome in cattle and Meadows *et al.* (2004) reported that little variation was to be found on the Y chromosome between seven breeds of sheep. This may be due to the relatively small amount of genetic information carried on the Y chromosome compared to other chromosomes (Haqq & Donahoe 1998; McClive *et al.* 2003), despite its important role in sex determination. An example where sex linked inheritance causes sexual dimorphism is the *dw* dwarfism gene in chickens (Hutt 1959). In all bird species the female is the heterogametic sex (ZW vs. males with ZZ) which allows the dwarfism gene, located on the w chromosome, to only be inherited by females where it acts to retard growth. Because it is impossible for males to inherit this gene, their growth phenotype remains normal and sexual dimorphism increases in populations where this gene is present.

The influence of autosomal genes, which comprise the majority of the genome (Bowman 1968; Williams & Carroll 2009), on sexual dimorphism, is less direct. Autosomal genes are inherited equally by both sexes and consequently, any variation contained within is passed on equally to each sex (Reeve & Fairbairn 1996). However, the expression of these genes can be regulated by sex-linked genes allowing them to contribute to the phenotypic differences observed between the sexes (Fairbairn & Roff 2006; Williams & Carroll 2009). Genetic (or parental) imprinting is another inheritance pattern that depends on sex, but the

phenotypic expression of these genes depends on the sex of the parent passing on the genes, not the sex of the individual. As a consequence, both male and female progeny express these gene(s) in the same way, thus they do not contribute to sexual dimorphism. Due to most known imprinted genes having only prenatal effects, it is thought that one of their roles is to restrict male growth *in utero* to avoid sexual dimorphism in birth weight causing birth difficulties. It is worth noting that although few imprinted genes have been studied for postnatal effects (Charalambous *et al.* 2008), the following imprinted genes have been linked with either growth or body composition, the *Callipyge* muscle hypertrophy (CLPG) gene in sheep and the Insulin-like Growth Factor 2 gene in sheep, cattle and pigs (de Koning *et al.* 2000; Engellandt & Tier 2002; McLaren & Montgomery 1999; Wrzeska & Rejduch 2004).

In quantitative genetic terms, it is necessary to consider the levels of heritable variance at different ages and also the nature of the covariance between age specific size traits to understand the evolution of body size (Wilson *et al.* 2005). We must take this one step further in order to understand the evolution of sexual dimorphism and consider the *between sex* variation in the levels of heritable variance and covariance between the traits (Fairbairn & Roff 2006; Lande 1980; Rice 1984; Robertson 1959). Genetic correlations can be estimated between sex limited traits (e.g. between male weight and female weight in this study) despite the fact that no individual can express both phenotypes. This is because while a male will not express a female trait (and vice versa), he has female relatives who do. The female relatives then provide information as to the male's genetic merit for the unexpressed female phenotype, just as male relatives can provide information on the female's genetic merit for their unexpressed male phenotype. Nevertheless, some caution is required when modelling sex limited traits since while the genetic covariance can be estimated from the performance of relatives, the same cannot be said for the environmental covariance and thus the total phenotypic correlation must remain undefined (Wilson *et al.* 2010). In a large review of 114 studies containing intersex genetic correlations from a wide variety of species including three plant, three fish, nine mammal, and 19 invertebrate species, and a wide variety of traits including size, fitness and behavioural traits, Poissant *et al.* (2010) found a negative relationship between the magnitude of sexual dimorphism and the intersex genetic correlation (Figure 2.4).

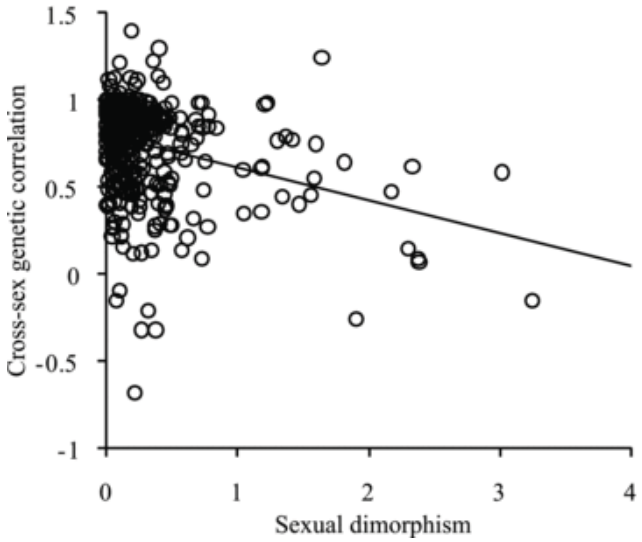

Figure 2.4: Crude relationship between the intersex genetic correlation and sexual dimorphism (Poissant *et al.* 2010).

2.6 The Estimation of Sex-specific Genetic Parameters

Of the large number of studies that have compared male and female heritability and/or estimated the intersex genetic correlation for the same trait, there are 12 studies that have been conducted on domestic sheep (Table 2.2). Twenty-one out of the 29 estimates contained in these studies found that female heritability is larger than found in males, though only two out of the 23 that reported standard errors were significant (95% confidence interval). Eisen and Hanrahan (1972) and Hanrahan and Eisen (1973) estimated the heritability of sexual dimorphism in live weight as a single trait based on mice breeding programs selecting for divergent growth in each sex. These estimates were at the low end of the heritability scale, ranging from 0.06±0.01 to 0.07±0.09, suggesting that selection for sexual dimorphism is impractical in mice populations. Similar research in other mammalian species was not found.

Table 2.2: Male and female heritabilities for live weight and the genetic correlation between the two sexes for the same trait. Light grey shading indicates the non-significantly higher estimate, yellow shading if the difference is significant (95% confidence interval).

		age	male		female				
Breed	Model	(months)	h^2	se	h^2	se	rg	se	Reference
Merino	p	15	0.58		0.64				Young *et al.* 1960
Merino	p	3	0.35		0.32				Young *et al.* 1965
Merino		3	0.28		0.32				Pattie 1965
Rambouillet	s	3	0.07	0.13	0.06	0.12			Vesely & Robison
Rambouillet		8.5	0.23	0.15	0.30	0.15	0.81	0.21	1971
Romnelet		3	-0.10	0.11	0.12	0.14	1.00		
Romnelet		8.5	0.05	0.13	-0.01	0.12	1.00	0.16	
Romney	s	3	-0.06	0.04	0.20	0.06			Baker *et al.* 1979
		5	0.13	0.07	0.36	0.09			
		7	0.14	0.07	0.34	0.09			
		10	0.21	0.08	0.46	0.10			
		13	0.23	0.08	0.31	0.08			
		16	0.14	0.07	0.40	0.09			
Merino	a	12 (h)	0.28	0.07	0.56	0.09			Lax & Jackson 1987
		12 (m)	0.22	0.09	0.57	0.11			
		12 (l)	0.14	0.09	0.35	0.1			
Romney	s	3	0.1	0.02	0.06	0.02	0.88	0.08	Parratt *et al.* 1989
		autumn	0.17	0.03	0.14	0.03	0.88	0.08	
		spring	0.27	0.04	0.22	0.03	0.75	0.1	
Romanov	a	1.5	0.35	0.05	0.22	0.05			Maria *et al.* 1993
		3	0.21	0.02	0.31	0.02			
Romney	p	12	0.18		0.35		0.89	0.08	Bisset *et al.* 1994
Merino	s	3	0.39	0.08	0.37	0.08	0.89	0.11	Lewer *et al.* 1994
		4	0.25	0.1	0.34	0.07	1.20	0.28	
		11	0.27	0.09	0.43	0.08	1.11	0.13	
		14	0.27	0.09	0.48	0.09			
Merino	am	4	0.13	0.05	0.23	0.04	1.00		van Vleck *et al.* 2000
White Breeds	am	4	0.14		0.20		0.98		Näsholm 2004
Gotland Breeds		4	0.17		0.24		0.97		

p = parent offspring regression model
s = sire model
a = animal model without maternal effects
am = animal model with maternal effects
(h)/(m)/(l) = high, medium and low fleece weight lines
3 months = weaning weight

The variation found between studies shown in Table 2.2 can be partly attributed to the statistical models used to estimate the genetic parameters. Some estimates were not corrected for fixed effects and were calculated by (a) half sib correlation, (b) full sib correlation, and (c) parent offspring regression. These methods all estimate the additive variance as a proportion of total variance, but there are other sources of bias that they do not account for, some of which are genetic in origin (e.g. maternal effects and non-additive

variation; Bowman 1968). Parent offspring regression is the only one of these methods that was used in the sheep examples presented in Table 2.2. This type of regression can take one of three forms, where the regressions are calculated between the offspring and dam, offspring and sire and off-spring and mid-parent data.

Sire or dam models are a form of mixed model that accounts for the influences of fixed effects and uses a combination of either a sire offspring regression with the paternal half sib correlation or a dam offspring regression with a maternal half sib correlation to estimate genetic parameters. The downside of these models is that it ignores half of the relationships formed by the parents, which prevents full sib correlations being estimated in single sex data and the estimation of maternal and non-additive genetic effects. Animal models are similar to sire models but utilise all of the information provided from both sire and dam relationships. This allows greater utility for the analysis of sex-specific data, the analysis of full sib groups and the estimation of maternal and non-additive genetic effects. The animal model is used by Sheep Genetics for the estimation of breeding values for the Australasian sheep industry (Brown *et al.* 2000) and has been successfully used in sex-specific analyses by Koch *et al.* (1973) and van Vleck and Cundiff (1998) in cattle, by Eisen and Hanrahan (1972) and Hanrahan and Eisen (1973) in mice, and Lax and Jackson (1987), Maria *et al.* (1993) and van Vleck *et al.* (2000) in sheep.

Random regression is a relatively new model available to animal breeders to estimate genetic parameters and breeding values. The main advantage of this technique, when compared with the previous models, is that it can be used to analyse traits that change continuously over a trajectory (e.g. weight with time; Fischer *et al.* 2004b; Lewis & Brotherstone 2002; van der Werf 2001). This removes any inaccuracies incurred by the requirement to correct data (weights) to specific ages as is necessary with traditional animal models and allows the covariance structure between any two ages on the trajectory to be described, even for pairs of ages for which there are no observations (Meyer 1999 & 2004; Nobre *et al.* 2003b;). Because there are potentially ‘infinite’ time points and records per animal, this has been termed an ‘infinite dimensional’ analysis (Kirkpatrick *et al.* 1990).

A random regression analysis has two components. The first stage uses a fixed regression, typically in the form of Legendre polynomial, to describe the average shape of the growth curve for the whole population. The second stage uses random regressions to account for each individual's variation from the fitted growth curve. From this, coefficients for additive genetic effects, maternal effects and permanent environmental effects (random effects) can be estimated by:

$$G_0 = \Phi K \Phi' \quad \text{(equation 2.2)}$$

where Φ is a matrix of Legendre polynomials for a set of specific ages and K is the corresponding matrix of (co)variance random regression coefficients for the random effects (additive genetic, maternal genetic and the dams permanent environmental effect) [k = var(α)]. The order of polynomial depends on how a trait changes along the trajectory. For example, when an order of zero is considered, no changes are assumed for the trait over time and only an intercept (α_0) is fitted, i.e. breeding values are identical at all ages. With an order of one we consider a slope as well as the intercept ($\alpha_0 + \alpha_1$) for the changes of the trait along the trajectory and the slope indicates an increase or decrease of breeding value with age (van der Werf *et al.* 1998)

The ability to model genetic differences in the shape of each animal's growth curve is important when genetic variances and covariances change rapidly during certain periods on ontogeny (e.g. puberty; Kirkpatrick *et al.* 1990) and becomes even more important when comparing males and females as each sex reaches puberty at a different age (Taylor 1968). However, the accuracy of the genetic parameters estimated by random regression can be affected by the distribution of data along the dataset, particularly at the extremities, the presence of animals with missing data, and the quality of the pedigree available (Meyer 2005; Nobre *et al.* 2003a, 2003b; van der Werf 2001). Random regression can also require more computing resources than multitrait models due to denser incidence and coefficient matrices and the increased number of effects that require estimation as each effect is estimated all the way along the trajectory rather than at a limited number of specific age demarcations as found in traditional multitrait analysis of growth (Kirkpatrick *et al.* 1990; Meyer 1999, 2004; Nobre *et al.* 2003). Insufficient records for each animal to fit the polynomial required by the model also increases the computing requirements of random regression as records from related individuals have to be used to provide information on

additional ages (Meyer 2004). This type of analysis has also not been previously applied to single sex data.

Some authors have argued that differences in the scale of genetic variation between ages, traits or sexes in multivariate analysis can play an important part in determining the accuracy of genetic correlation estimates (Atchley 1984; Fairbairn & Roff 2006; Hill *et al.* 1999; James 1998). For example, James (1998) and Hill *et al.* (1999) found that the standardisation of wool fibre diameter records measured at different ages to a common genetic variance (i.e. the removal of a scale effect between the age groups) changed genetic correlation estimates between measurements in some instances. As such, genetic correlations of < 1.0 might only reflect a scale effect and not imply that genetic control of the trait was affected by age (Hill *et al.* 1999). These possibilities can be distinguished by transforming both groups to the same genetic variance and comparing the resultant estimates with those obtained from untransformed data. Using this method, Hill *et al.* (1999) found that after standardisation to a common genetic variance, there was up to a 0.65 drop in genetic correlation between wool traits, though the differences were rarely (two out of 15) significant owing to the large standard errors involved. This issue is irrelevant when comparing estimates of heritabilities obtained from univariate analyses because these are generated from the relative values of the additive genetic and phenotypic variances, thus cancelling out any scale effects. While it is well known that rams are larger than ewes, no attempts to account for scale differences in the genetic variances between the sexes of sheep have been published.

2.6.1 Prediction of the Response to Selection within each Sex and the Evolution of Sexual Dimorphism.

The breeder's equation (equation 2.3) can be used to predict the single trait phenotypic response to selection (R) that occurs in response to given levels of selection intensity applied to the trait (i), the heritability (h^2) and the phenotypic standard deviation (σ_p).

$$R = i \times h^2 \times \sigma_p \qquad \text{(equation 2.3)}$$

The second commonly found form of the breeder's equation predicts the correlated response to selection in a trait that occurs in response to selection upon a second, correlated trait. An example of when this equation would be used is when selection is only carried out in adult ewes. In this situation, the correlated response to selection (CR) in rams would equal the selection intensity applied to ewes for the trait multiplied by the square root of the heritability for the trait in ewes (h_{ewes}) multiplied by the square root of the heritability for the trait in rams (h_{rams}) multiplied by the genetic correlation between the two traits (r_g) multiplied by the phenotypic variation of the trait in rams ($\sigma_{p\ rams}$; equation 2.4).

$$CR_{ewes} = i \times h_{rams} \times h_{ewes} \times r_g \times \sigma_{p\ rams} \quad \text{(equation 2.4)}$$

Further derivations of the breeder's equations can be used to predict the response to selection within each sex (equations 2.5a & b; Cheverud *et al.* 1983 & 1985; Eisen & Hanrahan 1972; Lande 1980; Reeve & Fairbairn 2001) and the evolution of sexual dimorphism in response to selection for growth in each sex (equation 2.5; Cheverud *et al.* 1985).

$$R_{ram} = 0.5 \times (h^2_{ram} \times \sigma_{p\ ram} \times i_{ram} + h_{ram} \times h_{ewe} \times r_g \times \sigma_{p\ ram} \times i_{ewe}) \quad \text{(equation 2.5a)}$$

$$\text{or } R_{ewe} = 0.5 \times (h^2_{ewe} \times \sigma_{p\ ewe} \times i_{ewe} + h_{ewe} \times h_{ram} \times r_g \times \sigma_{p\ ewe} \times i_{ram}) \quad \text{(equation 2.5b)}$$

The equations for the response to selection in males or females account for both direct selection within sex (as described by equation 2.3), and the indirect selection that occurs in response to selection in the opposite sex (equation 2.4). This is important because some variables in the equation are inconsistent between the sexes, particularly the selection intensity which is generally much higher in males than females in domesticated sheep flocks. The response of sexual dimorphism to selection in each sex can be simply defined as the difference between male and female response to selection for the same trait (equation 2.5a – equation 2.5b) which can be summarised into a single equation (Cheverud *et al.* 1985) like so:

$$R_{SD} = 0.5 \times [h^2_{ram} \times \sigma_{p\ ram} \times i_{ram} - h^2_{ewe} \times \sigma_{p\ ewe} \times i_{ewe} + h_{ram} \times h_{ewe} \times r_g\ (\sigma_{p\ ram} \times i_{ewe} - \sigma_{p\ ewe} \times i_{ram})] \quad \text{(equation 2.6)}$$

While the prediction of the response to selection based on phenotype is useful in wildlife, the majority of pastoral livestock (except seedstock operations not utilising performance

recording and females in commercial flocks/herds) are selected using estimated breeding values (EBV). The response of each trait to selection using EBVs (R_{EBV}) is still influenced by the heritability of and selection intensity applied, and the genetic correlation(s) between traits limit the multivariate response. In addition to the heritability, the number of records available from relatives determines the accuracy of selection (r_{IA}). As such, differences between the ewes and rams in selection intensity and heritability, intersex genetic correlations, the additive genetic standard deviation (σ_a) and in the number and type of records available from relatives, could all contribute to a sex-specific response to selection using EBVs. The equation used to predict the response to selection using EBVs is given below:

$$R_{EBV} = i \times r_{IA} \times \sigma_a \quad \text{(equation 2.7)}$$

2.7 Bio-Economic Modelling of Lamb Production Systems.

Bio-economics can be defined as the use of mathematical models to relate the biological performance of a production system to its economic and technical/biological constraints (Alford 2004; Cacho 1993). The success of the these models depend on their ability to simulate each of, and the interactions between, the economic, environmental, nutritional, genetic and human managerial elements that influence the production system (Alford 2004; Amer & Emmans 1998; Cacho 1993; Jones *et al.* 2004; Morel & Kenyon 2006; Newman *et al.* 2000). The main advantage of bio-economic models is that they can infer the response in variables that are difficult and/or expensive to measure (e.g. feed intake; Emmans 1997). The structure of such components within the model is generally based on experimental results and assumes that these are representative of the flock being simulated. Because of the ability to simulate the key components of the production system, bio-economic models have been used to:

- Compare management options like the choice of stock class or species (Alford *et al.* 2003a & 2003b; Alford 2004), the timing of lambing (Morel *et al.* 2004) and selling policies (Morel *et al.* 2005a; Salmon *et al.* 2004). Commercial versions of bio-economic models, referred to as decision support systems (DSS), are available to assist farmer decision making in both Australia (Grazplan; Freer *et al.* 1997; Moore *et al.* 1997) and New Zealand (Q-Graze; MWNZ 2002; Woodward *et al.* 2001).

- Evaluate the risk to profitability from biological and/or economic variation like seasonal changes in prices received/paid (Archer & Amer 2009; Morel *et al.* 2005b; Morel & Kenyon 2006).
- Calculate economic values for traits included in the breeding objectives (Amer *et al.* 1999; Conington *et al.* 2000, 2001 & 2004; Oriade & Dillon 1997; Jones *et al.* 2004; Wang & Dickerson 1991).
- Identify correlated traits that can be used to select for hard to measure traits like feed intake (Amer & Emmans 1998).
- Identify gaps in our knowledge that require further research (Morel & Kenyon 2006).

The development of a bio-economic model starts with the mathematical description of the growth of each individual and their relationship with the environment (Cacho 1993). Growth is important because it is a key determinant of an individual's value and of the costs due to their feed requirements (Brody 1945; Taylor 1980). While many studies have generated growth curves from real data, the frequency of recording is rarely sufficient for modelling, particularly at ages where growth rate changes rapidly. These rapid changes in grow rate occur at two locations on the growth curve. The first is the increase that occurs soon after birth and the second is the decrease that occurs as the animal nears maturity. Unfortunately, industry flocks tend to only record between these ages as this is when weight is commercially relevant to them (determines slaughter age and when ewes can first be mated). By comparison, mathematical growth functions estimate the weight of the animal on a continuous scale. Both Lewis *et al.* 2002 and Lambe *et al.* 2006 have reviewed and compared the use of different growth models in sheep.

Some growth functions also allow the maximum growth under non-limiting conditions (potential growth) to be modelled. This avoids inaccuracies due to deficiencies in feeding, environment and health that occur in real data and provides a better representation of the true genetic potential for growth in the animals being modelled (Wellock *et al.* 2004). The earliest forms of such functions were single equations that were fitted directly to growth data as a function of time (e.g. Gompertz, 1825). Recent developments have allowed the interaction between the growth of an animal and its surrounding environment (e.g. climate,

pasture quality and quantity) to be modelled (e.g. Freer *et al.* 1997; Moore *et al.* 1997; MWNZ 2002; Woodward *et al.* 2001) at the cost of added complexity. In addition to the desired level of complexity, growth should be modelled as a continuous process that results in a single smooth sigmoidal shaped growth curve where (a) weight tends towards a final or asymptotic value with time; (b) growth rate has a maximum at some intermediate weight; and (c) the relative growth rate decreases as weight increases toward maturity (Lewis *et al.* 2002; Wellock *et al.* 2004).

The most widely used function used to describe animal growth is that developed by Gompertz (1825). As originally defined, this equation draws an asymptotic relationship between live weight and time without accounting for variation in feeding, environmental stressors or physiological status, though Amer *et al.* (1997) was able to incorporate a multiplier into the function to account for limiting growth conditions. The main advantage of the Gompertz function is that it only needs three parameters to describe the current state of the individual. Increasing the number of parameters increases the difficulty in ascribing any biological meaning to them and makes the accurate estimation of their values more difficult (Alford 2004; Cacho 1998). Other things being equal, using fewer parameters is always beneficial (Occam's razor), though some authors believe that the assumption that maximum growth occurs at a fixed point of maturity (defined as the point of inflection), an inevitable consequence of a three parameter function, to be a disadvantage (Wellock *et al.* 2004). The logistic function, as used by Nelder (1961) is similar to the Gompertz function except it utilises an additional variable and the point of inflection occurs at 0.5 of mature weight, in comparison to 0.368 of adult weight in the Gompertz function. An earlier system developed by Brody (1945) is more flexible in that it uses two functions which are applied either side of what is considered the point of inflection.

$$u_t = \exp(-\exp(G_0 - B \,.\, t) \qquad \text{(equation 2.8)}$$

The Gompertz equation given in equation 2.8 was used by Amer and Emmans (1998) and Jones *et al.* (2004) to predict the increase in protein that occurs with time in the body where u_t = the degree of protein maturity at time t, G_0 = initial condition and B is a general rate parameter. Protein often receives special attention because it is the most expensive nutrient

in metabolic, economic and environmental terms (Cacho 1993) and when the relative weights of it, lipid, carbohydrates and water are used to construct total empty body weight, the modelling of feed requirements is more accurate than the use of live weight on its own (Cacho 1993; Jenkins & Ferrell 1983; Lewis *et al.* 2002). Unfortunately, obtaining the necessary parameters required to model the growth of body components requires slaughter experiments in which body composition is measured. Such experiments are more expensive and consequently less common than the measurement of live weight (Lewis *et al.* 2002). A review of such experiments, for example Ferrell *et al.* (1979), Thompson and Butterfield (1985), Jenkins and Leymaster (1993), and Kirton *et al.* (1995b) also reveals that there is variation in the relative proportions of these components due to age, sex and breed that must be accounted for in each model. Some nutrition models also account for the increased dietary requirements that occur as a consequence of increased physical activity (including feeding and walking to water); temperatures outside of an animal's thermoneutral zone; excessive protein intake requirements; and low diet metabolisability (Jenkins & Ferrell 1983).

Once the feed requirements of each livestock class have been determined, the cost of supplying the feed must be estimated. The most common method, as utilised by Amer and Emmans (1998), Conington *et al.* (2000, 2001 & 2004), and Jones *et al.* (2004), is to calculate the net cost of feed from the cost of the land, fertilizer, seed and other input costs required (for a worked example see Appendix A of Jones *et al.* 2004). However, some of the costs used in these equations can be misrepresented if the appropriate consideration of economic and biological factors is not considered. Examples of this include that land is not something that can be simply acquired one year in order to increase production and disposed of the next and a certain amount of fertilizer is required to maintain productivity before any increases in production can be realised and will only have a response during the growing season. These are good examples of the interactions between biology and economics that must be described to accurately model a farming system.

By using a fixed area of land and assuming that the cost of feed production is equal across all scenarios, the pasture management component of the model can be removed, allowing a simplified model that is more suitable for evaluating livestock management or genetic

options. Feed costs are still indirectly included in the model as the opportunity costs involved in running one type of livestock over another. This method was successfully used by Alford *et al.* (2003a & 2003b) and Alford (2004) who compared two groups of beef cattle, one selected for feed efficiency and the other not. In these studies, the difference in feed intake between the two groups was made available to either more cattle or to a different class of livestock (sheep), thus giving a de facto value of feed from the value of additional animals. A further advantage of using models that establish the area of land available for pasture production up front, is that the seasonal variations in feed availability (and cost, where appropriate) can be modelled (e.g. Grazplan (Freer *et al.* 1997; Moore *et al.* 1997) and Q-Graze (MWNZ 2002; Woodward *et al.* 2001)). Other input costs like the cost of labour and health treatments, along with the prices received can also express seasonality in some production systems and have been shown to have marked effects on breeding objectives and farm system strategies in some studies (Archer & Amer 2009; Jones *et al.* 2004). The results of this type of model are more acceptable to the farming community as they directly replicates the type of decision that farmers are faced with when comparing the livestock production systems that they can run on their given amount of feed resources which is determined by land area, land type, pasture type and climate.

2.8 Literature Review Summary

This chapter suggested a possible role for sexual dimorphism in defining lamb production efficiency and reviewed the current knowledge on what determines the efficiency of lamb production (section 2.2), the presence of sexual dimorphism in the animal kingdom (section 2.3), the differences in how growth is regulated in ewes and rams, both physiologically (section 2.4) and genetically (section 2.5) and techniques that could be used to investigate how sexual dimorphism may be able increase lamb production efficiency (sections 2.6 and 2.7). It also identified gaps in our knowledge in these topics, some of which are investigated in this thesis. Chapters 3, 4 and 5 will test to what extent it is possible to select for divergent growth selection objectives in each sex and Chapter 6 models the actual value of incorporating sexual dimorphism in a typical lamb production system.

Chapter 3: Sex-specific Estimation of Heritability in Three Australasian Sheep (*Ovis aries*) Breeds

3.1 Abstract

This study estimated the magnitude of sexual dimorphism (sex-specific variation in growth and mature size) and sex-specific heritabilities for five weight and two scanning traits (fat and eye muscle depth) in three sheep breeds (Coopworth, Poll Dorset and White Suffolk) from industry supplied data. Rams were between 10 and 30% heavier than ewes depending on age, and had 4 to 6% lower fat depths and 21 to 22% lower eye muscle depths when corrected for live weight. There was a consistent, yet non-significant trend for heritability estimates to be larger for ewes than for males for all traits except fat and eye muscle depths in the Coopworth breed. These results have the potential to influence the accurate estimation of breeding values, to pursue selection objectives specific to each sex, to predict the response to selection in each sex and to derive optimal weightings placed on each trait within multitrait selection indices.

3.2 Introduction

Knowledge of genetic parameters like heritability (h^2) and genetic correlations (r_g) are required to make accurate predictions of the response to selection, genetically evaluate animals and design effective breeding programs (Lax & Jackson 1987; Safari *et al.* 2005 & 2007). As a result, there is a considerable amount of literature dedicated to estimates of genetic parameters in sheep (for a review see Safari & Fogarty 2003).

