

**Breeding strategies to make sheep farms
resilient to uncertainty**

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Breeding strategies to make sheep farms resilient to uncertainty

Ian James Rose

Thesis

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Abstract

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The sheep industry in Western Australian has had many challenges over the last 20 years which have caused sheep numbers to decline. This decline is because sheep farms are not resilient to uncertain pasture growth and commodity prices. One way to improve resilience and profitability of farming systems is through breeding of sheep. Therefore, this thesis had two aims; 1. Quantify the potential to select and breed sheep that are more resilient and 2. Quantify how sheep breeding can make farming systems more resilient. To determine if sheep can be bred to be resilient to varying pasture growth I investigated if live weight change is a heritable trait. I investigated live weight change in adult Merino ewes managed in a Mediterranean climate in Katanning in Western Australia. Live weight change traits were during mating and lactation. The heritability of live weight change was low to moderate. Therefore that live weight change could be a potential indicator trait for resilience to uncertain pasture growth. To include live weight change in a breeding goal, correlations with other traits are needed. I calculated the genetic correlations between live weight change during mating, pregnancy and lactation, and reproduction traits. Most genetic correlations were not significant, but genetically gaining live weight during mating in two-year old ewes and during pregnancy for three-year-old ewes improved reproduction. Therefore, optimised selection strategies can select for live weight change and reproduction simultaneously. To investigate optimal breeding programs to make sheep farms resilient to uncertain pasture growth and prices, I modelled a sheep farm in a Mediterranean environment. The economic value of seven traits in the breeding objective were estimated. Including variation in pasture growth and commodity prices decreased average profit and increased the economic value of all breeding goal traits compared to the average scenario. Economic values increased most for traits that had increases in profit with the smallest impact on energy requirements. I also compared optimal breeding programs for across 11 years for 10 regions in Western Australia with different levels of reliability of pasture growth. I identified two potential breeding goals, one for regions with low or high pasture growth reliability and one for regions with medium reliability of pasture growth. Regions with low or high reliability of pasture growth had similar breeding goals because the relationship between economic values and reliability of pasture growth were not linear for some traits. Therefore, farmers can customise breeding goals depending on the reliability of pasture growth on their farm.

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1

General Introduction

1.1 Introduction to the Western Australian sheep industry

The bulk of Western Australia's sheep are managed in the Warm-summer and Hot-Summer Mediterranean climatic zones (Squires, 2006). These zones are characterised by warm/hot dry summers and cool/mild wet winters. This combination of temperature and rainfall means that there is a period of no pasture growth during summer and autumn, with pasture growing mostly in late winter and spring. This distribution of pasture growth has implications for ewe management with most farmers lambing in June and July to match peak energy requirements during late pregnancy and lactation with peak pasture supply (Curtis, 2008). Most farmers manage self-replacing Merino flocks and 76% of ewes are mated to Merino rams and 24% are mated to terminal meat rams (Curtis, 2008). This mix in ram use enables farmers to produce enough Merino lambs to replace old ewes whilst improving meat income by selling faster growing lambs produced by cross breeding. This means that breeding programs for Merino ewes focus on wool production, whilst there are generally two lines of sires, one for wool and one for meat. In this thesis I focus on Merino breeders who are selecting sheep predominantly for wool production, selling wethers (male castrates) for meat between one and two years old. I focus on this segment of the market because it represents the bulk of sheep production in Western Australia.

The Western Australian sheep industry has had many challenges over the last 20 years. Sheep numbers in Western Australia have declined (Figure 1.1) as farmers reduce their sheep flock by selling more lambs for meat (Figure 1.2) and changing their preference to other enterprise types. This reduction in sheep numbers has occurred nationwide and is the main cause of the farm value of wool in Australian decreasing from AU\$4.7 billion to \$AU1.8 billion per year between 1992 and 2010 (Rowe, 2010). In comparison, a shift towards meat production and higher meat prices increased the farm value of meat from around \$AU0.5 billion per year to \$AU1.75 billion per year (Rowe, 2010). The decline in sheep numbers and wool production is due to a combination of social, economic and environmental factors. The biggest cause of the shift away from sheep production is the increase in the relative profitability of cropping. Most farms in the Mediterranean climate zones have mixed crop and sheep (Kingwell and Pannell, 2005). This mixed farming system is preferred because regions with a Mediterranean climate of mild wet winters and dry hot summers support dryland cropping that is complemented by sheep which graze the crop residues over summer and autumn and aid in weed

control (Ewing *et al.*, 1992). The decrease in sheep numbers over the last 20 years coincided with an increase in area sown to cereals by over 50 percent between 1990 and 2005.

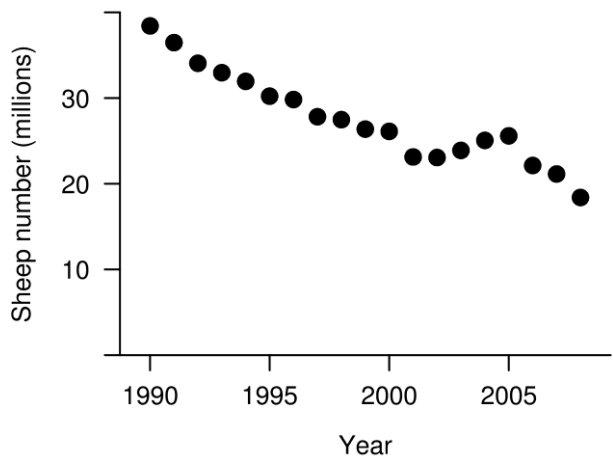


Figure 1.1 Number of sheep and in Western Australia between 1990 and 2008. (Australian Bureau of Statistics).