One aspect of genetic parameter estimation that has not received much attention is variation in heritability between the sexes. We know that sex is inherited genetically, specifically the inheritance of the Y chromosome by males and not by females. We also know that growth rate and terminal size differs between males and females (sexual dimorphism) in a large number of animal species including humans, sheep, cattle and goats (Roux 1992b). With the ongoing development of new reproductive technologies that can alter the sex ratio (sexed semen, sexed embryo transfer, etc.), the selective recording of traits according to sex

in the industry and the different roles for the majority of rams (sale) and ewes (replacements) in self-replacing production systems, knowledge of the intersex differences in the extent to which growth is inherited could become crucial information in the development of modern breeding programs.

Previous studies that have attempted to estimate the variation in the heritability of live weight between rams and ewes have had mixed results. Baker *et al.* (1979; weaning weight (at three months) in a Romney population), Lax and Jackson (1987; yearling weight in one out of the three Merino populations studied), Maria *et al.* (1993; three month weight and growth from 40 days to three months in a Romanov population), and van Vleck et al. (2000; four month weight in a composite breed) found that heritability estimates were larger for ewes than in rams. This trend was consistent in the studies conducted by Young *et al.* (1960; 15–16 month weight, Merino), Pattie (1965; weaning weight, Merino), Baker *et al.* (1979; 5, 7, 10, 13 & 16 month weights, Romney), Lax and Jackson (1987; weaning and yearling weight in two out of three Merino populations in the study), Lewer *et al.* (1994; weaning, eight month, yearling and 14 month weights, Merino), and Vesely and Robison (1971; weaning weight, Rambouillet and Romnelet) but the variation between the sexes in heritability was not significant. Young *et al.* (1965; weaning weight, Merino), Parratt *et al.* (1989; weaning, autumn and yearling weights, Romney) and Maria *et al.* (1993; weaning weight, Romanov) were the only studies to find larger heritability estimates for rams than ewes, though in each case the difference was small and not significantly different, partly due to the relatively small datasets analysed.

A wide range of methods was used to estimate the heritability in these studies. Young *et al.* (1960), Young *et al.* (1965), and Pattie (1965) used a parent-offspring regression, though Pattie (1965) also compared the results achieved from the realised divergence of selection lines selected for high and low weaning weight (regardless of sex). Baker *et al.* (1979), Lax and Jackson (1987), Parratt *et al.* (1989), Lewer *et al.* (1994), and Vesely and Robison (1971) used sire models, and Maria *et al.* (1993) and van Vleck *et al.* (2000) used the animal model approach. Of these approaches, the animal model is the most accurate because it accounts for all relationships between family members (e.g. sire-offspring, dam-offspring and between siblings). A mixed model containing animal effects can also be

extended to allow the estimation of the extent to which variation in the ability of the dam is due to variation in the additive effects of the genes (maternal heritability – m^2) and the permanent environmental (pe) influences on the dam's mothering ability including the non-additive genetic effects of the dam (Mrode 2005).

Animal models including maternal effects have been successfully used in other mammalian species by Eisen and Hanrahan (1972) and Hanrahan and Eisen (1973) in mice and by Koch *et al.* (1973) and van Vleck and Cundiff (1998) in cattle. This literature revealed similar results to those found in sheep – the direct heritability estimates for live weight were larger in males than females, though the difference was only significant for traits in the cattle estimates recorded after weaning (Koch *et al.* 1973; van Vleck & Cundiff 1998). No examples of sex-specific estimation of heritability for fat or muscle traits were found.

This study aims to estimate whether sexual dimorphism exists in live weight at five different ages and in fat and eye muscle depths at 7.5 months of age. Sex-specific heritabilities for each of these traits will also be estimated. Estimates are made for three breeds because of variations in the original genetic makeup of each breed (founder effect), where each breed evolved (natural selection) and the influence of domestication on the breed by humans (artificial selection towards different selection objectives in each breed; Bowman 1968; Zohary *et al.* 1998) that could lead to variation in sexual dimorphism. The data used was obtained from commercial ram producers and, as such, reflected sheep maintained under typical Australasian pastoral conditions.

3.3 Materials and Methods

3.3.1 Data

Data originated from the Sheep Genetics (SG) database and consisted of weights taken at five ages (Table 3.1) and post-weaning scanning data from Australian and New Zealand sheep. The breeds were selected on the basis of the number of weight records available for analysis and variation in breed history. Scanning data consists of Fat and Eye Muscle (EMD) depths at the C site of the 12th/13th rib and was obtained by SG accredited ultrasound scanners. Fat and EMD results obtained at post-weaning age were used in

preference to those recorded at one year old (yearling) due to the greater availability of data and because the lamb weights at this age are more representative of the average weight of slaughter lambs in New Zealand (Meat and Wool NZ Economic Service 2005) and Australia (ABARE 2007).

The Poll Dorset, White Suffolk and Coopworth breeds were chosen for use in this study based on the large numbers of weight records available on the SG database for these breeds and because of their roles in Australasian sheep production systems. The Poll Dorset and White Suffolk breeds are typically used as terminal sires where all progeny, regardless of sex, are sold and the Coopworth is used as a self-replacing maternal breed where most females are retained as replacements and most males sold. During data extraction in Microsoft Access™ (2003 edition), the age at measurement was calculated from the dates of birth and measurement, and then the data for each breed was split into different traits according to the age ranges given in Table 3.1.

Table 3.1: Sheep Genetics trait definitions and guidelines for trait measurement (Meat and Livestock Australia 2004).

Trait	Definition	Recommended Age Range
Weaning Weight	kg live weight at 100 days (3.3 months)	40 to 120 days
Post Wean Weight	kg live weight at 225 days (7.5 months)	80 to 340 days
Yearling Weight	kg live weight at 360 days (12 months)	290 to 430 days
Hogget Weight	kg live weight at 450 days (15 months)	410 to 550 days
Adult Weight	kg live weight at 540 days (18 months)	530 to 2315 days
Post Wean Fat	mm fat depth at 45kg live weight	80 to 340 days
Post Wean EMD	mm eye muscle depth at 45kg live weight	80 to 340 days

Records were omitted from the datasets in Access™ if they were missing essential information (e.g. sex, measurement age), if animals resulted from embryo transfer, if the birth rank was less than the rearing rank, and if an individual had less than 10 contemporaries of the same sex and from the same flock, birth year and trait management group, with which their performance could be directly compared. The number of records removed for each of these reasons is described in Table 3.2. The situation where the rearing rank (number of lambs successfully reared per ewe per lambing) exceeds birth rank (number of lambs born per ewe per lambing) of an individual can only be achieved artificially (by a recording mistake or by adoption, either voluntarily by the ewe or through

human interference) and the addition of extra lambs creates a situation where the genetic mother of the adopted lamb is not the same as the mother raising the lamb, thus creating conflict when estimating direct and maternal genetic effects. The situation for individuals resulting from embryo transfer is similar. The genetic mother of the embryo is recorded by SG and the recipient mother who raises the offspring is not. Also with embryo transfer there is evidence that the altered hormonal environment induced by embryo transfer influences pre- and post-natal growth (Wilson *et al.* 1995). Animals resulting from embryo transfer were identified either by a flag in the SG database or when the number of offspring per ewe per year exceeded the recorded birth rank. The datasets were further processed into a format that is suitable for analysis in ASReml (Gilmour *et al.* 2006) and contemporary groups were created from the farmer defined trait management group, birth flock and year. The summary statistics for each of the fixed effects in each dataset are shown in Table 3.3.

Table 3.2: The number of records remaining in the table after each data processing step.

	Number of complete records* obtained from SG database	Number of animals removed due to£:						Final Dataset Size
		Resulting from Embryo Transfer		Birth rank less than rearing rank		Less than 10 Contemporaries		
Coopworth								
Wean	40224	3677	9%	38	0%	519	1%	35990
Post-Wean	9609	1004	10%	6	0%	120	1%	8479
Yearling	22458	2350	10%	14	0%	462	2%	19632
Hogget	6737	665	10%	8	0%	274	5%	5790
Adult	433	49	11%	0	0%	12	3%	372
Poll Dorset								
Wean	109222	7434	7%	349	0%	1070	1%	100369
Post-Wean	106655	9432	9%	570	1%	930	1%	95723
Yearling	87837	11275	13%	215	0%	1803	2%	74544
Hogget	39136	8462	22%	45	0%	1124	4%	29505
Adult	2904	799	28%	4	0%	263	13%	1838
White Suffolk								
Wean	112300	7700	7%	270	0%	1980	2%	102350
Post-Wean	93244	6975	7%	225	0%	0	0%	86044
Yearling	56397	8452	15%	119	0%	3669	8%	44157
Hogget	13494	1370	10%	21	0%	889	7%	11214
Adult	846	80	9%	0	0%	124	16%	642

* Complete records are those containing all information required for analysis.

£ Records were removed in the order given in the table. The percentage values represent the percentage of data removed in each step.

Table 3.3: Summary statistics for the fixed effects present within sex in each dataset.

Age Group	Number in dataset		Average birth rank		Average rearing rank		Average dam age (years)		Number of contemporary groups	
Coopworth	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
Wean	17271	18719	1.79	1.75	1.63	1.62	3.37	3.34	217	219
Post-Wean	4409	4070	1.77	1.76	1.63	1.62	3.30	3.26	215	216
Yearling	9959	9673	1.81	1.82	1.67	1.67	3.53	3.39	178	137
Hogget	433	5357	1.89	1.71	1.57	1.59	3.80	3.08	23	48
Adult	0	372	-	1.85	-	1.74	-	3.26	-	8
Poll Dorset										
Wean	51956	48413	1.60	1.62	1.52	1.54	4.63	4.64	778	749
Post-Wean	56326	38737	1.60	1.62	1.51	1.54	4.64	4.66	812	642
Yearling	44379	30165	1.57	1.57	1.49	1.49	4.57	4.63	771	618
Hogget	19341	10164	1.54	1.51	1.46	1.43	4.55	4.51	380	267
Adult	296	1542	1.54	1.55	1.42	1.46	4.80	4.70	16	36
White Suffolk										
Wean	50935	51415	1.65	1.65	1.57	1.58	4.59	4.60	919	912
Post-Wean	47495	38549	1.64	1.64	1.57	1.57	4.57	4.61	1223	936
Yearling	25053	19104	1.60	1.61	1.53	1.53	4.50	4.55	680	557
Hogget	7290	3924	1.58	1.61	1.53	1.54	4.48	4.54	228	152
Adult	126	516	1.81	1.64	1.74	1.55	4.47	4.36	10	18

Pedigree files containing all available animals and relationships, regardless of the presence of records, were extracted from the SG database for each of the three breeds. Table 3.4 shows the family structure contained within each dataset. The total number of animals in each pedigree was 47897 Coopworth, 229584 Poll Dorset and 179226 White Suffolk. Base animals (parents without phenotypic observations) were assigned to genetic groups within the pedigree file. These assignments were allocated according to each base animal's birth year and sex, and this was similar to method described for the OVIS genetic evaluation software (used by SG) by Brown *et al.* (2000).

Table 3.4: Family structure for each of the datasets.

	Number of:										
							Maternal grandsires with records			Dams with records	
Age Group	Sires			Dams							
Coopworth	♂	♀	mixed*	♂	♀	mixed	♂	♀	mixed	♀	mixed
Wean	582	592	612	5141	6820	14464	394	412	424	5141	6820
Post-Wean	341	263	360	679	1010	5028	165	169	181	679	1010
Yearling	435	405	481	2459	3309	9338	321	338	349	2459	3309
Hogget	79	250	281	1160	1149	3997	204	210	220	1160	1149
Adult	n/a	41	n/a	2	n/a	n/a	29	29	30	2	n/a
Poll Dorset											
Wean	2302	2181	2392	9868	13864	46030	1377	1376	1484	9868	13864
Post-Wean	2427	1921	2520	7996	11793	46679	1255	1234	1351	7996	11793
Yearling	2268	1837	2468	5055	8327	42192	1380	1257	1486	5055	8327
Hogget	1140	801	1287	1425	2626	19285	609	586	657	1425	2626
Adult	53	171	186	118	126	1479	137	135	150	118	126
White Suffolk											
Wean	2367	2353	2486	11029	15025	44599	1737	1639	1852	11029	15025
Post-Wean	2474	2094	2576	8149	12073	42093	1468	1355	1564	8149	12073
Yearling	1700	1382	1857	18361	14442	26963	948	871	1034	2622	4465
Hogget	596	434	709	5735	3242	8105	275	262	312	225	485
Adult	26	53	71	109	419	521	16	41	48	26	26

* combined sex

3.3.2 Fixed Effects

The fixed effects included in the model were similar to those used in the OVIS program used by SG to estimate breeding values for the Australasian sheep industry (Brown *et al.* 2000) and in other recent Australasian estimates of genetic parameters for body weight and scanning results in sheep (Huisman *et al.* 2006; Johnson *et al.* 2006; Safari *et al.* 2007). Similarity between the published studies and that carried out here was maintained to allow comparison between the values estimated here with those in the literature.

ASReml calculated F values for each of the dense (< 100 levels) fixed factors included in the model which were monitored to ensure that any non-significant factors were removed from each analysis. The only fixed factor classified as sparse (> 100 levels) was contemporary group. The linear model used for the analysis of the weight traits was:

$$Y_{ijklm} = \mu + A_i + (BT \times RT)_j + EA_k + Sex_l + CG_m + e_{ijklm} \quad \text{(equation 3.1)}$$

Where:

Y_{ijklm} = an observation on weight at weaning, post-weaning, yearling and adult age ranges.

μ = the intercept of the model .

A_i = the fixed effect of the age of the animal at the time of measurement.

$(BT \times RT)_j$ = the fixed effect of the combination of birth rank (no. of lambs born by each dam per lambing) and rearing rank (no. of lambs reared to weaning by each ewe per lambing) (j = 11 (single single), 21 (twin single), 22 (twin twin), 31 (triplet single), 32 (triplet twin) and 33 (triplet triplet)).

EA_k = the fixed effect of the age of the dam (k = 1,…,5, corresponding to 2,3,4,5 and 6 years of age).

Sex_l = the fixed effect of gender (l = 1,2, corresponding to rams and ewes). Omitted in single sex analyses.

CG_m = the fixed effect of contemporary group. The number of groups in each dataset is described in Table 3.3.

The linear model used for the analysis of the scanning data was the same except that Y_{ijklmn} became either Fat or Eye Muscle depth and a covariate for live weight (kg) at the time of scanning (aka post weaning weight) was included in the model.

3.3.3 Estimation of Genetic Parameters

ASReml 2.0a software (Gilmour *et al.* 2006) was used to estimate variance components for each sex using restricted maximum likelihood methodology that employed an average information algorithm to concurrently provide estimates of standard errors for the parameters (Gilmour *et al.* 1995). An animal model including the fixed effects described in 3.3.2 and all known pedigree relationships was fitted. Three versions of the model were tried:

(a) With no maternal genetic effect or permanent environmental effect of the dam fitted.

(b) With the maternal genetic effect fitted but not the permanent environmental effect of the dam.

(c) With both the maternal genetic effect and the permanent environmental effect of the dam fitted.

Covariances between each of the random effects were assumed to be zero (e.g. no direct-maternal genetic correlation) because of the difficulty in estimating such correlations from

field data (Maniatis & Pollott 2003), particularly when each dataset was separated by sex in this study.

Convergence in each model was reached when the change in log likelihood between iterations reached 0.01 and log likelihood ratio tests were conducted to determine the most suitable model for each trait. An animal model including maternal genetic and permanent environmental effects (model c on previous page) is:

$$y = Xb + Zu + Wm + Sp + e \qquad \text{Equation 3.2}$$

Where y = a vector of observations, b = a vector of fixed effects (as described in 3.3.2), u = a vector of random direct genetic effects, m = a vector of random maternal (indirect) effects, p = a vector of permanent environmental influences on a dam's ability, e = a vector of random residual effects and the maternal non-additive genetic effects of the dam. X, Z, W and S are incidence matrices relating records to fixed, direct genetic, maternal genetic and permanent environmental respectively (Mrode 2005). This model can be reduced into model b above by removing the Sp (permanent environmental) term and into model a by removing both Sp and Wm (maternal genetic) terms.

A pragmatic approach was used to test the differences between the heritability estimates obtained in males and females. Because the estimates were obtained from different data, the comparison of log likelihoods obtained from the REML analysis was not practical. The distribution around each heritability estimate was assumed normal because of the large number of records involved, and therefore the standard errors approximated by ASReml were used to create confidence intervals. The significance level used in each confidence interval was 95%.

3.3.4 Calculation of Least Square Means for each Sex

Least square means for each sex were estimated by the 'predict' function in the ASReml software (Gilmour *et al.* 2006). These predictions are formed from a linear function of the vector of fixed and random effects in the linear model described in 3.3.3 to obtain adjusted means for each sex for the trait being analysed. The age at which the means were estimated for each trait were the same for both sexes though there was variation between breeds, reflecting the different data distributions in each breed. The least square means for the

scanning traits were corrected for age and weight within breed to allow accurate comparisons between the sexes.

3.4 Results

3.4.1 Least Squares Means for Rams and Ewes

Least square means correcting for the fixed factors described in section 3.3.2 are shown in Figure 3.1 (weights) and Table 3.5 (scanning results). These results show that sexual dimorphism exists in all of the traits analysed and when the relative values for the two sexes are compared (male weight/female weight), the amount of sexual dimorphism increases with age until they become adults where it decreases again. The amount of sexual dimorphism in each trait is similar across the three breeds.

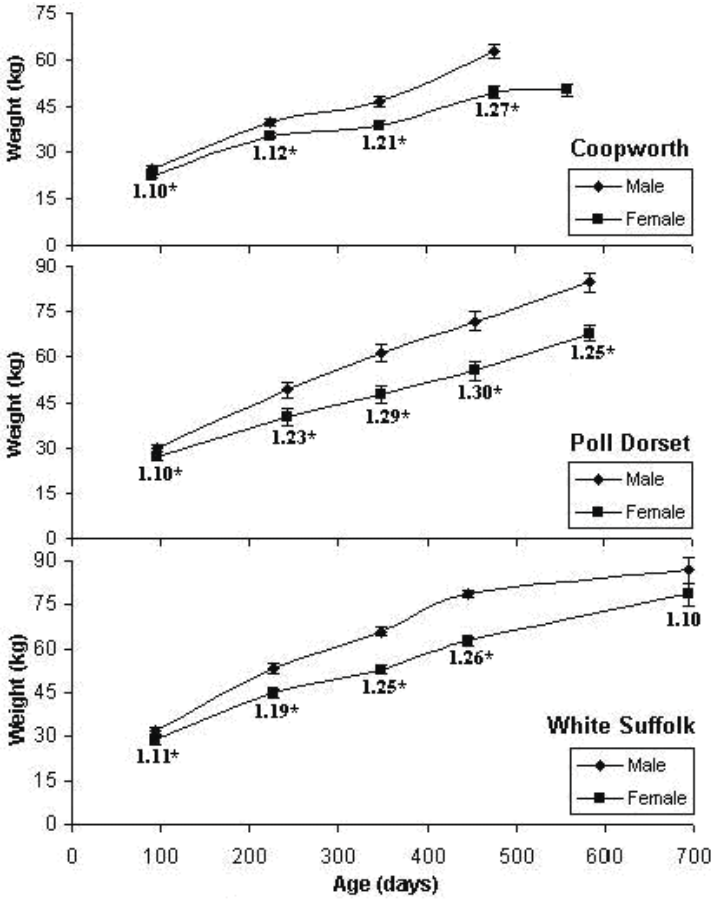

Figure 3.1: Male and female growth curves plotted from least square estimates for weaning, post-weaning, yearling hogget and adult weights. The values beneath the data points represent the degree of sexual dimorphism (male weight/female weight) and an asterisk indicates when the difference between the sexes exceeded the 95% confidence intervals shown by the error bars on the graph.

In all three breeds, ewes had deeper fat and eye muscle levels when the data was corrected for age and live weight at the time of scanning. When a similar analysis omitting live weight as a covariate was performed, the fat depth in ewes remained higher than in rams but in the Poll Dorset and White Suffolk breeds, the eye muscle depth was higher in rams compared to ewes.

Table 3.5: Least square means for scanning traits in male and ewes.

Breed	Trait	Sex	Depth (mm)	Male/Female
Coopworth	Fat	♂	2.36	0.78
		♀	3.02	
	EMD	♂	23.85	0.94
		♀	25.33	
Poll Dorset	Fat	♂	3.01	0.79
		♀	3.82	
	EMD	♂	28.89	0.96*
		♀	30.11	
White Suffolk	Fat	♂	3.04	0.78
		♀	3.91	
	EMD	♂	27.87	0.96
		♀	29.10	

* The difference between the sexes did not exceed a 95% confidence interval

3.4.2 Heritability Estimates for Rams and Ewes

For each of the weight traits, there was a non-significant trend that ewes have a higher heritability than rams (Table 3.6), though this was only significant for post-weaning weight in the Poll Dorset breed and yearling weight in the White Suffolk breed. The opposite effect, where the maternal heritability was greater in rams than ewes (non-significant) was observed in the majority (seven) of the nine datasets where this effect was estimated. Weaning weight in the White Suffolk breed was the only dataset where the difference between the sexes in the maternal heritability was significant and the exceptions to the male > female trend were weaning weight in the Poll Dorset breed and post-weaning weight in the White Suffolk breed. No trend or significant effects were apparent for the permanent environmental effects.

Table 3.6: Phenotypic variance (Vp), heritability (h^2), maternal heritability (m^2) and the variance due to the permanent environmental effect of the dams (p) for each of the weight traits. For each parameter, non-significant differences (95% confidence intervals) within each breed and age class are shown by identical superscripts.

Age	Breed	Sex	Vp	h^2	m^2	pe
Wean	Coopworth	♂	20.12[a]	0.308[a]	0.181[a]	0.119[a]
		♀	15.94[b]	0.394[a]	0.134[a]	0.122[a]
	Poll Dorset	♂	30.94[a]	0.280[a]	0.138[a]	0.131[a]
		♀	24.09[b]	0.338[a]	0.148[a]	0.128[a]
	White Suffolk	♂	31.71[a]	0.506[a]	0.265[a]	0.130[a]
		♀	23.83[b]	0.517[a]	0.191[b]	0.131[a]
Post-Wean	Coopworth	♂	22.25[a]	0.272[a]	0.220[a]	
		♀	17.06[b]	0.284[a]	0.104[a]	
	Poll Dorset	♂	52.36[a]	0.298[a]	0.189[a]	0.092[a]
		♀	30.98[b]	0.447[b]	0.160[a]	0.086[a]
	White Suffolk	♂	43.97[a]	0.416[a]	0.185[a]	0.121[a]
		♀	27.62[b]	0.482[a]	0.210[a]	0.105[a]
Yearling	Coopworth	♂	26.99[a]	0.323[a]	0.198[a]	
		♀	22.89[b]	0.364[a]	0.113[a]	
	Poll Dorset	♂	62.68[a]	0.295[a]	0.236[a]	
		♀	31.17[b]	0.350[a]	0.220[a]	
	White Suffolk	♂	49.31[a]	0.285[a]	0.195[a]	0.072[a]
		♀	32.87[b]	0.444[b]	0.133[a]	0.125[b]
Hogget	Coopworth	♂	60.75[a]	0.120[a]		
		♀	31.15[b]	0.411[a]		
	Poll Dorset	♂	76.14[a]	0.324[a]		
		♀	30.38[b]	0.368[a]		
	White Suffolk	♂	56.16[a]	0.249[a]		
		♀	33.37[b]	0.344[a]		
Adult	Poll Dorset	♂	57.88[a]	0.356[a]		
		♀	39.57[b]	0.487[a]		

The phenotypic variation was higher in rams than ewes for all weights ($p < 0.05$; Table 3.6). This effect is partially explained in all datasets by the presence of a positive correlation between phenotypic variation and weight. The relative proportions of each variance component (residual, additive, maternal and permanent environmental) in both

sexes are compared (Figure 3.2) in order to identify the differences that lead to the variation between the sexes in heritability, maternal heritability and permanent environmental variation. These comparisons revealed that ewes had lower (relative) residual variance with one exception (post-weaning weight in the Coopworth breed) and higher (relative) additive variance than rams in all datasets. The relative proportions of maternal and permanent environmental variances were small and relatively even across the two sexes. Similar comparisons of the different animal models (with and without maternal and permanent environmental effects) revealed that the proportion of residual variance was reduced when maternal effects were added to the model. The addition of permanent environmental effects reduced the maternal variance and the proportion of additive variance showed little variation regardless of model used.

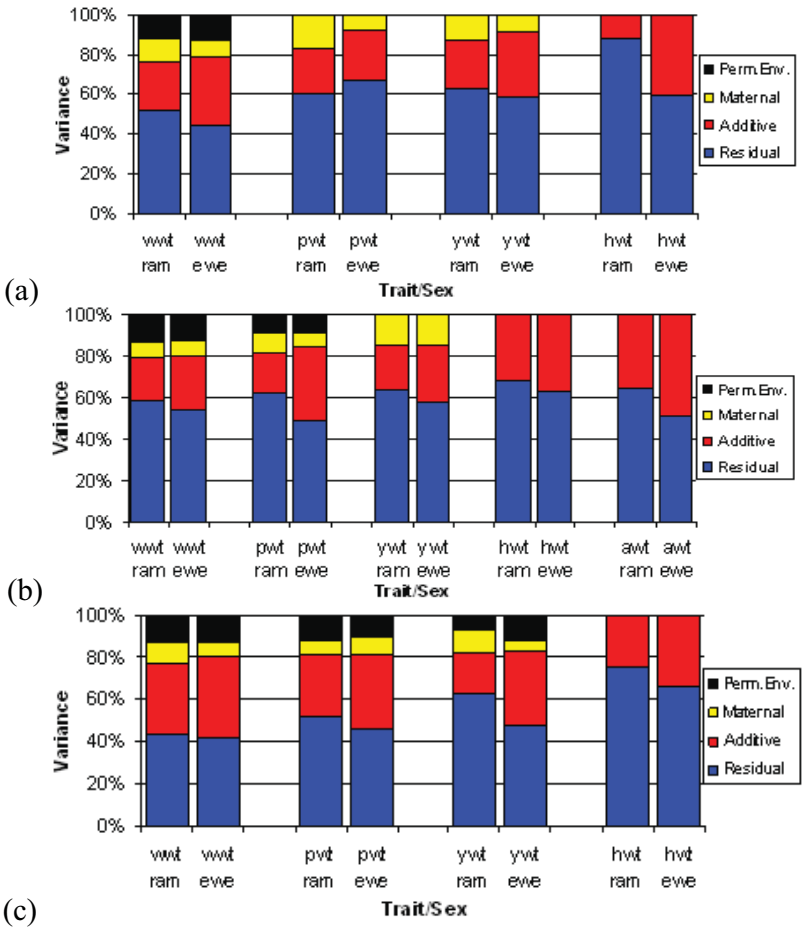

Figure 3.2: Relative proportions of variance components across mixed-sex, male and female datasets for each of the weight traits analysed. The three breeds shown are (a) Coopworth, (b) Poll Dorset, and (c) White Suffolk and the acronym of each weight is; wwt – weaning, pwt - post weaning, ywt – yearling and hwt – hogget.

The phenotypic variance in fat depth (Table 3.7) was significantly higher in ewes than in rams and was higher in rams than ewes for eye muscle depth (the Coopworth being the only breed where this difference was not significant). The trend of ewes having larger heritability estimates than rams was repeated for both fat and eye muscle depths in the Poll Dorset breed and for fat depth in the White Suffolk breed. However, these results were not consistent across breeds with the heritability estimates being larger in rams than ewes for fat depth in the Coopworth breed and in eye muscle depth in both the Coopworth and White Suffolk breeds.

Table 3.7: Phenotypic variance (Vp), heritability (h^2) and maternal heritability (m^2) for the scanning traits. For each genetic parameter, non-significant differences (95% confidence intervals) within each breed and age class are shown by identical superscripts.

Trait	Breed	Sex	Vp	h^2	m^2
Fat	Coopworth	♂	0.22^a	0.360^a	
		♀	0.31^b	0.305^a	
	Poll Dorset	♂	0.39^a	0.246^a	0.083^a
		♀	0.57^b	0.394^b	0.068^a
	White Suffolk	♂	0.37^a	0.300^a	
		♀	0.56^b	0.337^a	
EMD	Coopworth	♂	3.39^a	0.385^a	
		♀	3.07^a	0.320^a	
	Poll Dorset	♂	4.41^a	0.362^a	0.073^a
		♀	4.07^b	0.373^a	0.068^a
	White Suffolk	♂	3.97^a	0.365^a	
		♀	3.76^b	0.361^a	

3.5 Discussion

Rams were found to be heavier than ewes at all ages in this study and the magnitude of this difference increased with age until maturity. The estimates of sexual dimorphism at maturity were potentially biased by a lack of data in this age group and it is possible that compensatory growth (increased late growth to compensate for restricted growth earlier in development; Wilson *et al.* 2005) in females could also reduce sexual dimorphism, though the lack of data at maturity prevented any valid conclusions being reached on its presence. There are two factors that are likely to contribute to the increase in the magnitude of sexual

dimorphism prior to adulthood. Firstly, Mignon-Grasteau *et al.* (2000) suggested that any increase in sexual dimorphism with age could have a scale effect, where the difference between the sexes increases as the animals get older and heavier. However, if the reduction in sexual dimorphism observed in adults (as described above) is a real effect then it contradicts this hypothesis. Secondly, there was a noticeable jump in sexual dimorphism (~1.1 to ~1.2 in 125 days) between the weaning and post-weaning in the Poll Dorset and White Suffolk breeds, and between the post-weaning and one year of age in the Coopworth breed. This suggests that sexual dimorphism increases in response to the changes in physiology associated with sexual maturity (puberty; Badyaev 2002; Gatford *et al.* 1998).

The sexual dimorphism of body weight in this study, between 1.1 and 1.3 depending on age and breed, were within the range of values calculated from literature that reported both ewe and ram weights from the same flock (Appendix 1). The levels reported in literature varied between 1.03 and 1.54 depending on age, breed and feeding level (Cotterill & Roberts 1979; Kirton *et al.* 1995a; Lee *et al.* 1990; Lewis *et al.* 2002; Mousa *et al.* 1999; Pattie 1965; Stanford *et al.* 2001; Thompson *et al.* 1985; Thonney *et al.* 1987; Young *et al.* 1965). Typically, animal growth is reported to occur in a sigmoidal fashion (s-shaped curve), with an initial period of slow growth after birth followed by a longer period of faster growth that slows as an individual reaches its mature size (Brody 1945). This pattern was not observed in this study (Figure 3.1) because of the absence of data below 40 days of age and a lack of adult data.

The sexual dimorphism of fat and eye muscle depths in this study were found to be at the low end of the ranges found in the literature (fat 0.70 - 1.18 and EMD 0.94 - 1.09; Cotterill & Roberts 1979; Johnson *et al.* 2005; Kirton *et al.* 1995a; Stanford *et al.* 2001). Stanford *et al.* (2001) also found that the level of sexual dimorphism in both scanning traits was sensitive to the age at the time of measurement and to correction for live weight. For example, there were no significant fat depth differences between the sexes obtained at 120 days of age unless the data was adjusted for differences in live weight and males had larger eye muscle depths before 90 days of age, but not after. The data used in the current study was corrected for live weight and was, on average, from animals 225 days of age.

Thompson *et al.* (1985) expressed surprise at the lack of published estimates of sexual dimorphism in livestock as they can assist in the understanding of the differences between rams and ewes in their behavioural, feeding, growth and body composition characteristics. From sexual dimorphism studies of wild animals, we have learned that polygyny (mating ratios of one male to many ewes) is correlated with sexual dimorphism (reviewed in Jarman 1983) and that male growth is more susceptible to feed shortages than females (Clutton-Brock *et al.* 1982; Post *et al.* 1999). Both of these examples have potential impacts upon the management of sheep production systems. If rams are more susceptible to feed shortages than ewes, it is advisable to preferentially feed them when there are feed shortages. Domestic sheep also exhibit polygyny but no studies have been published linking sexual dimorphism (or ram mature size) with mating capacity.

The accurate derivation of selection indices will also be influenced by the variation in phenotypic variation and heritability between the sexes detected in this study. Sex-specific weightings on traits may be required to compensate for variation in selection response, particularly if selecting for sex-specific roles in a production system. For example, in a self-replacing lamb production system, most ewes are retained as replacement breeding stock, while most rams are slaughtered at a young age. Both of these roles would have quite different breeding objectives and variation in the selection response may allow some leeway for the differing objectives to be met.

Despite the presence of published studies utilising animal models with maternal effects to estimate genetic parameters for a single sex in sheep (van Vleck *et al.* 2000), cattle (Koch *et al.* 1973; van Vleck & Cundiff 1998), and mice (Eisen & Hanrahan 1972; Hanrahan & Eisen 1973), some doubt existed regarding the suitability of these models for this type of analysis. This was due to the absence of female data in the male only datasets and the reduction in the size of the maternal half sib groups (by 50% assuming a 50:50 sex ratio), both of which contribute to the estimation of genetic parameters (Bijma 2006; Maniatis & Pollott 2003). The comparison of the relative proportions of the variance components in each of the three models described in section 3.4.2 revealed that the relative proportion of additive genetic variance remained unchanged across the three models within each sex,

suggesting that the estimation of maternal effects in an animal model did not adversely affect the estimation of heritability.

The trend (some significant) for ewes to have larger heritability estimates than rams for weight traits is consistent both here and in most examples found in literature (Baker *et al.* 1979; Bisset *et al.* 1994; Lax & Jackson 1987; Lewer *et al.* 1994; Maria *et al.* 1993; Näsholm 2004; Pattie 1965; van Vleck *et al.* 2000; Vesely & Robison 1971; Young *et al.* 1960). The consistency of the trend suggests that ewes do have larger heritabilities than rams but the lack of significance indicates that the difference is small. Comparison of the relative proportions of the variance components in both sexes revealed that the larger heritability estimates in ewes was due to their lower (relatively) residual variance and larger (relatively) additive genetic variance than rams which was consistent with the findings of Baker *et al.* (1979), Parratt *et al.* (1989), and Maria *et al.* (1993). The larger phenotypic variation found in rams was found to be largely a function of their greater size, similar to that observed by Maria *et al.* (1993). The correlation between phenotypic variation and size (which increased with age) cancelled out any expected decrease in phenotypic variation due to increasing selection (Bulmer 1971) with age (via both natural and artificial means). All mixed-sex genetic parameters estimated in this study were within the range of estimates reviewed by Safari *et al.* (2005), though they tended to be on the high side.

Although most results found in literature were in agreement with those obtained in this study, there were a number of limitations which prevented their results from being directly comparable. Firstly, they used different breeds to those used in this study, though van Vleck *et al.* (2000) did use a composite population containing an estimated ¼ Suffolk which is one of the ancestral breeds of the White Suffolk (Australian White Suffolk Association Inc. "Website of the Australian White Suffolk Association Inc" 2006). Vesely and Robison (1971) compared rams in feedlots with ewes on pasture which made it impossible to separate the sex difference from the genotype by environment effect. Maria *et al.* (1993) and van Vleck *et al.* (2000) also used feedlots after weaning for both sexes and analysed average daily weight gain not weight at a specific age, though Maria *et al.* (1993) also analysed weaning and post-weaning weights. Finally, Young *et al.* (1960), Pattie (1965), Young *et al.* (1965), Vesely and Robison (1971), Baker *et al.* (1979), Lax and

Jackson (1987), Parratt *et al.* (1989), Bisset *et al.* (1994), and Lewer *et al.* (1994) used mixed models that ignored some of the familial relationships (e.g. parent-offspring and sire models). A literature search revealed no studies estimating sex-specific genetic parameters in sheep for fat and eye muscle depth.

The use of industry data ensured that these results are directly relevant to the conditions found "on-farm" and that there was sufficient data to generate accurate results. However, industry data can have greater measurement error and more missing observations than data collected by skilled technicians using accurately calibrated equipment in research flocks. The reduction in dataset and family group size within each dataset due to separating the datasets by sex would also have a detrimental effect upon the accuracy of the estimates generated, though this effect could be reduced by studying more fertile breeds.

Some of the datasets analysed in this study contained significantly more records from one sex than the other, which prevented the estimation of genetic parameters of similar accuracy in each sex. The sale of rams can prevent the collection of their data as adults and the role of each breed within the sheep production system also appeared to influence the sex-specific recording. In terminal sire breeds (Poll Dorset and White Suffolk) rams were preferentially recorded over ewes, particularly at older ages. This was possibly due to the absence of adult roles for ewes from these breeds in commercial flocks whereas the size of adult rams help determine their value at sale. Both sexes appeared to be recorded equally in the Coopworth breed until slaughter weight was reached (post-weaning age ~ 225 days of age; Meat and Livestock Australia 2004). After the post-weaning age, male recording was neglected once traits important to a maternal breed like the Coopworth and only recordable in females (e.g. reproductive ability) were exhibited at older ages.

The low percentages of animals recorded for more than two traits in each of the breeds reduced the accuracy of the comparisons of corrected weights and genetic parameters in different age groups. Ideally, the same animals would have been recorded in each age group so that the true differences between the traits could be identified with the genetics and preceding environment standardised in both age groups. Similarly, if data from only mixed-sex twins and triplets was analysed in this study, each pair would have the same parents

thus would be similar genetically, have similar maternal environments (the estimates of which were similar anyway) and have been exposed to the same natural environmental factors (climate, feed supply, etc). This would effectively standardise the fixed effects used in the models in this study, across sex, thus allowing the model to be simplified and more accurate estimation of the differences between the sexes to be carried out. The downside of this approach is that it would reduce the amount of animals available for analysis and would be difficult to achieve in lowly fecund breeds like the Merino.

The environmental influences acting upon each sex were assumed to be equal for animals born in the same flock, year and contemporary group in this study. Unfortunately, this is not entirely accurate because ewes and rams have to be grazed separately after sexual maturity to prevent interbreeding and pregnancy, which would distort ewe weights and is undesirable from the breeder's perspective. The alternative of castration is also undesirable for the ram breeders who supplied this data and would also alter the growth rate and body composition of the animals involved (Johnson *et al.* 2007; Lee *et al.* 1990). As a consequence, the separate grazing conditions could lead to a genetic by environmental effect that is impossible to detect and reduce the accuracy of these results. Management of each sex in "matching" paddocks where each sex has equal access to water, food, space and shelter would reduce this effect but there is no information available regarding whether this occurred for the animals analysed in this study.

3.6 Conclusion

This study estimated the magnitude of sexual dimorphism and sex-specific genetic parameters for five weight and two scanning traits (fat and eye muscle depth) in three sheep breeds (Coopworth, Poll Dorset and White Suffolk) from industry supplied data. Rams were heavier than ewes at all ages and ewes (after correcting for differences in live weight) were fatter and had deeper eye muscles. A trend that ewes had larger heritabilities than rams in all traits except fat and eye muscle depths in the Coopworth breed was detected and phenotypic variation was larger in rams than ewes. The greater phenotypic variation in rams was due, in part, to the greater size of rams compared with ewes.

These results could potentially influence the accurate estimation of breeding values, the selection objectives for each sex, the response to selection in each sex and the weightings placed on each trait within multitrait selection indices. Further analysis, involving the use of models analysing two or more traits at once, is required to estimate the genotypic correlations between the sexes and between the traits and sexes (Chapter 4). This will allow the magnitude of the differences between the sexes to be quantified.

Chapter 4: Estimation of Intersex Genetic Correlations in Three Australasian Sheep (*Ovis aries*) Breeds

4.1 Abstract

This study estimated intersex genetic correlations for five weight and two scanning traits (fat and eye muscle depth) from large industry datasets representing the Coopworth, Poll Dorset and White Suffolk sheep breeds. Genetic correlations were estimated between ewes and rams for the same trait, between traits within each sex, between traits for data containing both ewes and rams and between ewes and rams for different traits (ewe trait x, ram trait y). The genetic correlations estimated between ewes and rams (intersex) for the same trait were similar across the three breeds and decreased with advancing age (at weaning 0.93 – 0.97, as hoggets 0.75 – 0.80, depending on breed). Intersex genetic correlations for eye muscle and fat depths measured post-weaning were also estimated and found to be significantly less than unity (eye muscle depth 0.87 – 0.89 and fat depth 0.71 – 0.88, depending on breed).

These results reveal that there is variation between the sexes in the genetic control of growth in sheep and as a consequence, sex-specific responses to selection can be achieved in these traits which lead to the evolution of sexual dimorphism. In commercial breeding programs this could have implications for accurate genetic evaluation and the design of breeding programs, particularly where sexually divergent selection objectives exist.

4.2 Introduction

Traditional attempts to select for increased efficiency of meat production (amount of lean tissue produced/amount of feed consumed) in pastoral livestock species has been focused on 'bending' the growth curve where selection is applied to maximise early growth to slaughter age while minimising any increase in mature size (Fitzhugh 1976; Robertson 1987). The reason for this is that total feed requirement is correlated with body weight and the length of an animal's life (Taylor 1980). Feed requirements can, therefore, be reduced by fast growth to slaughter and smaller mature size. Unfortunately, the response to

selection for “curve bending” animals is slow due to the high genetic correlations that exist between growth to slaughter and mature weight (Brash *et al.* 1994; Fischer *et al.* 2004b; Mousa *et al.* 1999).

Bowman (1968) suggested that the differences between the sexes in body weight and, if it exists, in how growth is inherited, could have important applications in the meat production industry but did not specify any possible mechanisms how this may occur. Increasing sexual dimorphism (sex-specific variation in growth rate and terminal size) would allow divergent selection objectives in each sex to be targeted. For example, in a typical self-replacing lamb production system, most female offspring are retained as herd/flock replacements, whereas most males are destined for slaughter (Amer *et al.* 1999). Therefore, producing a fast growing male who reaches slaughter weight rapidly from the smallest possible mature female should increase the efficiency of the production system. This strategy will still be limited by the genetic correlation between growth to sale and mature weight which limits “curve bending”, but by analysing and utilising each trait in the relevant sex (e.g. post-weaning weight in rams and either hogget or adult weight in ewes), the genetic correlation should be lower than the mixed-sex value that restricts “curve bending”.

The results in Chapter 3 suggested that variation may exist between the sexes in how growth is inherited and the estimation of genetic correlations between the sexes will allow the magnitude of these differences to be estimated. If the genetic correlation between the sexes for the same trait is less than unity or the genetic correlation between different traits measured within each sex (e.g. weaning weight in rams and adult weight in ewes) are different to the genetic correlations estimated between the same traits from data containing both ewes and rams, then it would appear that some of the genetic controls for growth are different in each sex and that sex-specific genetic parameters may be required for the accurate prediction of response to selection, genetic evaluation and the design of breeding programs (Lax & Jackson 1987; Safari *et al.* 2005 & 2007).

Vesely and Robison (1971), Lax and Jackson (1987), Parratt *et al.* (1989), Lewer *et al.* (1994), Mousa *et al.* (1999), and van Vleck *et al.* (2000) have previously estimated intersex

genetic correlations in sheep and the estimates ranged between 1.2 (eight month weight; Lewer *et al.* 1994) to 0.75 (yearling weight; Parratt *et al.* 1989). Similar studies have also been reported in other mammalian species including mice and cattle. Theron and Scholtz (1994) and van Vleck and Cundiff (1998) estimated genetic correlations between the sexes for live weight at weaning (1.0, both studies) and at one year of age (0.79 and 0.92, respectively) in a wide range of cattle breeds. Hanrahan and Eisen (1973) estimated values between 0.87 at six weeks and 1.12 at eight weeks for live weight in an experimental line of mice. Given that estimates above 1.0 are biologically impossible and that the majority of estimates had high standard errors, these results reflect the relatively low numbers of animals available in each of these research flocks, herds and group of mice. This study was able to avoid this issue by obtaining data from a large number of industry flocks which also has the benefit of ensuring that the results obtained are representative of what would be found in a commercial application.

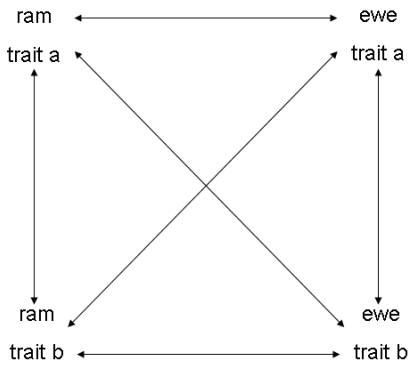

Figure 4.1: The correlations estimated in this study. Intersex genetic correlations are represented by the horizontal arrows, within sex by vertical arrows and different traits for each sex by the diagonal arrows.

This study quantified the genetic differences between ewes and rams for growth traits by estimating the genetic correlations between the sexes for the same trait (horizontal arrows in Figure 4.1), between traits within sex (vertical arrows) and between different traits in each sex (diagonal arrows). Estimates were derived from large datasets representing three different breeds grown under typical Australasian pastoral conditions. Different breeds were compared to establish whether variation in founder effects and in the natural and artificial selection history of each breed influenced the degree with which traits are related between the sexes. The genetic parameters obtained were then used to investigate the

evolution of sexual dimorphism in sheep and compare selection strategies designed to increase the feed efficiency of lamb production systems.

4.3 Materials and Methods

4.3.1 Data

The datasets representing the Coopworth, Poll Dorset and White Suffolk breeds that were utilised in Chapter 3 were again used in this study. Table 4.1 contains the resulting pedigree structure of the data used to estimate intersex genetic correlations for the same trait which is expanded upon in Appendix 2 to describe the pedigree structure shared between different traits in mixed-sex (both ewes and rams), single sex (ewes or rams) or across sex analysis. With few exceptions (predominantly post-weaning weight in the Coopworth breed), the number of records, sires and dams, and the percentage of sires and dams with progeny of both sexes, decreased with advancing age.

Table 4.1: Family structure of each dataset including the percentage of sires and dams with both ewe and ram progeny recorded.

		Sires		Dams	
	Individuals	Number of	% with both ♀ & ♂ progeny	Number of	% with both ♀ & ♂ progeny
Coopworth					
Wean	35990	612	92%	14464	43%
Post-Weaning	8479	360	67%	5028	24%
Yearling	19632	481	74%	9338	30%
Hogget	5790	281	17%	3997	2%
Poll Dorset					
Wean	109222	2392	87%	46030	38%
Post-Weaning	106655	2520	73%	46679	30%
Yearling	87837	2468	67%	42192	25%
Hogget	39136	1287	51%	19285	15%
Adult	2904	186	20%	1479	4%
White Suffolk					
Wean	112300	2486	90%	44599	41%
Post-Weaning	93244	2576	77%	42093	33%
Yearling	56397	1857	66%	26963	22%
Hogget	13494	709	45%	8105	11%
Adult	846	71	12%	521	2%

4.3.2 Fixed Effects

The fixed effects included in the bivariate models were similar to those fitted in Chapter 3 (see 3.3.2) which in turn were similar to those used in the OVIS program used by Sheep Genetics to estimate breeding values for the Australasian sheep industry (Brown *et al.* 2000) and in other recent Australasian estimates of genetic parameters for body weight and scanning results in sheep (Huisman *et al.* 2006; Johnson *et al.* 2006; Safari *et al.* 2007). For the estimation of genetic correlations between ewes and rams, age was fitted as an interaction with sex to account for the faster growth of rams identified in Chapter 3 (Figure 3.1). Both the eye muscle and fat depth traits were corrected for live weight at the time of measurement.

4.3.3 Estimation of Genetic Parameters

ASReml 2.0a software (Gilmour *et al.* 2006) was used to fit bivariate models in a similar manner to the fitting of univariate models described in Chapter 3. The animal model (with or without the maternal genetic effect and/or the permanent environmental effect of the dam) fitted to each trait was dependent upon the results of log likelihood ratio tests conducted on the univariate analyses reported in Chapter 3 except for when convergence issues occurred and the model was simplified by the removal of a random effect. Equation 4.1 is an example of a multivariate animal model that includes both maternal genetic and permanent environmental effects:

$$\begin{bmatrix} Y_1 \\ Y_2 \end{bmatrix} = \begin{bmatrix} X_1 & 0 \\ 0 & X_2 \end{bmatrix} \begin{bmatrix} b_1 \\ b_2 \end{bmatrix} + \begin{bmatrix} Z_1 & 0 \\ 0 & Z_2 \end{bmatrix} \begin{bmatrix} u_1 \\ u_2 \end{bmatrix} + \begin{bmatrix} W_1 & 0 \\ 0 & W_2 \end{bmatrix} \begin{bmatrix} m_1 \\ m_2 \end{bmatrix} + \begin{bmatrix} S_1 & 0 \\ 0 & S_2 \end{bmatrix} \begin{bmatrix} p_1 \\ p_2 \end{bmatrix} + \begin{bmatrix} e_1 \\ e_2 \end{bmatrix}$$

(equation 4.1)

where Y_i = a vector of observations for the i^{th} trait, b_i = vector of fixed effects (as described in 4.3.2), u_i = vector of random animal effects, m_i = vector of random maternal (indirect effects), p_i = vector of permanent environmental influences and e_i = vector of the random residual effects. X_i, Z_i, W_i and S_i are incidence matrices relating records of the i^{th} trait to fixed, animal, maternal genetic and permanent environmental, respectively (Mrode 2005). The residual covariance between traits measured in opposing sexes was fixed at zero within the model as this parameter is impossible to estimate without some animals having records

for both traits (Wilson *et al.* 2010) which would require them to be both a ewe and a ram. Pedigree files containing all animals with records and genetic groups were used for each breed (the same pedigree file as used for the univariate analysis described in Chapter 3).

A pragmatic approach was used to test the differences between the genetic correlation estimates obtained in this chapter. Because most of the correlations that were compared were obtained from different data, the comparison of log likelihoods obtained from the REML analysis was not possible. The distribution around each estimate was assumed normal and the standard errors approximated by ASReml were used to create confidence intervals. A 95% significance level was used to identify whether correlation estimates from different data sets were significantly different, i.e. whether their 95% confidence interval was overlapping.

4.3.4 Prediction of the Response to Selection within each Sex and the Response of Sexual Dimorphism to Sex-specific Selection.

The response per generation to phenotypic selection in each sex, including the response resulting from selection applied directly to that sex and the correlated response from selection applied in the opposite sex, was predicted by equations 4.2a and b (Cheverud *et al.* 1985; Lande 1980):

$$Rram = 0.5\ (h^2_{ram}\ \sigma_{p\ ram}\ i_{ram} + h_{ram}\ h_{ewe}\ r_g\ \sigma_{p\ ram}\ i_{ewe}) \quad \text{(equation 4.2a)}$$

$$\text{or } Rewe = 0.5\ (h^2_{ewe}\ \sigma_{p\ ewe}\ i_{ewe} + h_{ewe}\ h_{ram}\ r_g\ \sigma_{p\ ewe}\ i_{ram}) \quad \text{(equation 4.2b)}$$

Where R_{ram}/ R_{ewe} is the response to phenotypic selection in rams or ewes, h^2_{ram}/ h^2_{ewe} is the heritability in rams or ewes, $\sigma_{p\ ram}$ and $\sigma_{p\ ewe}$ is the phenotypic standard deviation of the trait in rams and ewes, i_{ram} and i_{ewe} is the selection intensity of rams and ewes, h_{ram} and h_{ewe} is the square root of the heritability in rams and ewes and the r_g is the genetic correlation between rams and ewes. The selection intensity for each sex was obtained from 10 year averages (1999-2008) in the Sheep Genetics Database (Sheep Genetics, unpublished data, 15/5/2009) and were 2.421 (ram, all breeds), 0.798 (ewe, Coopworth) and 0.830 (ewe, Poll Dorset/White Suffolk), which correspond to two, 53 and 48% selected, respectively. The response of sexual dimorphism to selection for growth can be defined as the difference between the ewe and ram responses to selection for the same trait obtained using equations

4.2a and b. As such, the difference between ewe and ram response to selection can be predicted using equation 4.3 (Cheverud *et al.* 1985):

$$RSD = 0.5\ [h^2_{ram}\ \sigma_{p\ ram}\ i_{ram} - h^2_{ewe}\ \sigma_{pewe}\ i_{ewe} + h_{ram}\ h_{ewe}\ r_g\ (\sigma_{p\ ram}\ i_{ewe} - \sigma_{p\ ewe}\ i_{ram})] \quad \text{(equation 4.3)}$$

The response of each trait within each sex to selection using EBVs (R_{EBV}) was predicted using selection index theory (Hazel 1943) via the MTindex spreadsheet developed by van der Werf (2005). In the selection index model, traits were unique to ewes or rams and were assumed correlated across sex with equal economic values reflecting the equal emphasis placed on growth in each sex in typical current breeding objectives. For each trait, rams had their own record, one sire record and 20 half sibling records (assumed mating ratio of one ram per 40 ewes, one lamb per ewe recorded and a 50:50 sex ratio) contributing towards the accuracy of the ram EBV and consequently the accuracy of selection (r_{IA}). Records from the same trait recorded in females (i.e. dam and 20 other half sibling records) also provided information as a correlated trait to the ram trait. The opposite applied when the response to selection was predicted in ewes. The additive genetic standard deviation (σ_a) was obtained from the square root of the heritability times the phenotypic standard deviation of each trait. Economic values were considered equal initially to simulate current selection. Selection for sexual dimorphism was then simulated by giving ewe hogget weight (representing the mature weight of ewes) a negative value (-$0.50 or -$1) and ram post weaning weight (representing sale weight in ram lambs) a positive value ($2). These values are artificial and should in no way be considered representative of the true economic values of these traits. Typical selection intensities from the Sheep Genetics Database were again used. The equation used to predict the response to selection using EBVs is given below:

$$R_{EBV} = i \times r_{IA} \times \sigma_a \quad \text{(equation 4.4)}$$

4.4 Results

4.4.1 Genetic Correlations

The genetic correlations between ewes and rams for the same trait are less than unity for all traits and breeds and, with the exceptions of those between yearling and hogget weights in the Poll Dorset and White Suffolk breeds, decreased with age (Table 4.2). High standard errors (>0.20) indicating insufficient data for the accurate estimation of genetic correlations were found for analyses involving adult weight in all breeds and for hogget weight in the Coopworth breed. These results have been listed as n/a (not available) in Table 4.2. Before one year of age, the maternal genetic and dams permanent environmental correlations were high in all three breeds (range 0.93 – 1.00), though the maternal genetic correlation decreased with age from the post-weaning age group onwards (to 0.70 - 0.79 in the hogget age group).

Table 4.2: Genetic correlations between ewes and rams for the same trait.

	Coopworth		Poll Dorset		White Suffolk	
Wean Weight	0.93	±0.03	0.97	±0.01	0.97	±0.01
Post-Wean Weight	0.94	±0.09	0.82	±0.03	0.80	±0.03
Yearling Weight	0.84	±0.06	0.74	±0.04	0.59	±0.06
Hogget Weight	n/a		0.80	±0.06	0.75	±0.16
Fat Depth	0.71	±0.10	0.79	±0.02	0.88	±0.02
Eye Muscle Depth	0.87	±0.07	0.89	±0.02	0.89	±0.02

The genetic correlations between weight measurements obtained at different ages were highly variable (range: 0.94 to 0.14, see Table 4.3) and this variation was not influenced by whether estimates were obtained from single sex data (ewes or rams) or mixed-sex data (ewes and rams) with rare exceptions (rams > ewes between Coopworth weaning and hogget weights and ewes > rams between Poll Dorset post-weaning and yearling weights (95% confidence interval)). Breed type appeared to influence the results, with the range of genetic correlations narrower (0.92 to 0.50) and the average higher (0.76) in the maternal breed (Coopworth) than in either of the terminal sire breeds (Poll Dorset range: 0.34 to 0.94, average: 0.55 and White Suffolk range: 0.14 to 0.87, average: 0.63).

Table 4.3: Genetic correlations estimated between weights measured at different ages in mixed-sex and single sex datasets.

		Genetic correlations									
Trait a	Trait b	Mixed-sex		Ram Only		Ewe Only		Ram a -Ewe b		Ram b - Ewe a	
Coopworth											
Weaning	Post-Wean	0.88	±0.03	0.79	±0.06	0.85	±0.04	0.92	±0.04	0.76	±0.10
Weaning	Yearling	0.81	±0.03	0.75	±0.05	0.81	±0.03	0.70	±0.06	0.54	±0.08
Weaning	Hogget	0.65	±0.03	0.81	±0.04	0.61	±0.04	0.51	±0.08	n/a	
Post-Wean	Yearling	0.84	±0.04	0.81	±0.04	0.72	±0.07	0.68	±0.11	0.65	±0.13
Post-Wean	Hogget	0.78	±0.09	n/a		0.73	±0.09	0.50	±0.11	n/a	
Yearling	Hogget	0.83	±0.05	0.84	±0.02	0.77	±0.05	0.79	±0.06	0.63	±0.05
Poll Dorset											
Weaning	Post-Wean	0.49	±0.03	0.40	±0.04	0.53	±0.03	0.34	±0.05	0.45	±0.04
Weaning	Yearling	0.51	±0.03	0.41	±0.05	0.54	±0.04	0.44	±0.05	0.43	±0.05
Weaning	Hogget	0.56	±0.05	0.55	±0.06	0.62	±0.06	0.58	±0.05	0.44	±0.08
Post-Wean	Yearling	0.86	±0.01	0.87	±0.01	0.94	±0.01	0.66	±0.05	0.59	±0.05
Post-Wean	Hogget	0.59	±0.05	0.67	±0.06	0.60	±0.06	0.55	±0.06	0.57	±0.06
Yearling	Hogget	0.88	±0.01	0.86	±0.02	0.89	±0.02	0.41	±0.08	0.65	±0.07
White Suffolk											
Weaning	Post-Wean	0.62	±0.02	0.61	±0.03	0.68	±0.02	0.51	±0.04	0.47	±0.04
Weaning	Yearling	0.54	±0.03	0.48	±0.05	0.56	±0.04	0.45	±0.05	0.44	±0.06
Weaning	Hogget	0.65	±0.05	0.51	±0.09	0.65	±0.08	0.43	±0.01	0.37	±0.11
Post-Wean	Yearling	0.79	±0.02	0.83	±0.02	0.80	±0.02	0.45	±0.05	0.53	±0.06
Post-Wean	Hogget	0.63	±0.07	0.69	±0.07	0.44	±0.12	0.14	±0.13	0.57	±0.13
Yearling	Hogget	0.82	±0.04	0.87	±0.05	0.86	±0.03	0.40	±0.15	0.57	±0.12

The average genetic correlations obtained from across sex data (trait a in ewes, trait b in rams) were 0.16 - 0.18 lower (0.53) than the average of those obtained from either single sex (♂ 0.69, ♀ 0.70) or mixed-sex data (0.71). These estimates were estimated directly in ASREML but similar results (within a 95% confidence interval) were found via the multiplication of the intersex genetic correlation for the same trait (given in Table 4.2) with the between trait genetic correlation obtained from data containing both ewes and rams (given in Table 4.3). The relationship between these correlations is explained diagrammatically in Figure 4.2. Breed type was again found to influence the results, with the range of genetic correlations narrower (0.51 to 0.92) and the average higher (0.80) in the maternal Coopworth breed than in either of the terminal sire breeds (Poll Dorset range: 0.34 to 0.94, average: 0.64 and White Suffolk range: 0.14 to 0.87, average: 0.64).

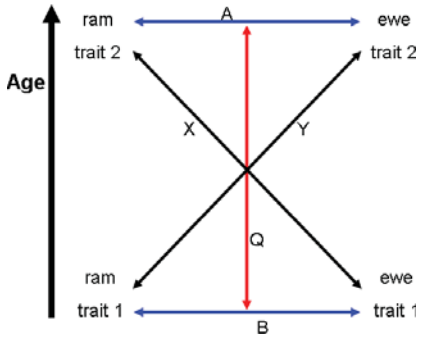

Figure 4.2: Intersex genetic correlations are represented by A and B, between age correlations (mixed-sex) by Q and different trait for each sex by X or Y.

The genetic correlations between either fat depth or eye muscle depth and weight at various ages (Table 4.4) was found to be low and negative (0 to -0.46 depending on the age at which weight was recorded) and the genetic correlations between fat depth and eye muscle depth were moderately low and positive (0.24 to 0.47). No consistent differences (95% confidence interval) were detected between estimates obtained from mixed-sex (average: -0.09), ram only (-0.08), ewe only (-0.09) and across sex data (-0.07). Breed type effects were again detected, with the average genetic correlation between weight and either fat or eye muscle depth higher (-0.06) in the maternal Coopworth breed than in either of the terminal sire breeds (Poll Dorset: -0.18 and White Suffolk: -0.17). The average genetic correlation between fat depth and eye muscle depth was higher (0.40) in the maternal Coopworth breed than in either of the terminal sire breeds (Poll Dorset: 0.31 and White Suffolk: 0.28). The range of genetic correlations obtained from different data (mixed, single or across sex) was similar across breeds.

Table 4.4: Genetic correlations estimated between weights (trait a) measured at different ages and fat/eye muscle depth (trait b) measured in the post-weaning age group in mixed-sex and single sex datasets. Trait pairs not significantly different (95% confidence interval) from zero not included.

		Genetic correlations									
trait a	trait b	Mixed-sex		Ram Only		Ewe Only		Ram a - Ewe b		Ram b - Ewe a	
Coopworth											
Weaning	Fat	-0.35	±0.05	-0.37	±0.08	-0.21	±0.08	-0.28	±0.09	-0.29	±0.07
Yearling	Fat	-0.17	±0.07	n/s		-0.19	±0.09	n/s		-0.18	±0.09
Fat	EMD	0.47	±0.06	0.45	±0.08	0.41	±0.09	0.42	±0.11	0.25	±0.10
Poll Dorset											
Weaning	Fat	-0.19	±0.02	-0.19	±0.04	-0.18	±0.03	-0.12	±0.05	-0.22	±0.05
Yearling	Fat	-0.19	±0.03	-0.12	±0.04	-0.17	±0.04	n/s		-0.24	±0.05
Hogget	Fat	-0.13	±0.05	n/s		-0.17	±0.07	n/s		-0.30	±0.08
Fat	EMD	0.31	±0.02	0.24	±0.03	0.43	±0.03	0.29	±0.04	0.30	±0.03
Weaning	EMD	-0.16	±0.02	-0.16	±0.03	-0.18	±0.03	-0.19	±0.05	-0.15	±0.04
Post-Wean	EMD	-0.18	±0.02	-0.13	±0.03	-0.18	±0.03	-0.21	±0.05	-0.15	±0.04
Yearling	EMD	-0.19	±0.03	-0.11	±0.04	-0.26	±0.06	n/s		-0.33	±0.05
Hogget	EMD	-0.27	±0.04	-0.26	±0.06	-0.46	±0.06	-0.31	±0.09	-0.36	±0.07
White Suffolk											
Weaning	Fat	-0.18	±0.02	-0.19	±0.03	-0.22	±0.03	-0.19	±0.04	-0.17	±0.04
Yearling	Fat	-0.20	±0.04	-0.18	±0.05	-0.17	±0.05	-0.19	±0.06	-0.18	±0.06
Hogget	Fat	-0.27	±0.07	-0.33	±0.09	-0.24	±0.10	n/s		n/s	
Fat	EMD	0.29	±0.02	0.27	±0.03	0.32	±0.03	0.30	±0.03	0.24	±0.02
Weaning	EMD	-0.16	±0.02	-0.15	±0.03	-0.14	±0.03	-0.16	±0.04	-0.15	±0.04
Post Wean	EMD	-0.20	±0.02	-0.14	±0.03	-0.16	±0.03	-0.10	±0.04	-0.25	±0.04
Yearling	EMD	-0.21	±0.03	-0.22	±0.05	-0.15	±0.05	-0.20	±0.06	n/s	
Hogget	EMD	-0.29	±0.07	-0.21	±0.09	-0.29	±0.10	n/s		n/s	

n/s = not significantly different from zero

4.4.2 Response to Selection by Ewes or Rams and by Sexual Dimorphism.

Table 4.5 shows the response to selection that would be expected from typical current selection policies where there is no variation in the economic value of each trait between the sexes. In both phenotypic and estimated breeding value based selection, a greater response is expected in rams than in ewes for weight and eye muscle depth, the fat depth response is greater in ewes than in rams and the unequal response in each sex leads to a correlated increase in sexual dimorphism in each of these traits.

Table 4.5: Response per generation by ewes, rams and by sexual dimorphism to current selection for growth (equal economic values in each sex).

			Response to selection by					
			Ewes		Rams		Sexual Dimorphism*	
Breed	Trait		Phenotypic	EBV	Phenotypic	EBV	Phenotypic	EBV
Coopworth	Wean	kg	1.67	2.31	1.85	2.47	0.18	0.16
	Post Wean	kg	1.47	2.10	1.72	2.38	0.25	0.28
	Yearling	kg	1.92	2.73	2.00	2.85	0.09	-0.12
	Fat	mm	0.23	0.32	0.24	0.30	-0.01	0.02
	EMD	mm	0.90	1.19	1.08	1.35	-0.18	-0.16
Poll Dorset	Wean	kg	2.72	3.47	3.57	4.50	0.85	1.03
	Post Wean	kg	1.71	2.73	2.13	3.06	0.42	0.32
	Yearling	kg	1.74	2.71	2.68	3.68	0.94	0.97
	Hogget	kg	2.23	3.69	3.42	4.64	1.19	1.25
	Fat	mm	0.32	0.22	0.26	0.25	0.06	-0.03
	EMD	mm	1.05	1.43	1.17	1.48	-0.11	-0.06
White Suffolk	Wean	kg	1.99	2.72	2.35	3.17	0.37	0.45
	Post Wean	kg	1.75	2.55	2.60	3.67	0.85	0.92
	Yearling	kg	1.79	2.91	2.25	2.98	0.46	0.07
	Hogget	kg	1.69	2.80	2.08	2.99	0.40	0.19
	Fat	mm	0.35	0.51	0.28	0.39	0.07	0.13
	EMD	mm	1.09	1.12	1.14	1.13	-0.05	-0.01

***** The response in sexual dimorphism is defined as the response in the larger sex – the response in the smaller sex. For weight, rams were larger than ewes and for both eye muscle depth and fat depth, ewes were larger than rams (see Table 3.5 in Chapter 3).

Table 4.6 shows the response to EBV selection if post weaning weight was selected for in rams (economic value = $2) and hogget weight was selected against in ewes (economic value = -$0.50 or -$1.00). Selection using equal economic values is also shown for comparative purposes. The response to selection increased with the difference between the economic values applied to ewes and rams.

Table 4.6: Response per generation by ewes, rams and by sexual dimorphism to selection for sexual dimorphism.

	Economic Value[#]		Response to selection by		
Breed	Ewe hogget weight	Ram post wean weight	Ewe hogget weight	Ram post wean weight	Sexual Dimorphism*
Coopworth	$1.00	$1.00	2.89	2.01	0.88
	-$0.50	$2.00	1.51	-0.68	2.19
	-$1.00	$2.00	2.99	0.62	2.36
Poll Dorset	$1.00	$1.00	4.04	1.60	2.44
	-$0.50	$2.00	3.59	0.40	3.19
	-$1.00	$2.00	4.24	0.96	3.28
White Suffolk	$1.00	$1.00	4.54	1.28	3.26
	-$0.50	$2.00	4.50	0.30	4.20
	-$1.00	$2.00	4.89	0.64	4.25

***** The response in sexual dimorphism is defined as the response in ram post weaning weight – the response in ewe hogget weight.

[#] Artificial economic values not expected to representative of the true economic values of these traits.

4.5 Discussion

The genetic correlations estimated from mixed-sex data in this study are within the range of estimates reviewed in Safari *et al.* (2005) and with three exceptions (yearling weight in the Poll Dorset (0.74) and White Suffolk breeds (0.59), and hogget weight in the Coopworth breed (0.71)) the intersex genetic correlations were within the range (0.75 to >1.0) found in the studies of Vesely and Robison (1971), Lax and Jackson (1987), Parratt *et al.* (1989), Bisset *et al.* (1994), Lewer *et al.* (1994), van Vleck *et al.* (2000), and Näsholm (2004). This suggests that the results in this study are representative of values typically found from this type of analysis.

The similarity of results achieved in each of these studies might be considered surprising given the considerable variation between the studies in experimental design, population size, breeds used and types of statistical models used. The use of sire models by Vesely and Robison (1971), Lax and Jackson (1987), Parratt *et al.* (1989), Bisset *et al.* (1994), and Lewer *et al.* (1994) prevented the estimation of maternal effects and appeared to result in relatively high standard errors for each of their estimates (commonly > 20% of the estimate). The high standard errors would also have been a consequence of smaller population sizes used in the published studies compared with those used in the current study. Only the smallest dataset used in the current study (hogget weight in the Coopworth breed) was small enough to fall within the range of population sizes (3600-12000) used in previously published research (Bisset *et al.* 1994; Lax & Jackson 1987; Lewer *et al.* 1994; Parratt *et al.* 1989; van Vleck *et al.* 2000; Vesely & Robison 1971) with the exception of Näsholm (2004) who used 24000 and 36000 records per breed. As a consequence, it was difficult for any of the published studies to find intersex genetic correlations less than unity and the majority of the estimates found by Lewer *et al.* (1994) were biologically impossible (> 1.0). Intrinsic to across sex experimental designs are a series of limitations which have been dealt with in more detail in the previous chapter. These include the halving (assuming a 50:50 sex ratio) of the number of progeny per parent that occurs as a consequence of analysing each trait within a single sex, the absence of dams in the male only data and absence of rams in female only data.

The animal model used in this study and by Mousa *et al.* (1999), van Vleck *et al.* (2000), and Näsholm (2004) utilises all of the information from both the sire and dam relationships and allows the estimation of maternal effects like the permanent environmental effect of the dam and the maternal genetic effect. However, both Mousa *et al.* (1999) and van Vleck *et al.* (2000) analysed lambs grown in feedlots not on pasture as used here and failed to report standard errors. Mousa *et al.* (1999) also analysed the correlation between live weight and average daily gain, a trait not considered in this study. The differences in trait definition, growing environment (feedlot) and individual population variation, lead to higher intersex genetic correlations for weaning weight and lower for yearling weight in both Mousa *et al.* (1999) and van Vleck *et al.* (2000) than was found in this study. The maternal genetic correlations for all traits (where reported) were non-significantly larger in this study than reported by Mousa *et al.* (1999) and van Vleck *et al.* (2000), but otherwise similar in being positive and of moderate to high magnitude. No permanent environmental correlations were reported in the literature for comparison with the high correlations observed in the current study. The highly positive correlation observed between the sexes for both the maternal and permanent environmental effects is logical because the maternal influence is a function of the ewe and should be available equally to lambs regardless of sex. One possible exception to this is if there is a consistent preference for one sex in multiple births or one sex exhibits dominant behaviour over the other, interfering with the ability of the second sex to receive the same maternal benefits. There is no evidence to suggest that this occurred.

Genetic correlations of less than unity between ewes and rams for the same trait can be partly explained by ewes being physiologically less mature during growth than rams of the same age (Taylor 1968). The largest effect of this phenomenon is likely to be on the carcass composition traits (fat or eye muscle depth) which are highly age dependent and those influenced by the timing of puberty (Taylor 1987). Because age has a larger influence upon food costs than physiological maturity (Brody 1945), the variation in maturity is unlikely to affect the efficiency of a self-replacing production system, but could influence the relative rate that each sex reaches market specifications in a terminal sire production system.

Variation in the range of the additive genetic variation present in each trait or sex upon the magnitude of estimated genetic correlations was not investigated in the current study. However, James (1998) and Hill *et al.* (1999) found in some instances, the standardisation of wool fibre diameter records measured at different ages to a common genetic variance (i.e. the removal of a scale effect between the age groups) changed genetic correlation estimates between measurements. As such, genetic correlations of < 1.0 might only reflect a scale effect and not imply that genetic control of the trait was affected by age (Hill *et al.* 1999). These possibilities can be distinguished by transforming both groups to the same genetic variance and comparing the resultant estimates with those obtained from untransformed data (James 1998). Using this method, Hill *et al.* (1999) found that after standardisation to a common genetic variance, there was up to a 0.65 drop in genetic correlation between wool traits, though the differences were rarely (two out of 15) significant owing to the large standard errors involved. While no standardisation of genetic variances were performed in this study, roughly half of the bivariate analyses for the same trait across sex had genetic variances within 95% confidence intervals of each other in each sex. Comparison of this observation was not possible because James (1998) did not report the genetic variances present in each age group analysed and Hill *et al.* (1999) did not report the standard errors for each of their genetic variances.

Ever since Darwin proposed the theory of sexual selection to explain the evolution of sexual dimorphism (Darwin 1875), researchers have tried to identify the genetic parameters responsible in order to model the selection response of sexual dimorphism. To this end, an adaptation of the breeder's equation has been used by some researchers to predict the response of sexual dimorphism to phenotypic selection applied to either or both sexes (Cheverud *et al.* 1983 & 1985; Lande 1980; Reeve & Fairbairn 1996). While not representative of the large proportion of the livestock industry that relies on multitrait selection on BLUP breeding values, the prediction of the response to phenotypic selection provides an interesting insight into how sexual dimorphism may have evolved in the wild. Michelena *et al.* (2006) suggested a number of reasons why domestic sheep are a good model species in which to study the evolution of sexual dimorphism. These include that they already possess high levels of sexual dimorphism, they are easier to manage and record parentage and trait values than wild species, groups of same-sex and mixed-sex can

easily be formed and observed under controlled conditions and are similar to Bighorn sheep (*Ovis Canadensis*) whose sexual dimorphism has been intensively studied (e.g. LeBlanc *et al.* 2001; Poissant *et al.* 2008). The ease of recording, in turn, leads to a greater availability of records which reduces the error involved in the estimation of the parameters contained within the equation. For example, both Cheverud *et al.* (1985) and Reeve and Fairbairn (1996) assumed both sexes had equal heritability in their simulations of the evolution of sexual dimorphism because of the lack of data available to distinguish between the sexes for this parameter. So despite domestic sheep not being typically maintained in the wild and, as a consequence, have different reasons for selection (mostly artificial selection for optimising production versus natural selection for fitness), they provide a good model in which the genetic parameters controlling the evolution of sexual dimorphism can be estimated.

This study also showed that sexually dimorphic responses to selection will also occur when sheep are selected using estimated breeding values, which is common in the seed stock component of the industry. This has many potential implications for livestock breeding, particularly in those flocks where sex bias in recording, selection intensity and/or selection objectives exist. In fact, given the potential importance of genetic correlations estimated between and within sex to the design of breeding programs for meat production, Thompson *et al.* (1985) considered the lack of research into this topic surprising. Only one study, Parratt *et al.* (1989), has previously attempted to estimate across sex and trait (ewe trait *x*, ram trait *y*) genetic correlations in sheep, though Vesely and Robison (1971), Lax and Jackson (1987), Parratt *et al.* (1989), Lewer *et al.* (1994), Mousa *et al.* (1999), and van Vleck *et al.* (2000) reported intersex genetic correlations for the same trait. No literature reporting intersex genetic correlations involving either fat or eye muscle depth was found.

For flocks where one sex is recorded preferentially over the other, the correlated response to selection in the non-recorded sex will be lower than the direct response to selection in the sex where the records were obtained due to the intersex genetic correlations being less than unity (Reeve & Fairbairn 2001) and less accurate selection accuracy that occurs as a consequence of less family information being available to estimate breeding values. Based on the large proportion of datasets used in this study that deviate from the expected 50:50

sex ratio, it would appear that this type of recording (sex biased) is commonplace within the industry. The lack of variation between genetic correlations between traits estimated from only ewes, only rams or data containing both sexes but recorded for both traits was consistent with the results found by Lewer *et al.* (1994), though Baker *et al.* (1979) found that the genetic correlations between traits estimated from ewe data were generally higher than those estimated from rams. The lack of variation in this study implies that breeding programs that utilise reproductive technologies to produce progeny of predominantly one sex will not be adversely affected by unrepresentative genetic correlations obtained from mixed-sex data.

The variation in selection response between ewes and rams has potential implications where divergent selection objectives could be used to optimise selection in sex-specific roles that are known to exist in some production systems. For example, the majority of rams are destined for slaughter while most ewe lambs are destined to be flock replacements in a self-replacing production system due to the ability of one ram to mate with many ewes. Therefore, if a higher selection emphasis is placed on growth in rams than ewes, male progeny would reach sale weight earlier and ewe mature weight would be maintained or reduced. This would have three benefits. Firstly, the age at which market weight is reached and the carcass fat levels would both be reduced in faster growing male progeny. Both of these factors would contribute to a reduction in the overall feed requirement of this class of sheep (Taylor 1980). Secondly, fast male growth allows flexibility to deal with seasonal pricing and feed availability (Archer & Amer 2009). Thirdly, because the feed requirements of adults is correlated with size (Brody 1945; Taylor 1980) and the feed intake of the ewe can comprise over 80% of the total feed costs in a production system (Thompson 1991), the maintenance or reduction in ewe mature weight could lead to a significant reduction in feed costs. However, where divergent breeding objectives do not exist, the use of single sex estimated breeding values is counterproductive if breeding values estimated from both sexes are available. This is due to single sex estimated breeding values being less accurate than those estimated from mixed-sex data because there is no dam or daughter data available for rams, no sire or son data for ewes and the number of siblings contributing data is halved (assuming a 50:50 sex ratio). However, due the high intersex genetic correlations,

data from the opposite sex would still contribute to the breeding value in the same manner as a highly correlated trait would.

To decrease feed costs in a self-replacing production system, it is desirable to select for sexual dimorphism between the following traits recorded by Sheep Genetics (Brown *et al.* 2000): post-weaning weight, fat depth and eye muscle depth in rams and adult weight in ewes. Post-weaning weight, fat depth and eye muscle depth are indicator traits for slaughter weight, the level of carcass fatness and muscling which are the traits that determine the price paid by a meat company for each animal (Atkins *et al.* 1991). Unfortunately, there was insufficient data to estimate accurate genetic correlations involving adult weight in this study, so hogget weight was used instead as it is highly correlated (according to the studies reviewed in Safari & Fogarty 2003) and the next oldest trait available. However, care must be taken to avoid a correlated reduction in hogget lambing performance when selecting for a reduction in hogget weight (Bowman 1968; Taylor 1987).

4.6 Conclusion

This study has shown that the intersex genetic correlations, particularly after weaning, are sufficiently low to explain the evolution of sexual dimorphism in sheep, both domesticated and in the wild. The existence of variation in selection response between ewes and rams, and the correlated response in sexual dimorphism also has potential benefits and implications in commercial breeding programs, particularly those where sex bias in recording, selection intensity and/or selection objectives exist. Analysis of the datasets used in this project (commercial data obtained for performance recording) has revealed that the preferential recording of one sex over the other is common, but varies depending on trait and breed. Unfortunately, the results of this study have revealed that the correlated selection response in a non-selected sex would be less than if both sexes were selected. The difference in selection response between ewes and rams also has potential benefits where divergent selection objectives could be used to optimise selection in sex-specific roles that are known to exist in some production systems, for example, where all rams are slaughtered and the majority of ewes kept as breeding replacements. The bio-economic modelling of a production system is required to see if this difference is large enough to be practical (Chapter 6).

Chapter 5: Description of Sex-specific Lamb Growth using Random Regression

5.1 Abstract

Random regression was used to evaluate the difference between ewes and rams in the genetic parameters that determine the growth trajectory. This allowed us to show that a 4th order Legendre polynomial (cubic) was the optimum for modelling the average growth curve in both ewes and rams in these data, that phenotypic variation is larger in rams throughout the trajectory (range: 21.77 to 90.43 in ewes, 35.97 to 167.20 in rams) and the heritability is larger in ewes than rams until 410 days of age (range: 0.27 to 0.38 in ewes, 0.20 to 0.38 in rams). The greater heritability in rams post 410 days is a possible consequence of the use of polynomials in the model and may explain why the overall heritability trend in rams increased with time, while the trend in ewes remained effectively constant throughout the trajectory. The phenotypic variation in both sexes increased with age. The analysis of the genetic correlations and eigenvalues of each random regression coefficient revealed that there is some direct additive genetic and maternal genetic variation available to alter the shape of growth curve in both sexes. Overall, random regression accurately estimated sex-specific genetic parameters for a population containing three or more records per individual, with the exception of estimates obtained at the edge of the trajectory. These genetic parameters showed that the heritability for live weight in ewes was larger than in rams at ages younger than 410 days of age and the phenotypic variation was larger in rams at all ages.

5.2 Introduction

The genetic analysis of growth in livestock typically analyses weight recorded in specific age demarcations. In Australia, these age groups are defined by Sheep Genetics (Meat and Livestock Australia 2004) and univariate and multiple trait analyses using these age groups are reported in Chapters 3 and 4. Due to these age demarcations, some animals are recorded for the same trait in the Sheep Genetics database even though there can be over six months

difference in age (the age range in the post weaning age group is 80 to 340 days), yet others are recorded as different traits despite having a much smaller age difference. For example, if animal *A* is recorded at 405 days of age, it will be recorded in the yearling age group (with an average age of 360 days) and if animal *B* is recorded at 435 days of age, it will be recorded as a hogget (average 450 days) despite there only being 30 days difference in age between the two animals. Random regression avoids this issue by estimating genetic parameters as a continuous function over a trajectory. For example, in this study the genetic parameters for weight can be derived every day between 50 and 500 days of age.

A random regression analysis comprises of two parts. Firstly, a fixed regression is used to describe the average shape of the growth curve for the whole population and secondly, a random regression is used for each individual to account for their variation from the average growth curve described by the fixed regression. With the fit of an animal model within the random regression of an animal's additive genetic effect on the change of phenotype over time, it is possible to derive genetic parameters at any time on the growth trajectory (Lewis & Brotherstone 2002). Because random regression estimates the genetic and environmental effects at the exact age they are recorded, any inaccuracies incurred by the requirement to correct data (weights) to specific ages as occurs in traditional multitrait methods is avoided (Meyer 2004). The ability to model genetic differences in the shape of each animal's growth curve is important when genetic variances and covariances change rapidly during certain periods of ontogeny (e.g. puberty; Kirkpatrick *et al.* 1990), and this might become even more important when comparing ewes and rams as some of the ontogenic changes (e.g. puberty) occur at different ages in each sex (Taylor 1968).

There are some disadvantages of random regression which have prevented its widespread use in genetic evaluation. Random regression can be more computationally intensive than multitrait models due to denser incidence and coefficient matrices and the increased number of effects requiring estimation with higher order functions (Kirkpatrick *et al.* 1990; Meyer 1999 & 2004; Nobre *et al.* 2003). The computing requirements for a random regression model can also be increased by the presence of animals with an insufficient number of records to apply the desired order of polynomial within the animal model (Meyer 2004; Nobre *et al.* 2003). As a consequence, records from related individuals have

to be used to provide information on additional ages, raising the computational requirements. Combined with the extensive nature of the sheep industry typically preventing the collection of more than two to three records per animal (Fischer & van der Werf 2002), this initially resulted in random regression only being applied to research flocks where there was greater amounts of recording per animal (e.g. Lewis & Brotherstone 2002). Application to industry data (e.g. Fischer *et al.* 2004a, 2004b & 2006) came later. These studies found that the heritability varied at different points along the growth trajectory, suggesting that live weight early in a lamb's life is a different trait to live weight later in life and that these differences have a genetic component and that the correlations decreased as the age difference increased (Fischer *et al.* 2004b & 2006; Lewis & Brotherstone 2002). Attempts to analyse growth with random regression in other species (including fish, cattle and pigs) have been reviewed by Schaeffer (2004). Random regression has not been previously used to estimate genetic parameters for growth of livestock using single sex data.

The aim of this study is to use random regression analysis to evaluate the difference between ewes and rams in genetic parameters that determine the growth trajectory. This will allow us to detect not only differences in the average growth curve, but also differences in the genetic variability between ewes and rams for different parts of the growth trajectory. The potential to exploit such differences in breeding programs will be discussed.

5.3 Materials and Methods

5.3.1 Data

A subset of the Poll Dorset data used in Chapters 3 and 4, including the data processing described in 3.3.1 was used in this study. The subset was formed by extracting only animals that possessed three or more weights recorded between 50 and 500 days of age. Insufficient data prevented the analysis of ages outside of this range. As a consequence of these restrictions, the dataset only contained 16% of the ewe records and 22% of the ram records analysed for the Poll Dorset breed in Chapters 3 and 4. The data structure is described in Table 5.1 and the distribution of records and the average weight (uncorrected for fixed effects) of each sex with age is shown in Figure 5.1. The data used in this study differs to

that used by Fischer *et al.* (2004b & 2006) and Fischer and van der Werf (2002) as the current data contains birth years 1987-2003 (as opposed to just 1990-2002) and a larger number of flocks with different data recording protocols. The wider range of flocks and birth years available in this study resulted in a dataset that was over 3.5 times larger (both in number of records and in the number of animals) than that used by Fischer *et al.* (2004b & 2006) and Fischer and van der Werf (2002).

Table 5.1: Data file structure.

Number of:	male	female
records	38399	20897
animals	12429	6853
animals with 3 records	11317	6515
animals with 4 records	1112	338
sires	1055	742
dams	9487	5487
recorded progeny per dam	1.31	1.25
contemporary groups	367	268
Average*:		
Weight (kg)	57.74	46.72
Age (days)	245.3	237.2

* Averages presented in table 5.1 are uncorrected for the influences of fixed effects

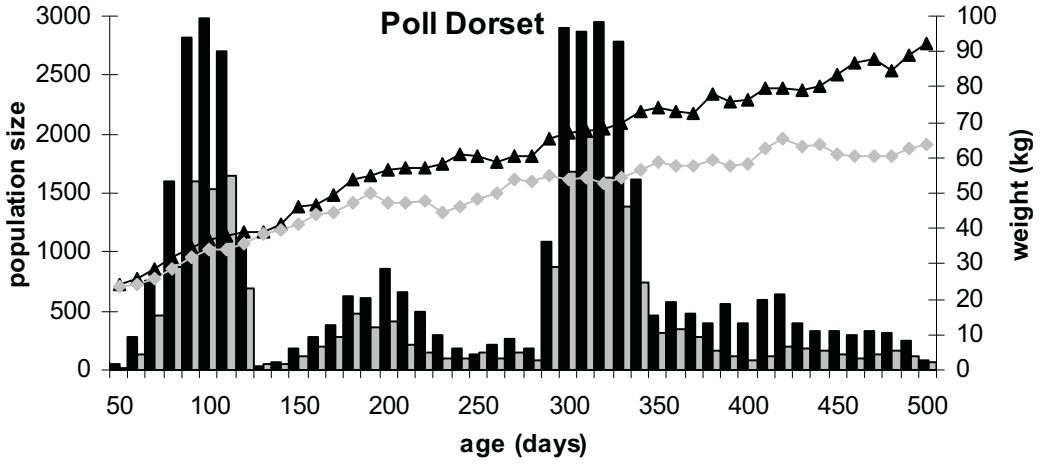

Figure 5.1: Numbers of records (columns, left axis) and uncorrected mean weights (lines, right axis) for individual ages in 10 day intervals. Black bars and lines depict males, grey females.

5.3.2 Fixed Effects

The fixed effects included in the models used in this study were similar to those fitted in Chapters 3 (see 3.3.2) and 4 (see 4.3.2) with the addition of Legendre polynomials fitted in the manner described by Fischer *et al.* (2004a, 2004b & 2006). The optimum order of Legendre polynomial required to model the population trajectory was determined by the comparison of residual variances estimated from models containing a range of orders. As a consequence, a 4th order polynomial (the same as used by Fischer *et al.* 2004a, 2004b & 2006) was nested within the levels of the birth by rearing type interaction and, separately, dam age to allow the corrections due to these effects to vary with age. Contemporary groups, as defined in 3.3.1, were fitted as a class variable unique across all ages of measurement. The same fixed effects model was used for different random effect models, making residual maximum likelihoods directly comparable using the methods described in section 5.3.7.

5.3.3 Random Effects

Previous applications of random regression to sheep data have fitted either three (direct genetic, maternal genetic and direct permanent environmental; Lewis & Brotherstone 2002) or four random effects (+ maternal permanent environmental; Fischer *et al.* 2004a, 2004b & 2006). Like Lewis and Brotherstone (2002), this analysis fitted the direct and maternal genetic effects and the direct permanent environmental effect. The direct and maternal genetic effects were found to be significant in the majority of the analyses carried out in Chapters 3 and 4, and the direct permanent environmental effect accounted for the environmental covariances between repeat records of any given individual within the data (Lewis & Brotherstone 2002). The direct and maternal genetic effects were assumed to be proportionate to the numerator relationship matrix.

5.3.4 Model of Analysis

The random regression model used in the analysis in this study was:

$$y_{ij} = F_{ij} + \sum_{m=0}^{kA-1} \alpha_{im}\,\phi_m(t_{ij}) + \sum_{m=0}^{kB-1} \gamma_{im}\,\phi_m(t_{ij}) + \sum_{m=0}^{kC-1} \rho_{im}\,\phi_m(t_{ij}) + \varepsilon_{ij} \qquad \text{(Equation 5.1)}$$

Where y_{ij} denotes the j-th record for animal i taken at age t_{ij} with t standardised ($-1<t<1$) for which Legendre polynomials are defined, and $\Phi_m(t_{ij})$ the corresponding m-th Legendre polynomial. F_{ij} represents the fixed effects pertaining to y_{ij}, including the regression on

orthogonal polynomials of age which were nested within rearing type and dam age. The variables α_{im}, γ_{im} and ρ_{im} are the m-th order RR coefficients for the direct additive genetic, maternal additive genetic and direct permanent environmental effects, respectively, and k_{A-1}, k_{B-1} and k_{C-1} are the corresponding order of (polynomial) fit for each effect. Finally, e_{ij} denotes the residual error. Residual effects were considered independently distributed, with heterogeneous measurement error variances in different trajectory intervals. Changes in measurement error variance over time were modelled as a step function with nine different classes depending on age (50–10, 101-150, …, 451–500 days). Repeated analyses considering different orders of polynomial fit for each random effect were carried out, with the choice of model determined by the criteria described in section 5.3.7.

For comparative purposes, typical univariate models as described in Chapter 3 and using the three random effects described in this chapter (direct and maternal genetic, direct permanent environmental) were performed on the datasets used in this chapter. Each trait was defined by the age ranges given by SG (Meat and Livestock Australia 2004) and utilised in Chapter 3.

5.3.5 Covariance Functions

The covariance functions for the each random effect was obtained by multiplying a matrix (K) containing the estimated variances and covariances between the random regression coefficients by a matrix containing Legendre polynomials (Φ) pertaining to a set of specific ages. The result is an estimated covariance matrix for that random effect for specific ages defined by Φ. This can be shown in matrix notation as

$$\hat{G}_0 = \Phi \, \mathrm{K} \, \Phi' \qquad \text{(Equation 5.2)}$$

Covariances between random regression coefficients pertaining to different random factors were assumed to be zero throughout (i.e. no direct–maternal genetic correlation) for a number of reasons. Firstly, such parameters are often difficult to estimate even in univariate analysis and debate surrounds the appropriate data structures required for such estimates to be performed (Maniatis & Pollott 2002). Furthermore, other studies have shown that fitting a sire×herd interaction accounts for the so-called direct–maternal covariance (Meyer 1997). In addition, random regression models invariably require a large number of parameters to be estimated, even without fitting covariances between random effects, so for parsimony

and consequent speed of analysis, these effects were not modelled. All estimates were obtained by residual maximum likelihood using ASReml 2.0a software (Gilmour *et al.* 2006).

5.3.6 Eigenvalues and Functions

Using the statistical program R (R Development Core Team), each covariance function was decomposed into its eigenvalues and eigenfunctions. Analysis of eigenvalues and eigenfunctions allow the identification of the independent components of genetic variance, each one determining an aspect of the growth trajectory of the population under investigation (Kingsolver *et al.* 2001; Kirkpatrick *et al.* 1990; Koehn *et al.* 2007). For example, the main eigenvalues can represent the variation in average growth, whereas the second eigenvalues can represent later growth which may be statistically different to average.

5.3.7 Model Selection

Comparison of models containing different polynomial orders fitted to the direct and maternal genetic random effects was based on Akaike's information criterion (AIC – equation 5.3) or Schwarz's Bayesian Information Criterion (BIC – equation 5.4). In both of these methods, the absolute size of the derived values is irrelevant and the differences between the derived values are important, with the model with the lowest difference being considered the best. The Schwarz's Bayesian Information Criterion takes into account model uncertainty which is ignored in the Akaike's information criterion. As a result the Schwarz's Bayesian Information Criterion is stricter than the Akaike's information criterion (Huisman & Veerkamp 2002).

$$AIC = -2 \text{ Log } L + 2p \qquad \text{(Equation 5.3)}$$

$$BIC = -2 \text{ Log } L + p \text{ Log } (n-x) \qquad \text{(Equation 5.4)}$$

Where p denotes the number of random (co)variance parameters to be estimated, n the number of observations, x the number of fixed effects, i.e. n-x is the residual degrees of freedom which was obtained from ASReml and Log L is the maximum Log Likelihood. Orders of fit greater than three were not considered because of the small number of animals

with four records (Table 5.1). The improvement in fit of each model is described by a reduction in either of the information criterion.

5.4 Results

The numbers of records and the average weights in each sex in 10 day increments along the time scale are displayed in Figure 5.1 which is displayed in the materials and methods section. Growth appeared to be almost linear with the exception of a moderate plateau effect observed in ewes after 200 days of age. It is also apparent that the spread of records is not uniform across time. Large peaks in recording occurred around 100 days (recommended age for recording weaning weight by SG (MLA 2004) and around 320 days (near the recommended age for recording yearling weight (360 days)), with a minor peak around 200 days (near the recommended age for recording post-weaning weight (225 days)).

Table 5.2 shows the Log Likelihood, AIC and BIC for each of the models fitted to data from each of the sexes. Models fitting Legendre polynomials of the order of $k = 3$ for both the direct additive genetic and maternal additive genetic effects and $k = 2$ for the direct permanent environmental effect were found to have the lowest AIC or BIC in both ewe and ram datasets.

Table 5.2: Log Likelihood (LogL) values and corresponding information criteria for analyses with different orders of polynomial fitted to each random effect. All LogL, AIC and BIC are expressed as differences from the preferred value.

			number of	ewe			ram		
k_A*	k_B	k_C	parameters	LogL	AIC	BIC	LogL	AIC	BIC
2	2	2	18	1792	3572	3524	4387	8762	8710
3	2	2	21	154	303	279	74	142	116
2	3	2	21	1169	2332	2309	1504	3001	2976
2	2	3	21	1146	2287	2263	1631	3257	3231
2	3	3	24	3986	7971	7971	1238	2475	2475
3	2	3	24	170	341	341	1199	2397	2397
3	3	2	24	0	0	0	0	0	0
3	3	3	27	1081	2168	2192	973	1951	1977

* k_A, k_B and k_c are the order of polynomial fitted to the direct additive genetic, maternal additive genetic and direct permanent environmental effects, respectively.

5.4.1 Random Regression Coefficients

Estimates of the covariance matrices are summarised in Table 5.3 for each sex. The intercepts of the polynomial regressions explained 83%, 85% and 99% of the direct additive genetic, maternal additive genetic and direct permanent environmental random effects in ewes, respectively, and 82%, 81% and 100% of the direct additive genetic, maternal additive genetic and direct permanent environmental random effects in rams.

Table 5.3: Estimates of covariances (lower triangle) and correlations (upper triangle) between random regression coefficients (0: intercept, 1: linear, 2: quadratic) together with eigenvalues (λ) of the covariance matrices for each sex.

	0	1	2	Eigenvalues	Proportion
Ewe					
	Direct Additive Genetic (k_A)				
0	26.82	0.70	-1.47	27.24	83%
1	6.97	5.29	0.45	4.88	15%
2	-3.23	-0.99	0.72	0.71	2%
	Maternal Additive Genetic (k_B)				
0	8.01	0.65	-0.49	8.15	85%
1	1.45	0.61	-0.96	1.26	13%
2	-0.10	-0.60	0.63	0.16	2%
	Direct Permanent Environmental (k_C)				
0	15.29	0.36		15.30	99%
1	0.56	0.16		0.15	1%
Ram					
	Direct Additive Genetic (k_A)				
0	44.70	0.76	-0.91	45.06	82%
1	15.43	8.72	0.41	8.40	15%
2	-2.10	-0.01	1.40	1.36	3%
	Maternal Additive Genetic (k_B)				
0	13.69	0.57	-0.84	13.91	81%
1	3.70	3.07	-0.52	2.92	17%
2	-0.16	-0.52	0.32	0.25	2%
	Direct Permanent Environmental (k_C)				
0	23.00	0.18		23.00	100%
1	0.24	0.08		0.08	0%

5.4.2 Covariance Functions

Estimates of the total variance for each random component were plotted against age for model 332 and are shown in Figure 5.2. For each component, the shape of the trajectory was similar in each sex except the additive genetic and maternal genetic variances for rams keep rising with age while ewes plateau above 350 days. The magnitude of each component was also larger in rams than ewes and fitted well with the univariate results also obtained

from the data used in this chapter. A sharp increase in measurement error was observed after 400 days of age where there was a relative absence of data. This also had a noticeable affect on the phenotypic variance.

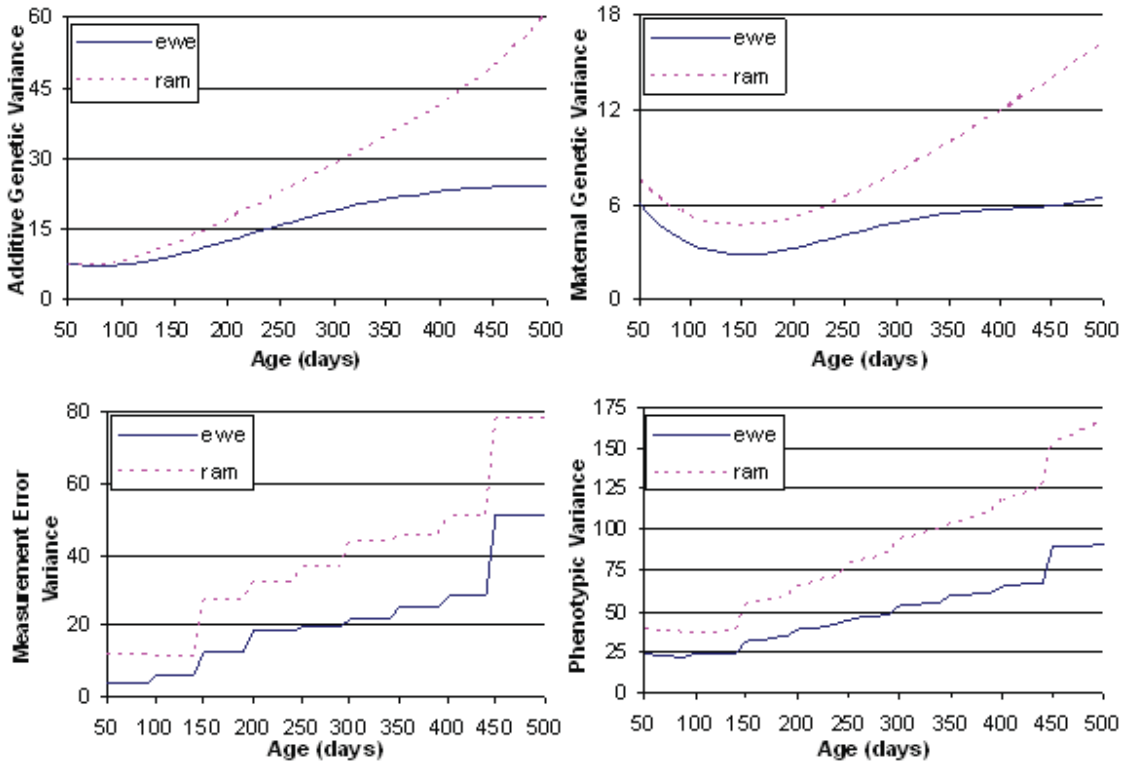

Figure 5.2: Estimates of the direct and maternal genetic, measurement error and phenotypic variances for each sex.

5.4.3 Heritability

The range of heritabilities estimated for ewes was 0.27 to 0.38 and 0.20 to 0.38 for rams and until 410 days of age, estimates were larger in ewes than rams (Figure 5.3). The heritability of ewes also remained relatively constant along the time trajectory, whereas the estimates in rams increased with time. These results are in partial agreement with the results obtained from this data using the age demarcations and methods described in Chapter 3 which found that ewes had higher heritability than rams at all ages. The overall trend shown by the maternal heritability and the direct permanent environmental estimates was a decrease with time and no consistent variation between ewes and rams was observed. All heritability estimates were found to be extremely sensitive to the presence or absence of the direct permanent environmental effect.

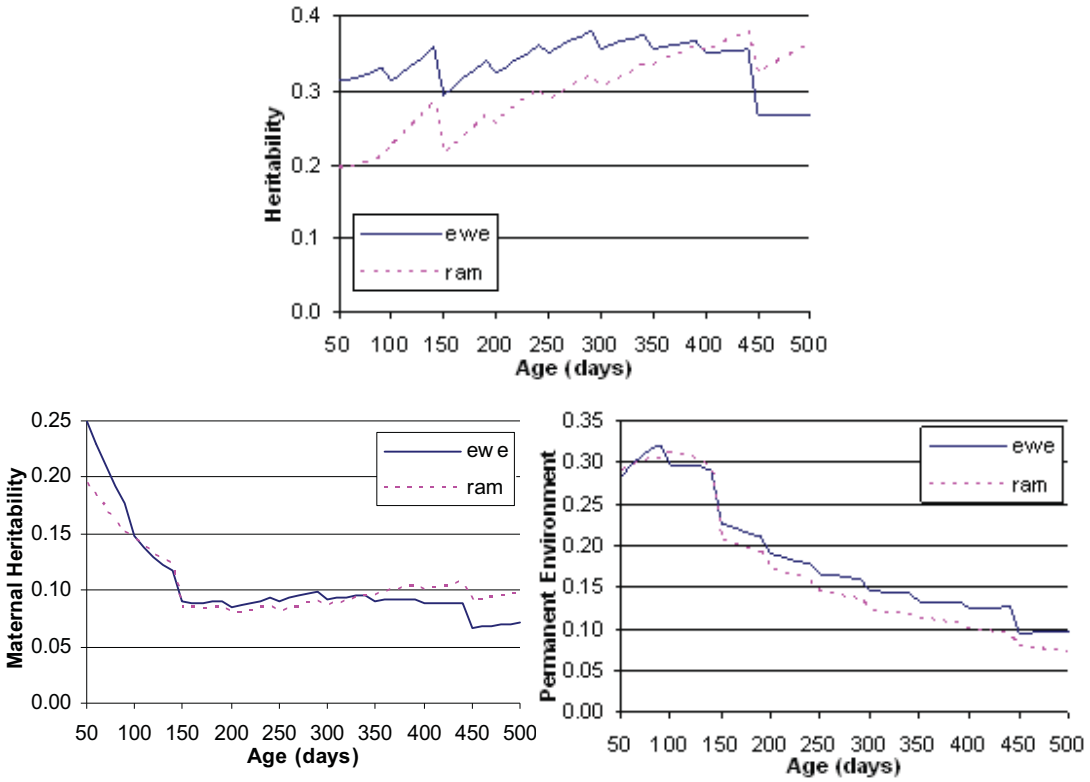

Figure 5.3: Estimates of the direct and maternal heritability and direct permanent environmental effects as a proportion of the phenotypic variance in each sex.

5.4.4 Correlations

Table 5.4 shows the phenotypic and genetic correlations between selected ages decreased as the age distance between weights increased. Some unrealistic (compared with their bivariate equivalents) genetic correlations (<0.2) at extreme age differences (>300 days) were estimated from the ewe data. Excluding the unrealistically low correlations in ewes, there was less than 0.1 difference between the correlations estimated in ewes and rams. Genetic correlations between weights at 200 days apart were also lower (0.37 ewes, 0.46 rams) at younger ages (50 vs. 250 days) than correlations between weights taken at older ages (300 vs. 500 days; 0.89 ewes, 0.86 rams). Unfortunately, due to the much greater computer requirements of random regression (three days per model) compared with the traditional animal model (<1 hour for each of the four age groups), time restraints prevented the estimation of intersex genetic correlations via bivariate random regression.

Table 5.4: Genetic (below diagonal) and phenotypic (above diagonal) correlations between weights measured at 50 day intervals for both ewes and rams.

Age	50	100	150	200	250	300	350	400	450	500
Ewes										
50	**1.00**	0.91	0.70	0.58	0.50	0.43	0.39	0.37	0.32	0.33
100	0.90	**1.00**	0.86	0.77	0.71	0.65	0.61	0.58	0.50	0.49
150	0.69	0.94	**1.00**	0.94	0.90	0.84	0.80	0.77	0.65	0.63
200	0.51	0.83	0.97	**1.00**	0.97	0.92	0.88	0.85	0.72	0.70
250	0.37	0.74	0.92	0.99	**1.00**	0.96	0.92	0.89	0.76	0.73
300	0.27	0.66	0.87	0.96	0.99	**1.00**	0.97	0.94	0.80	0.78
350	0.19	0.59	0.82	0.93	0.97	0.99	**1.00**	0.97	0.83	0.82
400	0.12	0.52	0.77	0.89	0.98	0.98	0.99	**1.00**	0.86	0.85
450	0.06	0.45	0.70	0.83	0.90	0.94	0.97	0.99	**1.00**	0.99
500	0.00	0.37	0.62	0.75	0.83	0.89	0.93	0.96	0.99	**1.00**
Rams										
50	**1.00**	0.98	0.75	0.66	0.59	0.53	0.51	0.48	0.43	0.43
100	0.88	**1.00**	0.82	0.76	0.70	0.66	0.63	0.60	0.54	0.52
150	0.69	0.95	**1.00**	0.95	0.89	0.84	0.82	0.78	0.69	0.66
200	0.55	0.87	0.98	**1.00**	0.95	0.91	0.89	0.85	0.75	0.72
250	0.46	0.82	0.95	0.99	**1.00**	0.96	0.94	0.90	0.81	0.78
300	0.42	0.77	0.92	0.97	0.99	**1.00**	0.99	0.95	0.85	0.83
350	0.39	0.74	0.89	0.95	0.98	0.99	**1.00**	0.97	0.88	0.86
400	0.38	0.70	0.84	0.90	0.97	0.97	0.99	**1.00**	0.91	0.90
450	0.38	0.65	0.78	0.84	0.88	0.92	0.96	0.99	**1.00**	0.99
500	0.38	0.60	0.70	0.75	0.80	0.86	0.91	0.96	0.99	**1.00**

5.5 Discussion

The direct comparison of these results with literature is impossible due to the absence of previous studies that compare the genetic parameters from each sex obtained using random regression. The magnitude of the results, however, are within the range of values obtained using the traditional animal model and reviewed by Safari and Fogarty (2003), and are also within the range of mixed-sex values obtained from other studies that utilised random regression to analyse growth in sheep (Fischer *et al.* 2004b & 2006; Fischer & van der Werf 2002; Kesbi *et al.* 2008; Lambe *et al.* 2006; Lewis & Brotherstone 2002).

The random regression results obtained in this chapter were also mostly in agreement with the traditional animal model results obtained from Chapters 3 and 4. At all ages, rams had greater phenotypic variance than ewes and the heritability, with the exception of ages over 410 days, was higher in ewes than rams. The increase in additive genetic and maternal genetic variances observed the later stages of the trajectory in rams and the increase in measurement error variance for both sexes at the same stage of the trajectory has been

observed in mixed-sex analyses by a number of researchers including Meyer (1998), van der Werf *et al.* (1998), Arango *et al.* (2004), Fischer *et al.* (2004b), and Kesbi *et al.* (2008). While some authors have linked this phenomenon to the relative absence of data at the edge of the trajectory, Fischer and van der Werf (2002) and Nobre *et al.* (2003) found that it still occurs when the data is evenly spread across the trajectory. As such, "end effect of polynomials" or "Runge's phenomenon" remains an unresolved problem for random regression models utilising Legendre polynomials. Some authors (Albuquerque & Meyer 2001; Fischer *et al.* 2004b; Kesbi *et al.* 2008; Lewis & Brotherstone 2002; Meyer 2005; Schaeffer & Jamrozik 2008) have suggested that using functions other than polynomials (e.g. splines) may solve this problem.

The maternal heritability and the direct permanent environmental effect were similar in each sex and decreased with age. The similarity in maternal heritability is expected as both sexes should be exposed to similar maternal environments given that, on average, each ewe will have equal numbers of male and female offspring. The lack of literature describing maternal effects and permanent environmental effects over an age trajectory makes comparison difficult, however both Vaez *et al.* (1996) and Fischer *et al.* (2004b) reported that these parameters decreased with time post weaning/puberty (>200 days) which is in agreement with these findings.

Unfortunately due to the much greater computing requirements of random regression compared with traditional bivariate models as found in this project and reported by Meyer (2002 & 2004) and Nobre *et al.* (2003b), the use of bivariate random regression models to estimate intersex genetic correlations were not attempted due to time constraints. Random regression models analysing weight data as separate traits are complicated by the requirement to model the growth trajectory of each sex separately which also requires the separate estimation of random effects in each sex as these are dependent upon the trajectory. The time taken for each analysis would have been affected by the size of the datasets used, both of which (ewe and ram) were larger than any other sheep dataset previously analysed (Fischer *et al.* 2004b & 2006; Fischer & van der Werf 2002; Kesbi *et al.* 2008; Lambe *et al.* 2006; Lewis & Brotherstone 2002). The computing requirements would have also been increased by the absence of data from crucial relatives in single sex

datasets (e.g. dam data in the male dataset). To reduce the computing requirement, the maternal permanent environmental random effect found in Fischer & van der Werf (2002), Fischer *et al.* (2004a, 2004b & 2006), and Kesbi *et al.* (2008) was omitted, thus replicating the model used by Lewis and Brotherstone (2002). This also simplified the estimation of maternal effects which is complicated in sex limited datasets. This issue is discussed in more detail in a previous chapter (Chapter 3).

Except for at the extremes of the trajectory, little variation between the genetic correlations estimated within each sex in this study was found which is in agreement with the results obtained by traditional multitrait models in Chapter 4 and by Lewer *et al.* (1994). However, there was considerable variation (up to 0.44) between the magnitude of the genetic correlations obtained in this study and those obtained for the Poll Dorset breed in Chapter 4. With the majority of the variation occurring in genetic correlations involving the ages nearest the edge of trajectory (weaning weight (100days) and hogget weight (450 days)), there is a possibility that the genetic correlations are affected by the increase in covariance functions at later ages discussed earlier, though the increase in direct additive genetic and maternal additive genetic variance was not noted in ewes. This hypothesis is supported by the unrealistic near zero genetic correlations between live weight at 50 days and greater than 350 days. Near zero genetic correlations between ages is unrealistic because growth is cumulative with time and therefore later weights are dependent on early weights (Schaeffer 2004).

Analysis of the relative proportions of eigenvalues for each random regression coefficient can also give insight into how closely linked early and late weight is. 17% and 18% of ewe and ram direct additive genetic variation, respectively, is explained by the second and third eigenvalues which suggests that there is some scope to alter the growth curve genetically, though there is little variation between the sexes. More variation between the sexes exists for the maternal additive genetic variation with 15% and 19% of the variation in ewes and rams, respectively, is explained by the sum of the second and third eigenvalues. This suggests that rams may be more dependent upon the maternal environment for their initial growth and that compensatory growth (Wilson *et al.* 2005) could occur later in life to make up for any growth restriction that occurs due to a limiting maternal environment. This is

supported by the findings in wild deer that growth in males is more likely to be influenced by the availability of food than in females (Clutton-Brock *et al.* 1982; Post *et al.* 1999). No variation (<1%) between the relative proportions of eigenvalues for the direct permanent environmental effect was detected. The remaining proportion of the total eigenvalues was explained by the first eigenvalue (intercept) which acts equally across all ages. This infers that the majority of the improvement resulting from selection on the direct additive genetic (82-83%) and maternal additive genetic (81-85%) variation would be equal throughout the trajectory regardless of at what age selection is applied. While this is in agreement with the moderate to high genetic correlations reported in each sex, a significant proportion of variation remains available to alter the growth curve. This conclusion replicates that already found by Lewis and Brotherstone (2002) and Fischer *et al.* (2004b & 2006) in sheep, Meyer (2002) in beef cattle, and Huisman and Veerkamp (2002) in pigs.

Any variation between the results reported in Chapters 3 and 4 compared with this chapter, the absence in ewes of the increase in additive genetic and maternal genetic variances that occurred at the later stages of the growth trajectory in rams and the difference in magnitude between the results found in this chapter and those reported by Fischer *et al.* (2004b) could be due to sampling. The data used in this chapter contained only 16% of the records available for ewes and 22% of the records available for rams in Chapters 3 and 4 (which included animals with < three records), the ewe dataset was roughly half the size of the ram dataset and the data used by Fischer *et al.* (2004b) was a subset of the data used here which comprised of roughly one third the number of records and animals. Conversely, the greater data density (number of records per individual) present in the random regression datasets would have also assisted the accuracy with which parameters were estimated compared with the estimates obtained using the traditional animal models. Furthermore, it is logical that the flocks with a greater recording density could have more accurate selection and, thus greater genetic progress which could bias the results.

Kirkpatrick *et al.* (1990) suggested that ideally data for the analysis of growth trajectories should be collected more frequently at ages where rapid changes in ontogeny occur (e.g. puberty) because genetic variances and covariance's can change rapidly at these stages of development. While this is very difficult to achieve when studying sexual dimorphism in

sheep, it is highly desirable because ewes and rams mature sexually and physically at different ages (Taylor 1968). The more frequent collection of data at these ages is difficult to achieve in large scale commercial data sets like those used in this study because some ages at which ontogeny changes occur are often not economically relevant to the producers, there is a significant cost in obtaining repeat records in extensive industries like the Australian sheep industry (Fischer *et al.* 2004b & 2006) and for the study of sex differences, assuming a 50:50 sex ratio, each dataset is halved. Some records/individuals are also omitted from random regression datasets because they fail to have enough records collected across the trajectory. The analyses of compensatory growth or fat levels are examples of when a greater frequency of data collection would be desirable. The analysis of the differences between the sexes in inheritance of fat deposition over time would be interesting from the perspective that low fat is desirable in sale animals but high fat is linked with feed efficiency and fertility in ewes (Ball & Thompson 1995; Fischer *et al.* 2006; Tolkamp *et al.* 2006). Previous mixed-sex analyses of fat (and eye muscle depth) over a trajectory using random regression have been carried out by Fischer *et al.* (2006) in sheep and by Hassen *et al.* (1998) in beef cattle.

Compensatory growth occurs when variable growth trajectories converge on a limited set of adult phenotypes and is assumed to occur as a plastic response to environmental conditions (e.g. increased growth after a period of starvation; Wilson *et al.* 2005). Unfortunately due to a lack of mature weight recording, it is not possible to analyse whether compensatory growth occurs or is equal in each sex beyond what was hypothesised from the maternal additive genetic eigenvalues. The lack of mature weight recording also prevented the complete testing of Lewis and Brotherstone's (2002) hypothesis that because the overall growth curve varies between ewes and rams, the estimation of the fixed regression coefficients within sex could result in a lower order of polynomial being sufficient to model deviations from the overall curve. While Figure 3.1 in Chapter 3 clearly showed that there are significant differences in the growth curve between ewes and rams, the order of polynomial sufficient to model deviations from the overall curve were identical in both sexes in this study. However, the use of polynomials to model growth trajectories is restricted by the inability of polynomials to reach an asymptotic value. This prevents the modelling of growth trajectories that reach a plateau at maturity (Arango *et al.* 2004).

5.6 Conclusion

This study involves the estimation of covariance functions for direct and maternal effects on growth over a 450 day trajectory within each sex using sheep data obtained from commercial producers. Random regression accurately estimated sex-specific genetic parameters for a population containing three or more records per individual, with the exception of estimates obtained at the edge of the trajectory. However, the requirement for three or more records per individual for random regression prevented the analysis of the majority of the data analysed in previous chapters which lead to a sampling bias and exacerbated the preferential recording of rams over ewes observed in previous chapters. Despite this, the greater phenotypic variation observed in rams, the similarity of genetic correlations across sex and the greater heritability in females until 410 days of age were in agreement with the results obtained from traditional animal models in previous chapters.

Chapter 6: A Bio-Economic Model to Evaluate the Potential Benefits of Sexual Dimorphism in a Self-replacing Lamb Production System.

6.1 Abstract

This study used a bio-economic model to show that divergent selection for growth in ewes and rams influenced the profitability of a self-replacing production system on the Northern Tablelands of New South Wales by between -$43 and $30 per 0.1 gain in sexual dimorphism, though negative values were rare. Variation in the feed efficiency of the system, which influenced the number of ewes that could be carried per hectare, was found to be the major influence on this variation. Variation throughout the year in feed availability and the prices received for lambs were also found to be important. The rare negative responses in profitability to increasing sexual dimorphism occurred when the ewe lamb sale weight was high compared with mature ewe weight. In this scenario, an optimal value of sexual dimorphism was reached (~1.3) because the length of time taken for highly sexually dimorphic ewe lambs to reach the desired sale weight exceeded the benefits gained from the lower feed requirements of the mature ewes.

6.2 Introduction

The concept of using sexual dimorphism (sex-specific variation in growth and/or mature size) in a breeding program to reduce the overall feed requirements of a production system was first discussed by Jaap (1969). He suggested that the use of a known recessive, sex linked dwarf gene in chickens could reduce the size of female parents by 30% and their feed requirements by 33%, with no adverse effects on reproductive rate, progeny growth (either sex if mated to a non carrier) or viability. Roux (1992b) found that bulls twice the size of cows would increase feed efficiency by up to 25% depending on the percentage of heifers required as replacements. Despite these studies and the extensive reviews of the evolution, genetic and physiological basis of sexual dimorphism present in the literature

(e.g. Glucksmann 1974), the influence of sexual dimorphism on the efficiency of lamb production has not been previously investigated.

From studies that reported the average weights of ewes and rams in the same flock, the range of sexual dimorphism, calculated as the ratio of ram weight to ewe weight, has been found to vary between 1.0 (Stanford *et al.* 2001) and 1.5 (Thompson *et al.* 1985) depending on breed, age and level of nutrition. Although no major genes influencing sexual dimorphism are known to exist in sheep (unlike chickens), the variation in sexual dimorphism suggests that it may be possible to obtain, via selection, flocks with greater sexual dimorphism. However, before implementing sexual dimorphism as a trait in a breeding program, it is appropriate to assess the potential economic value of sexual dimorphism in sheep production systems.

Bio-economic models can incorporate genetic, nutritional, management and economic factors that influence the profitability of livestock production systems (Jones *et al.* 2004). As such, this type of modelling is suitable for the evaluation of how sexual dimorphism may influence the profitability of a lamb production system because it can account for the interactions between the sources of income and loss. In contrast, Roux (1992b) and Schoeman (1996) used biological models to establish that the biological efficiency (amount of lean meat produced/amount of feed consumed) increased in conjunction with sexual dimorphism in South African beef cattle. These studies failed to consider the economic factors (e.g. variation in the cost of feed and prices received throughout the year) that affect the profitability of the production system. Numerous studies have been published which have used bio-economic modelling to describe sheep pastoral systems (e.g. Amer *et al.* 1999; Conington *et al.* 2000, 2001 & 2004; Jones *et al.* 2004; Morel *et al.* 2004, 2005a&b; Morel & Kenyon 2006; Salmon *et al.* 2004; Wang & Dickerson 1991). The main purpose of these studies has been the estimation of economic values of various traits in breeding programs and testing the robustness of these values to changes in nutrition, management and market prices (Jones *et al.* 2004).

The aim of this study was to develop a bio-economic model that describes a typical self-replacing lamb production system and use it to evaluate the impacts of variation in sexual dimorphism on profitability.

6.3 Materials and Methods

6.3.1 Production System

The production system simulated in this study is a 500 hectare self-replacing prime lamb production system on the Northern Tablelands of New South Wales. A representative farm for this region was simulated from available survey data and the impact of sexual dimorphism (ram/ewe weight), ranging from 1.0 (no difference) to 1.5 (rams 50% heavier than ewes) upon the efficiency and profitability of the production system was evaluated. The simulation of a given farm type and area replicates the decision and type of analysis an individual farmer (or their consultant) would use to evaluate the value of incorporating a new trait like sexual dimorphism into their breeding programs (e.g. feed efficiency in Alford 2004). Treating pasture production as a constant also simplifies the model by removing the requirement to estimate the cost of producing pasture.

The Northern Tablelands region consists of the Walcha, Uralla, Armidale-Dumaresq, Guyra, Glen Innes-Severn and Tenterfield local government areas, which takes in an area of approximately 3.12 million hectares (Alford *et al.* 2003b) and is home to the University of New England. The region is located between the latitudes of 28º 14'S and 31º 30'S and has an undulating to hilly topography with an average elevation of 800 metres rising to a maximum of 1400 metres. The climate is characterised by high summer rainfall (average 750 – 1000 mm/year) and a 200 day frosting interval from April through to October with intense cold winter conditions (Ayres *et al.* 2000). The typical lambing period in this region starts in the month of September (Alford 2004; Curtis 2007; Salmon *et al.* 2004).

A flock producing its own replacement breeding stock (ewes and rams) was simulated. The simulation of a self-replacing flock has many advantages. Firstly, it ensures that any variation is due to sexual dimorphism and not genetic differences between the sires and dams. Secondly, it avoids the complication of heterosis which occurs when two or more

breeds are crossed. Thirdly, each sex has clearly defined yet divergent roles in a self-replacing production system (most ewes become replacements, most rams are sold) unlike 1st cross systems where all progeny regardless of sex are typically sold. Fourthly, the number of self-replacing flocks in Australian lamb production systems is rising in response to an increasing emphasis on lamb production (Curtis 2007). Finally, while self-replacing flocks are relatively rare in lamb production systems, they provide a model for the sum of the Australian sheep industry where very few imports occur and therefore must be self-replacing.

6.3.2 Flock Structure

A typical NSW lamb production flock structure (including ram requirements, age structure and average weaning age and sale weight) was simulated using data (Table 6.1) obtained from the New South Wales Department of Primary Industries (2009) livestock gross margin budgets, the thesis of Alford (2004) and associated reports (Alford *et al.* 2003a&b). The sensitivity of the model to variation in ewe weight was also analysed. The age classes used in this study were similar to those described by Sheep Genetics (Meat and Livestock Australia 2004) and used in previous chapters.

Table 6.1: Key components of the simulated flock structure (obtained from (New South Wales Department of Primary Industries 2009).

Age at which first progeny were born (both sexes)	2 years
Number of matings before were cast for age (CFA)	4
Weaning rate (lambs born/ewes mated/year)	1
Weaning age	3 months
Sale carcass weight	21kg
Adult mortality	4%
Ram requirements (rams/ewe * 100)	2%

Each production unit simulated within the model contained 1 breeding ewe, her ram requirement (0.02), her progeny (1) and the number of hogget replacements required per ewe per year. The number of replacements was calculated from the flock age structure shown in Table 6.2. Only a single offspring per year was simulated to simplify the estimation of the feed requirements due to pregnancy and lactation. The simulation of multiples would have required the estimation of the relative proportions of singles, twins

and triplets in the average litter, which varies considerably between farms. The carrying capacity of the simulated property was calculated from the number of production units that could be carried when pasture availability was at its lowest relative to the feed requirements of a production unit at any point throughout the year.

Table 6.2: Flock age structure showing the number of ewes and rams in age group per 1000 ewes.

Age (yrs)	Ewe	ram
2	265	5.3
3	255	5.1
4	245	4.9
5	235	4.7
Total	1000	20

6.3.3 Magnitude of Sexual Dimorphism Simulated

Flocks with sexual dimorphism (ram/ewe weight) between 1.0 (both sexes the same weight) and 1.5 (rams 50% heavier than females) and reference weights (RW) between 55 and 70kg were simulated. The reference weights represent the mature empty body weight of both sexes if there is no sexual dimorphism present (=1.0) and the average empty body mature weight of both sexes where sexual dimorphism is present. Variation in the reference weight was included to test if the combined size of both sexes had any influence on the effects of sexual dimorphism. The mature weights of each sex at each level of sexual dimorphism were estimated by calculating the amount of deviation above and below the reference weight required to achieve the desired amount of sexual dimorphism. The changes in full body weight with sexual dimorphism in low reference weight (55kg) and high reference weight (70 kg) flocks are shown in Figure 6.1.

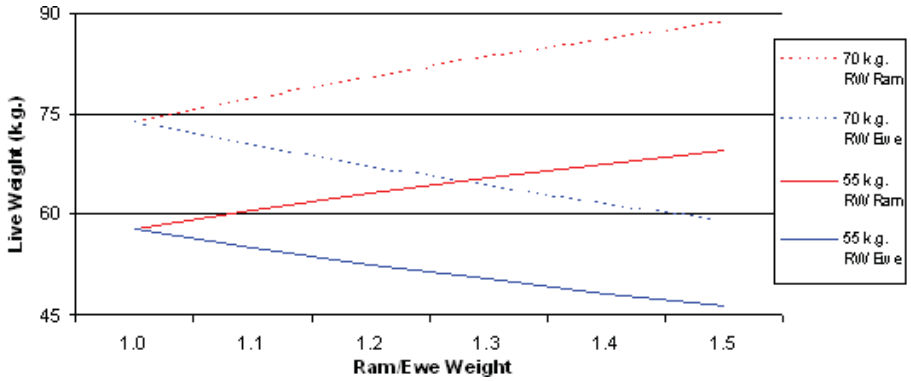

Figure 6.1: The magnitude of sexual dimorphism (ram/ewe weight) and mature weight (kg) of parents.

Existing sexual dimorphism in birth weight and chemical composition was accounted for within the model. The average birth weights of ewes and rams of typical self-replacing/ maternal breeds in the Sheep Genetics database was 4.71 and 5.01 kg, respectively (Daniel Brown 2009, *pers. comm.* 16 September). Table 6.3 shows the differences between ewes and rams in their chemical composition at maturity as described by Thompson and Butterfield (1985).

Table 6.3: Sexual dimorphism of the chemical composition of the sheep body at maturity (Thompson & Butterfield 1985).

	Ewes	Rams
Protein	13.4%	11.9%
Lipid	32.0%	41.0%
Water	51.3%	44.2%
Ash	3.3%	2.9%

6.3.4 Bio-Economic Model

The bio-economic model used to describe the effects of sexual dimorphism upon the profitability of lamb production in the Northern Tablelands region contained six major components: pasture availability, the energy required by individuals in the production system, the carrying capacity of the farm, the costs per animal, the income per animal and the overall gross margin or profit. The interactions between each of these components are described in Figure 6.2. Variation in the size of mature ewes and rams, including the effect of sexual dimorphism, influences the feed requirements (Brody 1945; Taylor 1980) and salvage value of adults (Robertson 1987; Thompson 1991), as well as the growth of progeny (Taylor 1980). While variation in the growth of progeny plays a minor role in determining the feed efficiency of the production system (faster growth to sale weight lowers their maintenance requirement**)**, the mature size/adult feed efficiency is a key determinant of the carrying capacity of a given enterprise (Thompson 1991). For the purposes of this simulation, the carrying capacity is defined as the number of production units that can be carried by a 500 hectare New England Tablelands farm modelled on the Glen Innes Agricultural Research and Advisory Station.

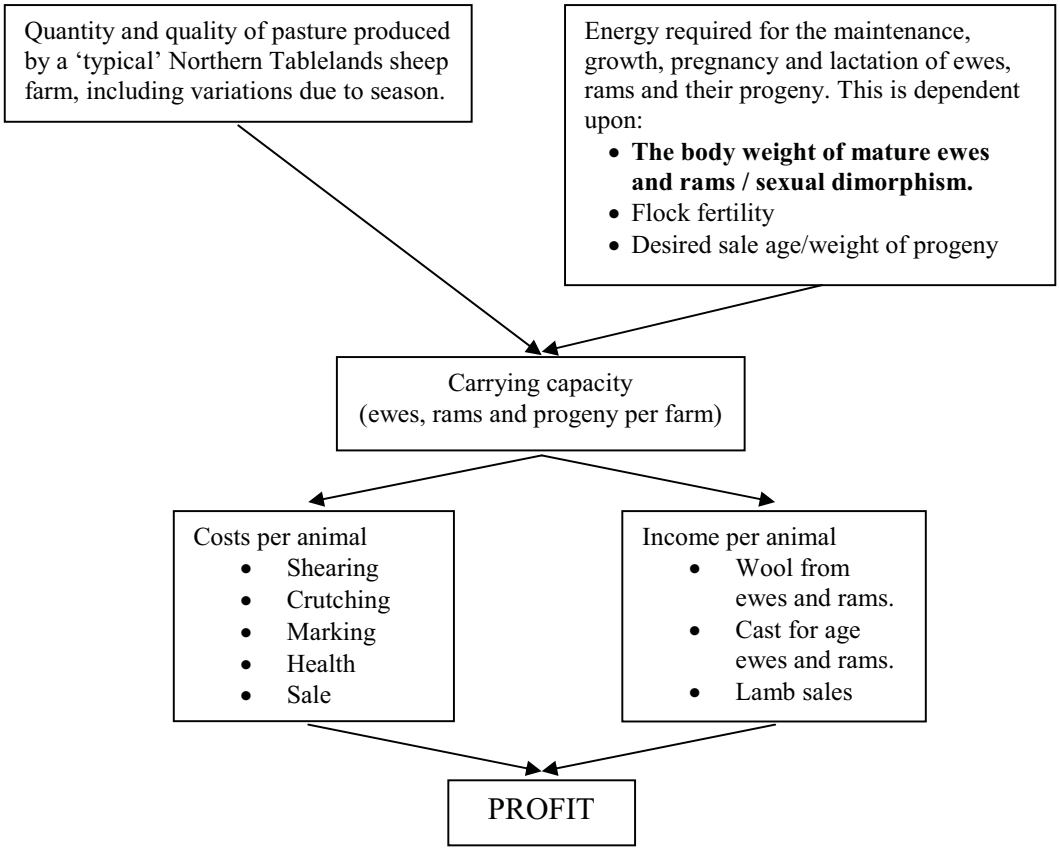

Figure 6.2: A lamb production bio-economic model used to evaluate the influence of sexual dimorphism on the profit achieved in the production system. User inputted variables are shown in bold type.

Pasture Availability

The available pasture production and composition of the farm was modelled using the GrassGro decision support system (Moore *et al.* 1997) based on the climate, soil and pasture characteristics of the Glen Innes Agricultural Research and Advisory Station. The Glen Innes Agricultural Research and Advisory Station is centrally located within the Northern Tablelands region and the soil type, pasture production and climate has been described by Ayres *et al.* (2000 & 2001). The majority of the grassland in the region is comprised of native grasses (including *Bothriochloa* and *Danthonia* spp.) with temperate, cool season perennials (e.g. white clover (*Trifolium repens*), perennial ryegrass (*Lolium perenne*) and phalaris (*Phalaris aquatica*)) introduced on approximately 25% of the farm

area. The resultant average annual pasture production curves from the GrassGro decision support system (Moore *et al.* 1997) are shown in Figure 6.3.

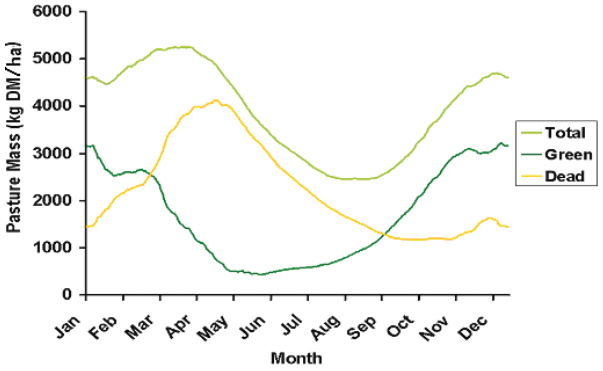

Figure 6.3: Annual cycle of green and dead pasture production along with total available pasture per hectare simulated for the New England Tablelands by the GrassGro decision support system (Moore *et al.* 1997).

By estimating the carrying capacity of a given amount of pasture (defined by farm location and size), the need to calculate the cost of pasture production is avoided. This results in a simpler model to estimate the influence of sexual dimorphism upon the profitability of the production system. For simplicity, no supplementary feeding was modelled.

Animal Growth

The average size of individuals in each stock class is important in determining the market value and feed requirements of each animal contained within the model. To estimate the average growth curve of each sex, an extended version of the Amer and Emmans (1998) model that utilises a Gompertz function (Gompertz 1825) to estimate the unconstrained growth of protein, fat, water and ash as a function of the degree of protein maturity, was used. The Gompertz equation used in the model to estimate the level of protein maturity (u_t) is:

$$u_t = \exp(-\exp(G_0 - (B_S\, t))) \qquad \text{Equation 6.1}$$

where t is time, G_o is the initial condition derived from the ratio of the initial protein content (P_o) and mature protein content (P_m), B_s is the scaled rate parameter used to express the general rate parameter in metabolic time and is derived using Equation 6.3 where B^* is a general rate parameter. The initial body protein (P_o – at birth) is estimated using the Newton-Raphson iteration method used by Wellock *et al.* (2003).

$$G_0 = \ln(-\ln(P_0/P_m)) \quad \text{Equation 6.2}$$

$$B_S = B^*/P_m^{0.27} \quad \text{Equation 6.3}$$

The weight of each chemical body component was estimated using the relationship defined by Emmans (1988) that states the degree of maturity of one chemical component has an allometric relationship with the degree of maturity of another chemical component. This allows for the weights of the chemical body components to be predicted using:

$$P_t = u_t \,.\, P_m \quad \text{Equation 6.4}$$

$$A_t = S.P_t \quad \text{Equation 6.5}$$

$$L_t = u_t^{bl} \,.\, Q \,.\, P_m \quad \text{Equation 6.6}$$

$$H_t = u_t^{bh}.R.P_m \quad \text{Equation 6.7}$$

where P_t, A_t, L_t and H_t are the weights of protein, ash, lipid and water in the body at time, t. The ratios of water, lipid and ash to protein at maturity are represented by Q, R and S respectively, are sexually dimorphic and were calculated from the values given in Table 6.3. The power constants for lipid and water had values of 2.23 (*bl* ewe), 2.13 (*bl* ram) and 0.855 (*bh*), respectively (Amer & Emmans 1998). The sum of protein, lipid, ash and water components give the empty body weight (*EBW* (kg)) which can be converted to full body weight (w (kg) – includes gut fill) using Equation 6.8 (Wellock *et al.* 2003). An example of the full body weight growth curve generated in the model for a 65 kg ewe is shown in Figure 6.4.

$$Wt_t = EBW_t/0.95 \quad \text{Equation 6.8}$$

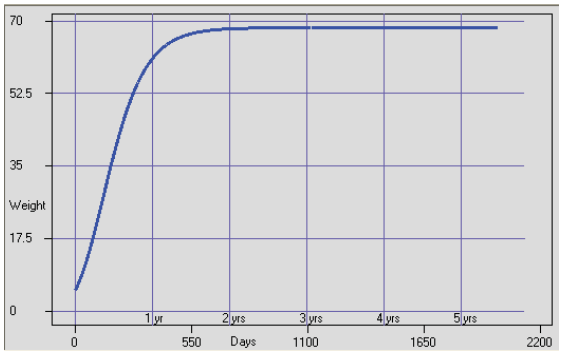

Figure 6.4: Screenshot from the model showing the growth curve generated for a 65 kg ewe.

Pregnancy and Lactation

The growth of the conceptus (a single foetus, membranes and fluids) follows the Gompertz function (Freer *et al.* 1997) (equation 6.1). The starting and mature (aka at birth) values for the conceptus required by the function were obtained from the chemical composition values of each conceptus component published by Rattray *et al.* (1974).

Milk available for consumption was simulated to occur for the first 120 days of an animal's life using the model presented by Emmans and Fischer (1986) and tested by Friggens *et al.* (1999) in beef cattle**.** Daily milk production (*dY/dt* – kg/day) was modelled using:

$$dY/dt = a\,(\exp(-\exp(G_0 - b.t))) \,.\, (\exp(-c.t) \qquad \text{Equation 6.9}$$

where *t* is days from lambing, *a* is a scalar, *b* is a growth rate parameter, *c* is a decay parameter and G_o is the initial state at $t = 0$, given by:

$$G_0 = \ln [\, -\ln(M_0/a)] \qquad \text{Equation 6.10}$$

where M_o is initial milk production at parturition. The patterns of fat, protein and lactose production across time were modelled based on the percentage contribution of each to total milk volume as shown in Table 6.5. The lactose composition of milk (kg per kg milk) followed a similar pattern to total milk production and thus was modelled using the same equation (6.10). Conversely, fat and protein composition decreased during the initial stages of lactation following parturition and then increased again as lactation progresses towards completion. Because the patterns of fat and protein composition are effectively a mirror image of lactose composition, it was modelled by removing the negative sign between the two exponents in the total milk production/lactose composition equation (equation 6.10).

Table 6.5 – The percentage contribution of fat, protein and lactose to total milk volume in single suckled ewes (Bencini & Purvis 1990).

Component	Percentage (%) ± S.E.
Fat	8.48 ± 0.23
Protein	4.85 ± 0.07
Lactose	5.16 ± 0.03

Nutritional Requirements

Individual animals simulated in this model consumed pasture to meet the nutritional requirements of four different physiological processes: maintenance, growth, pregnancy and lactation. A fifth process, wool growth, was omitted from the nutritional requirements model for simplicity as it has a relatively low nutritional requirement compared to the other processes (SCARM 1994), it has a low correlation with body weight (Safari & Fogarty 2003) which is the dependent variable in this study and is considered a by-product in a lamb production system. The omission of the energy requirements of wool production is not unusual according to SCARM (1994), as it is often accepted as an integral part of the maintenance requirements (like hair growth on other animals). The cost of shearing and value of wool sold was retained in the economic sub model because these values are influenced by the carrying capacity of the property.

The quantity of energy required on day, t (EN_t – MJ/day) was predicted using the method described in Emmans (1994):

$$EN_t = MR_t + (z_p\,(dP/dt)) + (z_L\,(dL/dt)) \qquad \text{Equation 6.11}$$

where z_P and z_L are the energy costs of protein and lipid deposition, 50 and 56 MJ/kg, respectively (Amer & Emmans 1998). Accounting for the higher cost of depositing fat compared with muscle is particularly important when modelling sexual dimorphism due to the variation between ewes and rams in body composition (Thompson & Butterfield 1985). dP/dt and dL/dt are the daily retentions of protein and lipid, respectively, required for growth (kg/day). MR_t is the predicted maintenance requirement of the animal at time, t (MJ/day; Emmans & Fischer 1986). To allow comparison of maintenance requirements between animals of different mature sizes, the maintenance value was made proportional to mature protein weight to the power of 0.73 ($P_m^{0.73}$) using Equation 6.12 (Emmans 1997) following Brody's (1945) rule for scaling mature maintenance needs.

$$MR_t = z_M \,.\, P_m^{0.73} \,.\, u_t \qquad \text{Equation 6.12}$$

where z_M is the energy constant for maintenance, given as 1.65 and is considered to be constant across animals and diets (Amer & Emmans 1998). u_t is the level of protein

maturity given in Equation 6.1. The nutritional requirements of a single ewe simulated in the model are shown in Figure 6.5.

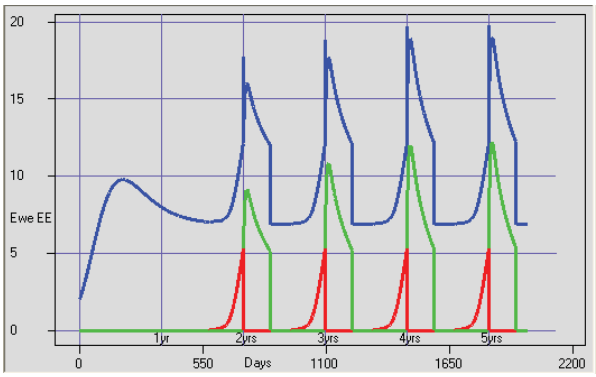

Figure 6.5: Screenshot from the model showing the nutritional requirements (MJ) of a 65 kg ewe. The blue line represents the total energy requirements (including growth and maintenance), green line represents lactation and red line represents gestation.

Energy Content of Feeds

The quantity of effective energy (*EE* – MJ/kg dry matter) contained in a kilogram of feed is determined using Equation 6.13 (Emmans 1994) where *ME* is the metabolisable energy and *DCP* is the digestible crude protein content of the feed.

$$EE = 1.15ME - 3.84 - 4.67DCP \quad \text{Equation 6.13}$$

The energy available from milk varies from that available from other feed sources because milk bypasses the first two compartments of the stomach, the rumen and reticulum, which are undeveloped in young ruminants and is channelled directly to the omasum and abomasum via a tube-like fold of tissue known as the oesophageal groove (McDonald *et al.* 2002). As a result, when modelling the consumption of milk in young ruminants, equations for monogastric animals (e.g. pig) should be used, for example, Equation 6.14 as given in Emmans (1994):

$$EE = (1.17ME) - [4.29(CPC/1000)] - 2.4 \quad \text{Equation 6.14}$$

where *CPC* is the crude protein content of milk and *ME* is the metabolisable energy content of milk (MJ/kg) and is calculated following Emmans (1994) as:

$$ME = DigE - 5.63(CPC/1000) \quad \text{Equation 6.15}$$

where *DigE* is the digestible energy content of milk which is considered to be 98.6% of the gross energy of milk (Walker & Kirk 1975). The gross energy of milk (*GE* – MJ/kg) was calculated from the equation presented by McDonald *et al.* (2002) that takes the percentage of fat (*F*), protein (*P*) and lactose (*L*) in milk into consideration:

$$GE = (0.0384F) + (0.0223P) + (0.0199L) - 0.108 \quad \text{Equation 6.16}$$

Costs of Production

The costs associated with a Northern Tablelands lamb production system were obtained from the NSW Department of Primary Industries Livestock Gross Margin Budgets (NSW DPI 2009; see Table 6.6). The values contained in the gross margin budgets were derived from a mixture of survey data (e.g. the costs of inputs and the frequency that they are required) and forecast commodity prices. Like the gross margin budgets, the bio-economic model used in this study did not include fixed or overhead costs such as depreciation, interest payments, rates and permanent labour, which have to be met regardless of the livestock numbers or type involved in the production system. Similarly, the cost of pasture production was assumed constant across each scenario and not required in the model. All dollar values quoted are in Australian Currency and exclusive of Goods and Services Tax.

Table 6.6: Cost per animal and number of replicates of each treatment required per year (data sourced from NSW Department of Primary Industries Livestock Gross Margin Budgets (NSW DPI 2009)

Treatment	Animal Class	Cost per treatment	No. of treatments required per year
Shearing	Ewes/Ewe Hoggets	$5.74	1
	Rams	$8.61	1
Crutching	Ewes/Ewe Hoggets	$0.85	1
	Rams	$1.71	1
	Lambs (mixed-sex)	$0.85	1
Wool Tax	Rams/Ewes/Ewe Hoggets	2%	1
Commission (Wool)	Rams/Ewes/Ewe Hoggets	$42.99*	1
Cartage/Packs (Wool)	Rams/Ewes/Ewe Hoggets	$28.57*	1
Drenching	Rams/Ewes/Ewe Hoggets	$0.35	2
	Lambs (mixed-sex)	$0.18	3
Dipping	Rams/Ewes/Ewe Hoggets	$0.56	1
Jetting	Rams/Ewes/Ewe Hoggets	$1.65	1
	Lambs (mixed-sex)	$1.38	1
Vaccination	Rams/Ewes/Ewe Hoggets	$0.22	1
	Lambs (mixed-sex)	$0.22	1
Marking/Mulsing	Ewe Lambs	$3.75	1
Marking	Ram Lambs	$1.35	1
Scanning	Ewes	$0.90	1
Cartage (sheep)	All sale sheep	$2.00	1
Commission (sheep)	All sale sheep	5%	1

* per bale (165 kg wool)

Sources of Income

Two sources of income were present in the model; wool production (including crutchings) and sheep sales. All sheep not kept for reproductive purposes were assumed sold and all sheep sold were assumed sold for slaughter, thus prices were on a per kilogram of carcass weight basis. Variation in value between stock classes (lamb vs. hogget vs. adult, ewe vs. ram) was incorporated for all products, where possible (hogget meat is classified as lamb). Variation throughout the year in the prices paid by the meat companies for each carcass grade was also taken into account (data obtained from the weekly Over the Hooks Reports for New South Wales (MLA 2009; Figure 6.6). The price and quantity of wool produced by each stock class was obtained from NSW Department of Primary Industries Livestock Gross Margin Budgets (NSW DPI 2009; Table 6.7).

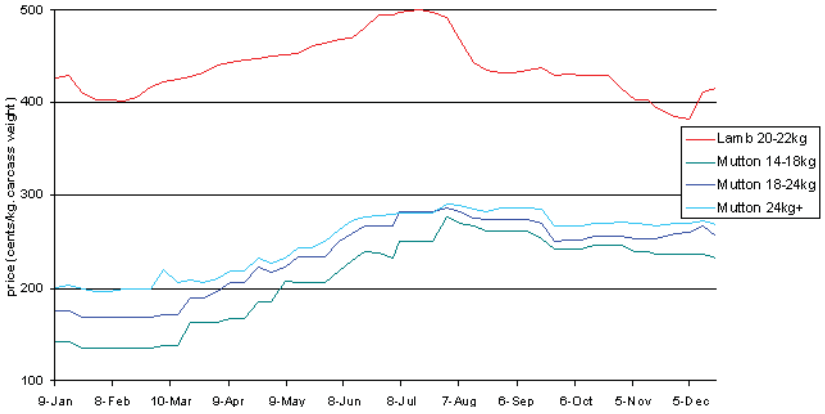

Figure 6.6: Variation in the price received for lamb (20-22 kg carcass only) and mutton throughout 2009. Data obtained from weekly Over the Hooks Reports for New South Wales (MLA 2009).

Table 6.7: Sources of wool income (values obtained from NSW Department of Primary Industries Livestock Gross Margin Budgets (NSW DPI 2009)

Product	Animal Class	Wool produced per animal	Value ($/kg)	Wool income per animal
Wool	Ewes	4.50 kg	$2.83	$12.74
	Rams	6.00 kg	$2.37	$14.22
	Ewe Hoggets	3.15 kg*	$2.83	$8.91
Crutchings	Ewes and Rams	0.30 kg	$1.37	$0.41
	Ewe Hoggets	0.21 kg*	$1.37	$0.29

* Hoggets wool weights were assumed to be 70% of adult wool weight as suggested by (Curtis 2007)

6.4 Results

The results showed that there was a general increase in carrying capacity and consequently, profitability with increasing sexual dimorphism (Figure 6.7), though there were exceptions at lower reference weights. Figure 6.8 shows the change in the shape and magnitude of the feed requirements curve just before lambing (circled) with increasing sexual dimorphism. At this stage of the year, pasture was limiting in all scenarios tested (thus determined carrying capacity) due to the gestation and lactation requirements of the ewes (see Figure 6.5). The presence of slow growing ewe lambs that had not reached sale weight at this time of year reduced the amount of feed available for the ewes and thus decreased carrying capacity. The presence of slow growing ewe lambs was explained by the relatively low mature weight of ewes in the 55 kg reference weight group with higher levels of sexual dimorphism. With a ram/ewe weight of 1.5, the mature weight (44.3 kg) was only just sufficient to produce the desired 21 kg carcass weight at maturity (with a 47% dressing percentage the maximum carcass weight at maturity was 21.8 kg). As such, results from a 55 kg reference weight and 1.5 sexual dimorphism were not recorded as it is impractical for any farmer to keep lambs through two winters before sale. The correlation between profit per hectare and carrying capacity was >0.99 for the higher reference weights (65 and 70 kg) and between 0.55 and 0.68 for the lower references weights (50 and 65 kg). The decrease in the overall magnitude of the flock energy requirements with sexual dimorphism is also visible in Figure 6.8.

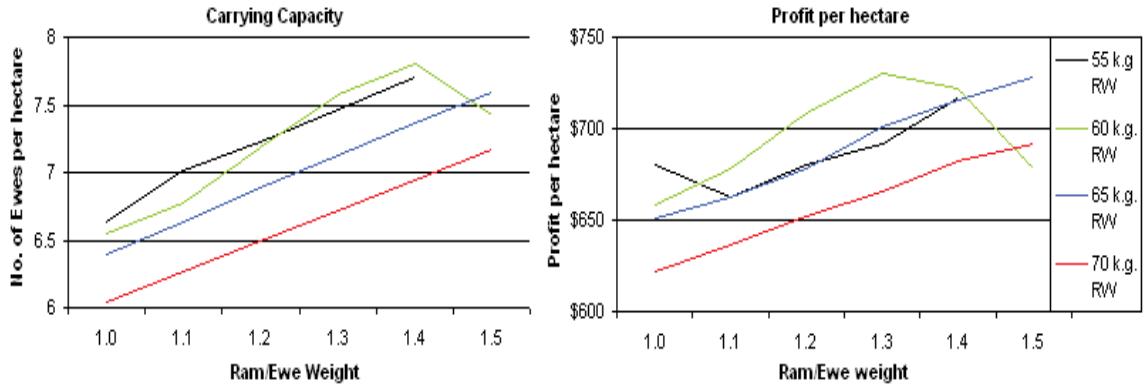

Figure 6.7: The variation in the carrying capacity and profit per hectare expected due to variation in sexual dimorphism (ram/ewe weight) on a 500 hectare New England Tablelands property (RW = reference weight).

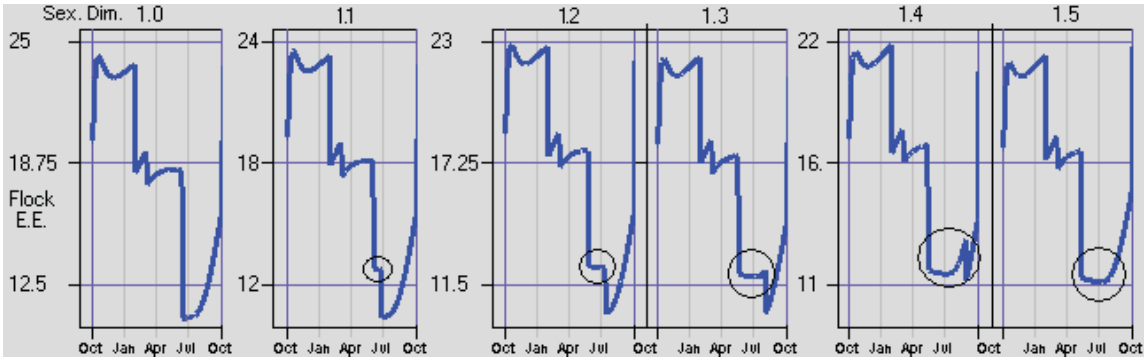

Figure 6.8: Comparison of the relative production unit energy requirements per year across differing levels of sexual dimorphism for a flock with a 60 kg reference weight.

The amount of profit per ewe decreases with increasing sexual dimorphism (Figure 6.9), which is the opposite of the profit per hectare result. The reason for this is the variation in price throughout the year as depicted in Figure 6.6 and the absence of any benefits accrued by increasing carrying capacity (as it is per ewe). At higher levels of sexual dimorphism, the age at which most ram lambs are slaughtered decreases (Figure 6.9) and thus, ram lambs reach market weights earlier in the year when they are worth less. The extent to which this phenomenon occurs is dependant on the reference weight of the flock.

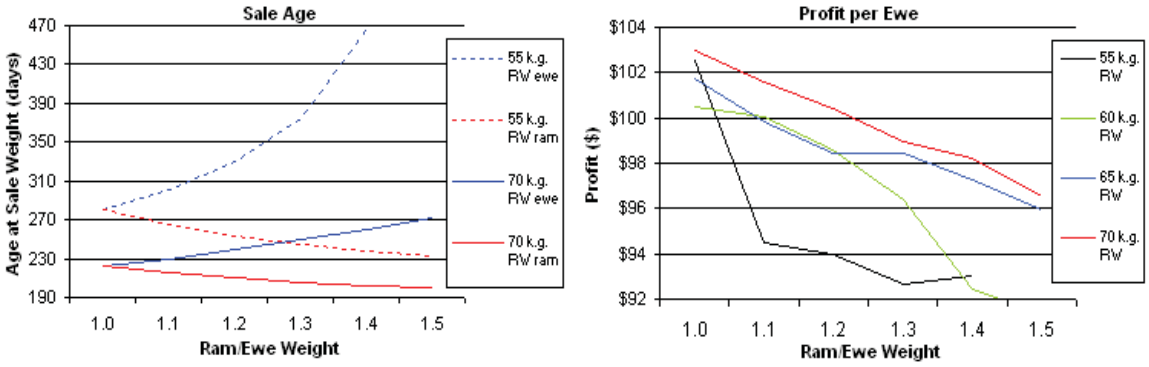

Figure 6.9: The effect of sexual dimorphism on the sale age (@ 21 kg carcass weight) in ewe and ram lambs and the profit expected per ewe.

6.5 General Discussion

In the farm scenario modelled, sexual dimorphism was found to have a positive effect on farm profit in flocks with a higher reference weight. This effect was achieved by feed efficiency increasing with sexual dimorphism, thus allowing the number of ewes that could be carried on a given farm area/amount of pasture production, to increase. Similar results were found by Roux (1992b) in beef cattle and Hutt (1959) in chickens and confirm the importance of simulating variation in feed availability and prices received as identified by Archer and Amer (2009). The presence of an optimum level of sexual dimorphism in flocks simulated with lower reference weights was due to the high sale weight of ewe lambs compared to ewe mature weight. Animals with high relative sale weights require a longer growing period with associated increases in lamb maintenance requirements (Dickerson 1970), reductions in the prices received after July (see Figure 6.6) and in feed availability due to both the increased ewe requirements for gestation/lactation (Figure 6.5) and low pasture production during winter (Figure 6.3). However, the set weight at slaughter used in the model (21 kg carcass weight) is not a realistic representation of the options available to the producer. The producer has the option of selling animals at lower weights. The lightest classification (16-19 kg carcass weight) requires a live weight 10 kg lighter, which can be reached between a month and a half to four months earlier depending on the reference weight and sexual dimorphism of the flock. However, 16-19 kg carcasses are worth five cents less per kg on average throughout the year and there is greater variation in the prices received throughout the year than at heavier weights (MLA 2009). Lambs with higher relative sale weights will also be penalised for the higher levels of fat that is deposited as a consequence of their greater maturity at the same weight (Taylor 1980), though this was not evaluated in this study due to the absence of a fat pricing structure in the weekly 'Over the Hooks Reports' (MLA 2009) used to obtain representative carcass values.

Roux (1992b) identified the importance of replacement rate in determining the benefits that can be obtained from incorporating sexual dimorphism in a breeding program. The number of ewes and rams required as replacements determines not only the amount of feed required to grow these animals to maturity before they begin production but also the number of ewes and rams available for sale. To achieve the maximum benefit from sexual dimorphism, the

number of ram replacements needs to be minimised and the number of ewe replacements maximised so that more large rams are available for sale and more smaller adult ewes are retained in the production system, though this may be in conflict with other objectives such as maximising replacement rate for genetic progress. While variation in replacement rate was not modelled in this study, Roux (1992b) found that a biological efficiency gain of 3% was possible with sexual dimorphism of 1.2 by increasing the rate of female replacements from five to 50% and a gain of 9% was possible with sexual dimorphism of 1.6 with the same increase in female replacement rate.

A number of traits influence the replacement rate of a flock including the length of time a ewe (or ram) remains in production (longevity), the number of lambs produced per ewe (fertility), and the level of mortality (both lamb and adult) in the flock. Longevity and adult mortality in the breeding flock determine the number of replacements that are required and fertility and lamb mortality determine the number of lambs available for selection into the breeding flock. The ratio of replacements required and lambs available for selection determines the number of non-selected lambs available for sale. For modelling purposes, fertility is a complicated trait because knowledge of the relative proportions of dry ewes and ewes carrying singles, twins or triplets is required. Unfortunately, at the same level of fertility the proportions can vary greatly between flocks, ewe parity, seasons and/or breeds (Friggens *et al.* 1999). Furthermore, the change in the these proportions from before birth to after weaning (accounting for lamb mortality) is also required for the accurate prediction of the lactation requirements (Amer *et al.* 1999), and variation between flocks, ewe parity, seasons and/or breeds have been shown to exist in flocks maintained under similar conditions (Gudex *et al.* 2005).

The bio-economic model used in this study assumed that selection for sexual dimorphism would be symmetrical with ewes losing the same amount of weight that the rams gained. This allowed the comparison of sexual dimorphism at the same reference weight which the results have shown to be important. However, with the appropriate weighting of sex-specific breeding values in a selection index, sexual dimorphism can be obtained through maintaining or slightly increasing ewe weight as long as the increase in ram weight exceeds the increase in ewe weight (if any). It is likely that this will be desirable in breeding

programs that value fertility, due to the positive correlation that exists between live weight and fertility (Safari *et al.* 2005 & 2007) and live weight and salvage value when she is cast for age (Conington *et al.* 2004). The non linearity of these relationships and degree of interrelationship (particularly with fertility influencing replacement rate and being influenced by live weight) suggest that a non linear selection index as suggested by Meuwissen and Goddard (1997) would be the most suitable option to incorporate sexual dimorphism into a breeding program which would increase the complexity of applying what is already a complex trait.

As used in this study, the model operates on the premise that live weight is positively correlated with feed intake (Morel & Kenyon 2006; Snowder & Vleck 2003; Thompson 1991) but does not account for the positive correlations between fat levels and feed intake at the same weight (rg 0.56) found by (Lee *et al.* 1992). Based on the positive correlation between fat and feed intake and the desirability of producing lean carcasses for sale, selection for sexual dimorphism in fat levels would also be desirable and according to the results presented in Chapters 3 and 4, possible. Fortunately, the negative correlations reported between fat and live weight in Chapter 4 suggest that selection for sexual dimorphism in live weight will have a desirable correlated response in fat levels, though this was not simulated in this study.

The omission of variation in fat levels did not affect the accuracy with which the feed requirements were predicted in this study. Comparison of the feed requirements for maintenance, growth, gestation and lactation presented by Amer *et al.* (1999) for a 60 kg ewe and single lamb revealed comparable results to those obtained in this study. The Standing Committee on Agriculture and Resource Management (SCARM 1994) recommends adding an extra 15% to the maintenance requirements of rams to account for the greater energy cost of depositing protein compared with fat and the higher proportion of protein and lower proportion of fat present in the ram body (Thompson & Butterfield 1985). By simulating the growth of each body component, the Amer and Emmans (1998) model directly accounts for the variation between the sexes in body composition, but at the cost of greater model complexity and data requirements.

Some models, including variations of the Amer and Emmans (1998) model used in this study incorporate information on various environmental factors, including climate, feed intake(including the energy cost of grazing) and feed quality (digestibility, crude protein), into the estimation of growth and feed requirements. If not accounted for, these factors can bias the results due to variation between individuals/mobs and the masking of each individual's innate ability to grow (Emmans & Kyriazakis 1999). The version of the Amer and Emmans (1998) model used in this study avoids this by estimating non limited growth which assumes optimal growing conditions. This allows individuals to be compared under identical conditions (Emmans & Kyriazakis 1999).

6.6 Conclusion

This study successfully designed and constructed a bio-economic model to evaluate the benefits of sexual dimorphism in a self-replacing lamb production system on a 500 hectare Northern Tablelands property. Despite the unique production environment simulated, the results of pasture production, energy requirements and economic sub models were comparable to those published previously and sexual dimorphism was found to have a positive effect on farm profit in flocks where the ratio of lamb sale weight to ewe weight was not limiting. The positive influence of sexual dimorphism upon profitability was achieved through increasing feed efficiency with sexual dimorphism, which allowed the number of ewes that could be carried on a given farm area/amount of pasture production to increase. Aside from the ratio of lamb sale weight to ewe weight, variation throughout the year in feed availability and the prices received for lamb were found to be important variables in the model. The influence of variation throughout the year in feed availability also suggests that different results are likely in different environments, though this effect, like the effects of variation in sale weight, replacement rates and fat levels, was not tested. The number and nature of the factors influencing the benefits of sexual dimorphism suggests that a non linear selection index would be the most suitable option to incorporate sexual dimorphism into a breeding program, though this adds more complexity to the application of an already complex trait.

Chapter 7: General Discussion

Traditionally animal breeding has placed a greater emphasis on traits that can increase net income, with little emphasis on the often positively correlated traits that influence the costs of production. For example, selection for faster growing lambs has also lead to larger ewes that require greater amounts of feed throughout the year, including the winter when feed in more scarce/valuable. As a consequence, the predicted economic outcomes of breeding programs have often been overly simplified and optimistic as the correlated response in some traits have been ignored (Ponzoni 1988). A major reason for the emphasis on traits influencing net income has been their ease of measurement, for example the weighing of lambs. By comparison, the measurement of feed intake is both difficult and costly (Amer & Emmans 1998; Snowder & Vleck 2003). This thesis proposed a mechanism by which sexual dimorphism could reduce feed costs in lamb production systems in Chapters 1 and 2. Although similar approaches have been suggested in chickens (Jaap 1969; Merat 1984) and feedlot cattle (Roux 1992b), this was the first instance where it has been proposed for a pastoral livestock production system. Livestock maintained on pasture have a lot more to gain than those fed concentrated feeds because of the difficulties and expense involved in the measurement of the pasture intake of individuals. Furthermore, the large maintenance requirement of the female parents, low reproductive rate (relative to pigs and poultry) and short lifespan of sheep make them ideally suited to benefit from any increase in female feed efficiency (Lambe *et al.* 2006; Robertson 1987; Thompson 1991).

The first three experimental chapters of this thesis sought to answer how similar, genetically, growth is in each sex. Chapter 3 also quantified the extent to which rams are larger than ewes. The results revealed that the difference in size between ewes and rams increased with age until rams were ~1.3 (ram/ewe weight) times larger than ewes, that ewes have larger heritability and smaller phenotypic variances than rams and that the intersex genetic correlations were less than unity and decreased with age. The prediction of the response to selection for growth using these results revealed that the response of rams to selection for growth was larger than in ewes given the typical selection intensities found in the industry (rams > ewes). The sole exception to these results was found when fat depth was analysed. For fat depth, ewes had deeper measurements (per kg live weight), lower

heritability and higher phenotypic variances than rams. This was the first time that sex-specific genetic parameters for fat and eye muscle depth in sheep have been reported. Little variation was observed between the Coopworth, Poll Dorset and White Suffolk breeds in the genetic parameters or selection responses estimated in this study, despite variation in selection history/objectives and in the founder effects present in each breed.

A bio-economic model was used in chapter 6 to simulate the influence of sexual dimorphism on the feed efficiency and the profitability of a self-replacing lamb production system. This model revealed that there was potential feed efficiency and financial gains to be made by increasing sexual dimorphism within a self-replacing flock and that these gains are dependant on the average combined weight of both sexes and variation throughout the year in feed availability and prices received. Variation in response due to the age structure of the flock (including replacement rate) and fertility were also discussed. This was the first time that a model incorporating financial considerations has been used to evaluate the value of sexual dimorphism in any livestock species (previous models have ignored the economic component) and it is also the first time that sheep have been evaluated for this trait.

The following sections of this discussion will review and discuss the technical and practical considerations that users must be aware of if sexual dimorphism is to be used as a trait in breeding programs. Other possible applications of sexual dimorphism in livestock breeding and future directions of research are also discussed.

7.1 Technical Considerations for the Genetic Evaluation of Sexual Dimorphism

There are two possible methods by which breeding values could be estimated to allow selection for sexual dimorphism. Lee and Pollak (1997) and Näsholm (2004) suggested treating male and female weights as separate traits, thus allowing weight in each sex to be incorporated individually into a selection index with appropriate weightings for divergent selection. The second approach involves the estimation of a single sexual dimorphism breeding value that quantifies the genetic difference in growth between ewes and rams at

relevant ages. The accuracy of both the sexed breeding values and the sexual dimorphism breeding value will be less than those obtained from mixed-sex data because each sex only has half (assuming a 50:50 sex ratio) the data and relatives with records available for analysis compared with their mixed-sex equivalents. As mixed-sex breeding values would still be required for breeders who ignore sexual dimorphism or production systems where it is not relevant, the production of either the sexed breeding values or the sexual dimorphism breeding value would be in addition to those currently estimated (Näsholm 2004) though no extra data collection is required.

Both of the sexed breeding value and sexual dimorphism breeding value methods have their own unique advantages and disadvantages. A single sexual dimorphism breeding value only involves the estimation and incorporation into the breeding program of one extra trait. However, this method lacks the ability to directly control the direction and magnitude of selection on each component trait (ewe and ram weights) represented by the breeding value (Gunsett 1984). For selection for sexual dimorphism to occur in sheep, it is not necessary for ewe weight to decrease as long as the increase in ram weight exceeds the increase in ewe weight. This may be desirable given the negative correlation between ewe weight and fertility and the economic value of ewe weight when she is cast for age. The sexed breeding value method allows the direction and magnitude of the selection response in each sex to be controlled via the appropriate weighting of economic values applied to the ewe breeding value and the ram breeding value in a selection index. The use of sexed breeding values also avoids any debate regarding the suitability of using ratios to describe sexual dimorphism in statistics and/or genetic selection (e.g. Gunsett 1984; Huhn 1992; Lovich & Gibbons 1992; Smith 1999; Newton Turner 1959).

7.2 Practical Considerations for the Use of Sexual Dimorphism in Breeding Programs

The presence of variation between ewes and rams in genetic parameters and in selection responses estimated using typical selection intensities obtained from the industry reveals that sexual dimorphism is likely to be increasing without most breeders' knowledge or

inclusion in breeding objectives. While Chapter 6 showed that this is beneficial in most self-replacing production systems, there are scenarios when it is desirable to select against sexual dimorphism (e.g. where sale weight is high relative to mature ewe weight or in terminal sire breeds). The increase in sexual dimorphism from typical mixed-sex selection for growth needs to be countered in these situations.

Selection against sexual dimorphism in terminal sire breeds would be desirable due to the lack of divergent roles and selection objectives between ewes and rams in these breeds and the desirability of reducing the diversity of terminal sired lambs offered for sale. Although this objective is contradictory to what is desirable in self-replacing maternal breeds, it would allow sexual dimorphism within a line/breed and a terminal sire to be used in conjunction to increase the overall feed efficiency and profitability of the industry. The feed efficiency of the flock producing the sexually dimorphic ewe would be increased as described in Chapter 6, while the adverse affect of sexual dimorphism on terminal ewe lamb growth (as discussed in Chapter 2) would be cancelled out in flocks using terminal sires. This allows the retention of the benefits that occur in a large sire, small dam terminal sire production system (Jones *et al.* 2004; Mousa *et al.* 1999) despite the presence of sexual dimorphism in the dam. The magnitude of the sexual dimorphism present between the parents in a terminal sire production system is not passed on to the progeny and, typically, the progeny are all destined for sale and not for further breeding. The lack of variation in the magnitude of sexual dimorphism and in the genetic parameters that determine its response to selection observed between the breeds utilised in this study (Coopworth, Poll Dorset and White Suffolk) was surprising given the variation between breeds in selection history and founder effects. Even though only a small sample of breeds (three) were analysed and the effect of heterosis on sexual dimorphism was not examined, this suggests that crossbreeding will not lead to rapid genetic gain in sexual dimorphism.

Including sexual dimorphism into the breeding objectives of some flocks is complicated by the unequal recording of traits across sex that is evident in the Sheep Genetics database. Combined with the variation in selection response between ewes and rams observed in Chapter 4, the unequal recording questions the accuracy with which selection is being carried out in some of these flocks. Also required for the accurate design of breeding

programs is knowledge of how sexual dimorphism interacts with other traits. For example, breeding for increased sexual dimorphism could result in smaller ewes having difficulty giving birth to larger ram lambs or slower growing ewes not reaching puberty early enough to allow hogget lambing. Fitzhugh (1976) and Roux (1992b) also suggested that restricting nutrition in growing ewes could also be used to promote sexual dimorphism. However, the positive correlation between ewe weight and other production traits, for example, fertility, makes this approach unattractive.

7.3 Other Possible Applications of Sexual Dimorphism in Livestock Breeding Programs

The feed efficiency advantages conferred by sexual dimorphism in sheep are also applicable in other livestock species (e.g. Jaap 1969 and Merat 1984 in chickens, and Roux 1992b in cattle). Species with large maternal maintenance requirements, low market weight compared with mature size, low reproductive rate and a short lifespan will benefit the most from this approach. Although cattle have a high relative market weight and a long lifespan, they should benefit from greater sexual dimorphism due to the large cow maintenance requirements and low fertility (Arango & Van Vleck 2002; Thompson 1991). At the other extreme, pigs and poultry have low maintenance requirements and high fertility (Thompson 1991) which would reduce the benefits of including sexual dimorphism in their breeding programs.

Sexual dimorphism in other traits may also be of benefit to Australasian sheep production systems. Fatter ewes have lower maintenance requirements (Ball & Thompson 1995; Francois *et al.* 2002; Knott *et al.* 2004; Lee *et al.* 1992) and leaner lambs are more valuable (Fischer *et al.* 2006), so selection for sexual dimorphism in fat levels is also desirable. Fortunately, correlated selection for fatter ewes and leaner lambs is likely to occur as a consequence of selecting for lighter ewes and heavier rams due to the negative genetic correlation between fat and live weight shown in Chapter 4. Wool production is another sector of the sheep industry that could benefit from selection on sexual dimorphism. It may be possible to breed specialist wool producing Merino wethers from ewes with a higher emphasis on reproductive traits, which in turn has a negative genetic correlation with fleece

weight (Safari *et al.* 2007). Conversely, selecting against sexual dimorphism in wool traits could be desirable given that the majority of the wool is produced by ewes or wethers, yet most wool measurements are recorded in rams, therefore reducing the intersex variation is important. Selection against sexual dimorphism in some traits and productions systems may be desirable as a method of reducing product diversity which can aid the efficiency with which the product is processed.

7.4 Future Directions

While this study established that it is possible to select for sexual dimorphism in sheep and that such a breeding objective would benefit a self-replacing lamb production system, there remains some unanswered questions. The incorporation of sexual dimorphism into the objectives of a breeding would validate this research and answer whether any undesirable correlations with other traits exist (e.g. between smaller ewes and birthing difficulties or fertility; Merat 1984; Roux & Scholtz 1992). Breeding programs that have selected for (and against) sexual dimorphism in other species (e.g. Eisen & Hanrahan 1972 and Hanrahan & Eisen 1973 in mice) do offer some insight into whether these correlations exist, as do the existing mixed-sex correlations between the relevant traits (particularly as both birth difficulty and fertility are already sex linked traits).

A breeding program selecting for sexual dimorphism in growth could also be used as a model to help explain how sexual dimorphism has evolved in the wild. Sexual dimorphism has received considerable attention from evolutionary biologists because it is the defining trait of sexual selection (as defined by Darwin 1875). However, studies of sexual dimorphism in the wild have been limited by the difficulty in recording sufficient animals for pedigree and traits (Michelena *et al.* 2006) and the complication of different environments utilised by each sex in some species (intersex niche divergence as suggested by Darwin 1875). Parentage and trait values recorded under similar environmental conditions for each sex are easier to obtain in domestic sheep, they posses good sexual dimorphism in easy to measure traits (e.g. weight, horn size) and they are closely related to Bighorn sheep (*Ovis Canadensis*) whose sexual dimorphism has been extensively studied (e.g. LeBlanc *et al.* 2001; Poissant *et al.* 2008).

7.5 Conclusions

This thesis proposed a mechanism by which sexual dimorphism could increase the feed efficiency and profitability of a self-replacing lamb production system, it showed that it was possible to breed for sexual dimorphism and quantified the improvement in feed efficiency and profitability possible by increasing sexual dimorphism in self-replacing lamb production systems. It also discussed what factors potentially influence the benefits of sexual dimorphism, other potential applications in livestock breeding, possible future research directions on this topic and the technical and practical considerations that must be considered if sexual dimorphism is to be used as a trait in breeding programs.

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Appendix 1: Estimates of sexual dimorphism in sheep from published literature.

Table A1.1: Estimates of sexual dimorphism derived from ewe and ram weights published from the same flock.

Breed(s)	trait	age	male	female	male/female	sig	Reference	Comments
Merino	weaning weight		62.9 kg	52.2 kg	1.21	-	Pattie 1965	SE* not reported
Merino	weight	180 days	60.3 kg	54.7 kg	1.10	-	Young *et al.* 1965	SE not reported
Romney, Southdown and crosses	weight	birth	4.5 kg	4.1 kg	1.1	y	Fourie *et al.* 1970	Fat, muscle and bone present in carcass also compared
		7 days	6.8 kg	6.0 kg	1.13	y		
		42 days	15.8 kg	13.5 kg	1.17	y		
		77 days	22.3 kg	19.2 kg	1.16	y		
		112 days	27.9 kg	24 kg	1.16	y		
		175 days	31.4 kg	26.7 kg	1.18	y		
		287 days	35.8 kg	32.1 kg	1.12	y		
		560 days	58.2 kg	48.5 kg	1.2	y		
		Maturity	61.7 kg	49.8 kg	1.24	y		
	dressing percentage	birth	46.6%	46.8%	1.00	n		
		7 days	50.8%	51.1%	0.99	n		
		42 days	53.9%	54.3%	0.99	n		
		77 days	54.1%	54.6%	0.99	n		
		112 days	52.4%	52.5%	1.00	n		
		175 days	50.6%	52.3%	0.97	n		
		287 days	51.2%	54.9%	0.93	y		
		560 days	56.1%	57.3%	0.98	n		
		Maturity	54.9%	56.1%	0.98	n		
Romney	weaning weight	81 days	21.4 kg	19.6 kg	1.09	-	Baker *et al.* 1979	SE not reported
	February weight	5m	32.7 kg	29.4 kg	1.11	-		
	April weight	7m	38.7 kg	33.6 kg	1.15	-		
	July weight	10m	41.8 kg	43.037.3	1.12	-		
	October weight	13m	45.9 kg	37.9 kg	1.21	-		
	January weight	16m	57.9 kg	49.0 kg	1.18	-		

Breed(s)	trait	age	male	female	male/female	sig	Reference	Comments
Crosses of:	pre wean growth		203 g/d	193 g/d	1.05	y	Cotterill & Roberts 1979	weaning age
Poll Dorset,	post wean growth		130 g/d	125 g/d	1.04	n		not recorded.
Suffolk, Lincoln,	dressing percentage		47.2 %	47.4 %	0.99	n		All carcass
Dorset Horn,	carcass length		58.0 cm	58.5 cm	0.99	y		measurements
Merino, Dormer	eye muscle length		56.4 mm	55.7 mm	1.01	n		@35kg fasted
& Border Leicester	eye muscle depth		27.5 mm	27.4 mm	1.00	n		live weight
	rib fat depth		4.0 mm	4.0 mm	1.00	n		
Merino	weight	adult	-	-	1.43	-	Thompson *et al.* 1985	Weight +ve line
			-	-	1.35	-		Random
			-	-	1.54	-	SE not reported	Weight –ve line
Various	slaughter weight		-	-	1.31	-	Thonney *et al.* 1987	
	days to slaughter		-	-	1.10	-		SE not reported
	wool weight		-	-	1.26	-		
Dorset x (Merino	growth	0-45 days	200 g/d	172 g/d	1.16	-	Lee *et al.* 1990	
x Border Leicester)		45-110 days	188 g/d	143 g/d	1.32	-		SE not reported
		110-145 days	298 g/d	252 g/d	1.18	-		
Romney	weight	45 days	24.8 kg	23.3 kg	1.06	-	Bisset *et al.* 1994	SE not reported
		70 days	44.3 kg	34.8 kg	1.27	-		for rams. Part of a
		360 days	49.4 kg	37.6 kg	1.31	-		Parasite trial.
Hampshire x Suffolk	weaning weight		20.8 kg	19.5 kg	1.07	-	Mousa *et al.* 1999	
Suffolk cross	weight	60 days	18.3 kg	17.7kg	1.03	n	Stanford *et al.* 2001	data not corrected
		75 days	23.1 kg	21.8 kg	1.06	n		for fixed effects
		90 days	27.3 kg	25.3 kg	1.08	n		but all lambs
		105 days	29.4 kg	26.2 kg	1.12	y		raised as twins by
		120 days	38.2 kg	34.0 kg	1.12	y		ewes between 2
		135 days	43.1 kg	37.5 kg	1.15	y		and 5 years old.
	eye muscle area	60 days	5.79 cm^2	5.75 cm^2	1.01	n		
		75 days	6.27 cm^2	6.28 cm^2	1.00	n		
		90 days	7.15 cm^2	7.42 cm^2	0.96	n		
		105 days	8.94 cm^2	8.48 cm^2	1.05	n		
		120 days	9.56 cm^2	9.39 cm^2	1.02	n		
		135 days	10.31cm^2	10.82 cm^2	0.95	n		

Breed(s)	trait	age	male	female	male/female	sig	Reference	Comments
Suffolk cross	eye muscle width	60 days	41.7 mm	41.5 mm	1.01	n	Stanford *et al.* 2001	continued
		75 days	42.6 mm	41.2 mm	1.03	n		
		90 days	45.9 mm	46.3 mm	0.99	n		
		105 days	51.9 mm	50.5 mm	1.03	n		
		120 days	50.8 mm	47.8 mm	1.06	n		
		135 days	53.9 mm	56.6 mm	0.95	n		
	eye muscle depth	60 days	18.2 mm	18.1 mm	1.01	n		
		75 days	19.9 mm	19.4 mm	1.03	n		
		90 days	19.7 mm	20.9 mm	0.94	n		
		105 days	25.0 mm	22.9 mm	1.09	n		
		120 days	24.2 mm	23.9 mm	1.01	n		
		135 days	24.9 mm	25.6 mm	0.97	n		
	fat depth	60 days	1.77 mm	1.72 mm	1.03	n		
		75 days	1.87 mm	1.88 mm	1.00	n		
		90 days	2.74 mm	2.96 mm	0.93	n		
		105 days	3.12 mm	3.04 mm	1.03	n		
		120 days	3.18 mm	3.42 mm	0.93	n		
		135 days	4.50 mm	3.80 mm	1.18	n		
Suffolk	weight	150 days	64.9 kg	54.5 kg	1.19	y	Lewis *et al.* 2002	
		adult	109.8 kg	86.3 kg	1.27	y		
White Breeds	weight	120 days	37.0 kg	33.5 kg	1.10	n	Näsholm 2004	
Gotland Breeds		120 days	37.4 kg	33.4 kg	1.12	n		
Texel Cross	dressing percentage	160/216 days	40 %	42 %	1.05	y	Johnson *et al.* 2005	Average of two
	fat depth		2.1 mm	3.0 mm	0.70	y		slaughter groups
	eye muscle area		11.8 cm^2	12.2 cm^2	0.97	y		hence two ages
	eye muscle width		58.1 mm	55.2 mm	1.05	y		
	eye muscle depth		26.7 mm	27.2 mm	0.98	y		

* SE = Standard Error

Appendix 2: The pedigree structure of each trait pair analysed in Chapter 4.

Table A2.1a: The number of individuals (with records), sires and dams – Coopworth

		Individuals			Sires			Dams		
Age/Sex a	Age/Sex b	Total	In Both		Total	In Both		Total	In Both	
Wean ♂	Post wean ♂	18111	3569	20%	605	335	55%	10396	2866	28%
Wean ♂	Yearling ♂	18655	8575	46%	612	424	69%	10517	5672	54%
Wean ♂	Hogget ♂	17363	341	2%	598	77	13%	10037	315	3%
Post wean ♂	Yearling ♂	11675	2693	23%	520	270	52%	7132	2317	32%
Post wean ♂	Hogget ♂	4747	95	2%	395	34	9%	3508	104	3%
Yearling ♂	Hogget ♂	10175	217	2%	466	59	13%	6332	207	3%
Wean ♀	Post wean ♀	19555	3234	17%	616	257	42%	11120	2617	24%
Wean ♀	Yearling ♀	20014	8378	42%	619	400	65%	11208	5532	49%
Wean ♀	Hogget ♀	19354	4722	24%	613	250	41%	10986	3470	32%
Post wean ♀	Yearling ♀	11311	2432	22%	485	199	41%	6923	2056	30%
Post wean ♀	Hogget ♀	8338	1089	13%	399	129	32%	5648	1047	19%
Yearling ♀	Hogget ♀	13021	2009	15%	465	209	45%	7731	1967	25%
Wean ♂	Wean ♀	35990	n/a		612	573	92%	14464	6286	43%
Wean ♂	Post wean ♀	21341	n/a		604	258	43%	11316	1673	15%
Wean ♂	Yearling ♀	26944	n/a		627	381	61%	12384	3608	29%
Wean ♂	Hogget ♀	22628	n/a		610	242	40%	11431	2277	20%
Post wean ♂	Post wean ♀	8479	n/a		360	248	67%	5028	1221	24%
Post wean ♂	Yearling ♀	14082	n/a		517	245	47%	7730	1522	20%
Post wean ♂	Hogget ♀	9766	n/a		446	160	36%	6234	734	12%
Yearling ♂	Yearling ♀	19632	n/a		481	366	74%	9338	2841	30%
Yearling ♂	Hogget ♀	15316	n/a		478	224	47%	8148	1747	21%
Hogget ♂	Hogget ♀	5790	n/a		281	50	17%	3997	60	2%
Wean ♀	Post wean ♂	23128	n/a		628	323	51%	11947	2063	17%
Wean ♀	Yearling ♂	28678	n/a		630	417	66%	12772	4165	33%
Wean ♀	Hogget ♂	19152	n/a		612	74	12%	10887	213	2%
Post wean ♀	Yearling ♂	14029	n/a		517	195	38%	7993	1183	15%
Post wean ♀	Hogget ♂	4503	n/a		323	28	9%	3282	57	2%
Yearling ♀	Hogget ♂	10106	n/a		445	52	12%	6222	120	2%
Wean (both)	Post wean (both)	37666	6803	18%	636	356	56%	14935	4557	31%
Wean (both)	Yearling (both)	38669	16953	44%	639	477	75%	15025	8777	58%
Wean (both)	Hogget (both)	36717	5063	14%	632	283	45%	14649	3813	26%
Post wean (both)	Yearling (both)	22986	5125	22%	565	295	52%	10599	3767	36%
Post wean (both)	Hogget (both)	13085	1184	9%	479	180	38%	7621	1405	18%
Yearling (both)	Hogget (both)	23196	2226	10%	527	256	49%	10388	2948	28%

Table A2.1b: The number of individuals (with records), sires and dams – Poll Dorset

		Individuals			Sires			Dams		
Age/Sex a	Age/Sex b	Total	In Both		Total	In Both		Total	In Both	
Wean ♂	Post wean ♂	75683	32598	43%	2870	1871	65%	45460	23541	52%
Wean ♂	Yearling ♂	78287	18048	23%	3130	1468	47%	48854	14986	31%
Wean ♂	Hogget ♂	65122	6175	9%	2766	702	25%	41462	5915	14%
Wean ♂	Adult ♂	52231	21	0%	2335	32	1%	33344	86	0%
Post wean ♂	Yearling ♂	79579	21125	27%	3074	1637	53%	49118	17407	35%
Post wean ♂	Hogget ♂	71961	3705	5%	2975	606	20%	45765	4297	9%
Post wean ♂	Adult ♂	56614	7	0%	2451	29	1%	36062	53	0%
Yearling ♂	Hogget ♂	56846	6874	12%	2499	939	38%	37206	7695	21%
Yearling ♂	Adult ♂	44606	69	0%	2298	39	2%	30857	97	0%
Hogget ♂	Adult ♂	19465	172	1%	1167	40	3%	14306	185	1%
Wean ♀	Post wean ♀	63175	23975	38%	2544	1570	62%	37931	17411	46%
Wean ♀	Yearling ♀	66843	11735	18%	2810	1235	44%	41447	10793	26%
Wean ♀	Hogget ♀	54105	4472	8%	2454	553	23%	34194	4193	12%
Wean ♀	Adult ♀	48982	973	2%	2217	148	7%	30776	875	3%
Post wean ♀	Yearling ♀	56629	12273	22%	2572	1201	47%	36072	10734	30%
Post wean ♀	Hogget ♀	46945	1956	4%	2339	396	17%	30747	2206	7%
Post wean ♀	Adult ♀	39379	900	2%	1959	134	7%	25461	756	3%
Yearling ♀	Hogget ♀	36989	3340	9%	2061	605	29%	26008	3843	15%
Yearling ♀	Adult ♀	31368	339	1%	1914	110	6%	22647	468	2%
Hogget ♀	Adult ♀	10896	810	7%	865	121	14%	8561	701	8%
Wean ♂	Wean ♀	109222	n/a		2392	2103	87%	46030	17516	38%
Wean ♂	Post wean ♀	90693	n/a		2670	1565	59%	45890	12222	27%
Wean ♂	Yearling ♀	82121	n/a		2915	1251	43%	47111	7899	17%
Wean ♂	Hogget ♀	62120	n/a		2557	571	22%	38068	3089	8%
Wean ♂	Adult ♀	53498	n/a		2343	143	6%	33785	636	2%
Post wean ♂	Post wean ♀	106655	n/a		2520	1828	73%	46679	14119	30%
Post wean ♂	Yearling ♀	86490	n/a		2944	1335	45%	48967	8728	18%
Post wean ♂	Hogget ♀	66489	n/a		2748	493	18%	41444	2398	6%
Post wean ♂	Adult ♀	57867	n/a		2460	139	6%	36484	622	2%
Yearling ♂	Yearling ♀	87837	n/a		2468	1652	67%	42192	10342	25%
Yearling ♂	Hogget ♀	54543	n/a		2459	639	26%	35588	3093	9%
Yearling ♂	Adult ♀	45921	n/a		2333	123	5%	31391	554	2%
Hogget ♂	Hogget ♀	39136	n/a		1287	667	51%	19285	2933	15%
Hogget ♂	Adult ♀	20883	n/a		1222	104	9%	15023	459	3%
Adult ♂	Adult ♀	2904	n/a		186	38	20%	1479	55	4%
Wean ♀	Post wean ♂	104738	n/a		2848	1772	62%	51157	15074	29%
Wean ♀	Yearling ♂	92792	n/a		3111	1366	44%	51585	9485	18%
Wean ♀	Hogget ♂	67754	n/a		2698	649	24%	40926	3681	9%
Wean ♀	Adult ♂	48709	n/a		2215	31	1%	30602	58	0%
Post wean ♀	Yearling ♂	83116	n/a		2945	1260	43%	47312	8324	18%
Post wean ♀	Hogget ♂	58078	n/a		2599	476	18%	36697	2476	7%
Post wean ♀	Adult ♂	39033	n/a		1948	26	1%	25173	53	0%
Yearling ♀	Hogget ♂	49506	n/a		2282	724	32%	32256	3815	12%
Yearling ♀	Adult ♂	30461	n/a		1870	35	2%	22059	65	0%
Hogget ♀	Adult ♂	10460	n/a		832	35	4%	8192	79	1%
Wean (both)	Post wean (both)	138858	56573	41%	2964	1961	66%	59966	32742	55%
Wean (both)	Yearling (both)	145130	29783	21%	3285	1604	49%	65903	22319	34%
Wean (both)	Hogget (both)	119227	10647	9%	2885	821	28%	55881	9434	17%
Wean (both)	Adult (both)	101213	994	1%	2437	155	6%	46497	1013	2%
Post wean (both)	Yearling (both)	136208	33398	25%	3217	1787	56%	64046	24824	39%
Post wean (both)	Hogget (both)	118906	5661	5%	3091	730	24%	58969	6994	12%
Post wean (both)	Adult	95993	907	1%	2557	150	6%	47231	927	2%
Yearling (both)	Hogget (both)	93835	10214	11%	2707	1078	40%	49898	11579	23%
Yearling (both)	Adult (both)	75974	408	1%	2523	148	6%	42811	861	2%
Hogget (both)	Adult (both)	30361	982	3%	1341	147	11%	19780	985	5%

Table A2.1c: The number of individuals (with records), sires and dams – White Suffolk

		Individuals			Sires			Dams		
Age/Sex a	**Age/Sex b**	**Total**	**In Both**		**Total**	**In Both**		**Total**	**In Both**	
Wean ♂	Post wean ♂	65684	32715	50%	2800	2063	74%	39010	23109	59%
Wean ♂	Yearling ♂	61722	14135	23%	2757	1328	48%	37479	12222	33%
Wean ♂	Hogget ♂	54769	3445	6%	2521	461	18%	33661	3528	10%
Wean ♂	Adult ♂	51012	71	0%	2385	27	1%	31478	89	0%
Post wean ♂	Yearling ♂	58551	13855	24%	2782	1410	51%	36567	12345	34%
Post wean ♂	Hogget ♂	52385	2378	5%	2615	474	18%	33489	2911	9%
Post wean ♂	Adult ♂	47591	71	0%	2490	29	1%	30698	80	0%
Yearling ♂	Hogget ♂	29371	2850	10%	1780	531	30%	20695	3287	16%
Yearling ♂	Adult ♂	25069	21	0%	1718	23	1%	18314	46	0%
Hogget ♂	Adult ♂	7381	66	1%	615	23	4%	5768	80	1%
Wean ♀	Post wean ♀	62497	27454	44%	2657	1813	68%	37009	19717	53%
Wean ♀	Yearling ♀	59486	10952	18%	2645	1109	42%	35989	9963	28%
Wean ♀	Hogget ♀	52902	2430	5%	2439	367	15%	32536	2286	7%
Wean ♀	Adult ♀	51660	323	1%	2366	56	2%	31704	307	1%
Post wean ♀	Yearling ♀	49197	8376	17%	2453	1041	42%	31471	8047	26%
Post wean ♀	Hogget ♀	41517	950	2%	2239	307	14%	27013	1375	5%
Post wean ♀	Adult ♀	38840	278	1%	2108	54	3%	25283	294	1%
Yearling ♀	Hogget ♀	21500	1454	7%	1465	365	25%	15850	1764	11%
Yearling ♀	Adult ♀	19401	204	1%	1403	43	3%	14577	226	2%
Hogget ♀	Adult ♀	4316	183	4%	462	36	8%	3481	192	6%
Wean ♂	Wean ♀	112300	n/a		2486	2245	90%	44599	18450	41%
Wean ♂	Post wean ♀	89468	n/a		2690	1793	67%	43522	13078	30%
Wean ♂	Yearling ♀	69955	n/a		2657	1110	42%	38965	6861	18%
Wean ♂	Hogget ♀	54849	n/a		2446	373	15%	33022	1674	5%
Wean ♂	Adult ♀	51500	n/a		2378	57	2%	31631	254	1%
Post wean ♂	Post wean ♀	93244	n/a		2576	2002	77%	42093	13744	33%
Post wean ♂	Yearling ♀	66504	n/a		2705	1169	43%	38641	6396	17%
Post wean ♂	Hogget ♀	51398	n/a		2556	370	14%	32530	1377	4%
Post wean ♂	Adult ♀	48049	n/a		2485	57	2%	30828	268	1%
Yearling ♂	Yearling ♀	56397	n/a		1857	1231	66%	26963	5832	22%
Yearling ♂	Hogget ♀	28856	n/a		1768	380	21%	20237	1252	6%
Yearling ♂	Adult ♀	25507	n/a		1730	34	2%	18521	157	1%
Hogget ♂	Hogget ♀	13494	n/a		709	325	45%	8105	872	11%
Hogget ♂	Adult ♀	7864	n/a		633	28	4%	6093	73	1%
Adult ♂	Adult ♀	846	n/a		71	10	12%	521	11	2%
Wean ♀	Post wean ♂	98882	n/a		2846	2004	70%	46946	15299	33%
Wean ♀	Yearling ♂	76340	n/a		2785	1287	46%	41479	8348	20%
Wean ♀	Hogget ♂	58697	n/a		2515	454	18%	34776	2539	7%
Wean ♀	Adult ♂	51566	n/a		2373	26	1%	31620	73	0%
Post wean ♀	Yearling ♂	63475	n/a		2664	1148	43%	37185	6208	17%
Post wean ♀	Hogget ♂	45832	n/a		2352	357	15%	29366	1515	5%
Post wean ♀	Adult ♂	38701	n/a		2113	26	1%	25215	44	0%
Yearling ♀	Hogget ♂	26319	n/a		1590	403	25%	18766	1341	7%
Yearling ♀	Adult ♂	19188	n/a		1402	21	1%	14442	43	0%
Hogget ♀	Adult ♂	4082	n/a		457	18	4%	3322	33	1%
Wean (both)	Post wean (both)	128181	60169	47%	2910	2176	75%	53457	33194	62%
Wean (both)	Yearling (both)	121208	25087	21%	2897	1466	51%	52064	19307	37%
Wean (both)	Hogget (both)	107671	5875	5%	2643	575	22%	47062	5627	12%
Wean (both)	Adult (both)	102672	394	0%	2505	74	3%	44689	428	1%
Post wean (both)	Yearling (both)	107748	22231	21%	2908	1545	53%	50301	18553	37%
Post wean (both)	Hogget (both)	93902	3328	4%	2731	577	21%	45548	4624	10%
Post wean (both)	Adult	86431	349	0%	2593	76	3%	42163	437	1%
Yearling (both)	Hogget (both)	50871	4304	8%	1948	637	33%	29591	5301	18%
Yearling (both)	Adult (both)	44470	225	1%	1886	60	3%	26949	371	1%
Hogget (both)	Adult (both)	11697	249	2%	745	56	8%	8334	304	4%