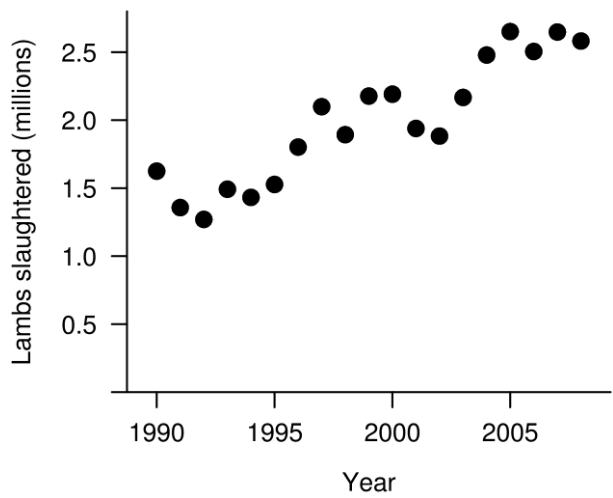


Figure 1.2 Number of lambs slaughtered in Western Australia between 1990 and 2008. (Australian Bureau of Statistics).

Cropping has become more profitable because it has had higher rates of productivity gain (Zhao *et al.*, 2008; Nossal and Sheng, 2010). These productivity gains are from more crop options such as lupins and canola, and improved varieties such as wheat varieties with different flowering times that suit more environments (Beare *et al.*, 1999; Zhao *et al.*, 2008). Additionally, cropping has become easier with the introduction of new herbicides (Gill and Holmes, 1997) large machinery that provides economies of scale benefits (Liao and Martin, 2009) and new machinery technology such as direct drill sowing (Kokic *et al.*, 2006) and GPS-based controlled traffic systems (Fuschbichler and Kingwell, 2010). Alternatively, sheep technology has remained relatively stagnant, and although the introduction of live sheep export created a new market option for farmers, the benefits of cropping often have outweighed those of sheep.

In addition to improved crop technologies, the number of farms is decreasing (Figure 1.3) while the average size of farms is increasing. This increase in farm size has meant higher debt levels for farmers particularly due to the high interest rates during the 1980s and 1990s (Australian Bureau of Agriculture and Resource Economics, 2001). This increase in debt has caused farmers to turn to cropping to increase farm income. Additionally, management of larger farms has become more complex due to increased availability of technology, crop choice, rotation options, marketing and information services (Kingwell, 2011). Therefore, farmers have become more selective in how they allocate their time and investments.

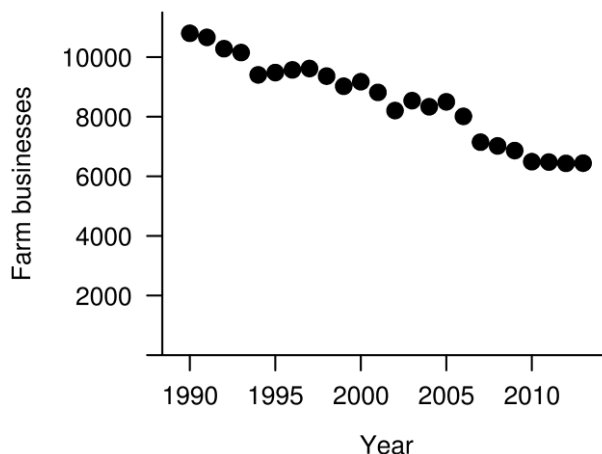


Figure 1.3 Number of farm businesses in Western Australia between 1990 and 2013. (ABARE farm survey data available on AgSurf.)

Farm benchmarking suggests that the labour requirement for sheep is high compared to cropping (Holmes and Sackett, 2009). Additionally, many farms in Western Australia experience problems in attracting and retaining farm labour (Rabobank, 2007). Therefore, when farm management labour is scarce, sheep management can place high demands on that labour. Moreover, because of the dominance of cropping in Western Australia over recent decades, many young farmers who have specialised in cropping, have limited experience, knowledge and skills for managing sheep (Dymond, 2006). This means that some farmers, because of time pressures or limited knowledge, are managing low maintenance sheep systems.

These time pressures as well as fluctuation in pasture growth between years have caused most farmers to manage set stocking systems with low stocking rates set for poor seasons to increase resilience to uncertain pasture supply (Doyle *et al.*, 1993). This type of management means that pasture utilisation in most years is low and pasture is lost through decay from spring to autumn (Doyle *et al.*, 1996). Given the strong relationship between stocking rate and profit (White and Morley, 1977; White *et al.*, 1980; Young *et al.*, 2010), there is potential on many farms to increase stocking rates and make more money from sheep. Additionally, there is an optimal stocking rate which if exceeded farm profits decrease (White and Morley, 1977; White *et al.*, 1980) and soil health is compromised (Moore *et al.*, 2009). This optimal stocking also varies depending on the season, particularly when available pasture fluctuates (White and Morley, 1977; White *et al.*, 1980). Farming systems in Western Australia are characterised by fluctuating levels of pasture biomass (Rossiter, 1966). Additionally, combine harvesters are becoming more efficient and leaving less grain behind making crop stubbles an unreliable feed resource (Landau *et al.*, 2000). Therefore, increasing stocking rate reduces the resilience of farming systems to low pasture growth in poor seasons causing farmers to adopt conservative stocking rates.

This shift away from sheep towards crop has created many challenges for farmers including poor soil health, herbicide resistant weeds in crops and salinity. Although continuous cropping is profitable in the short term, long periods of cropping have negative impacts on soil health and soil nitrogen reserves (Reeves and Ewing, 1993). Additionally, crop dominant farming increases herbicide resistance which develops when overuse of herbicides causes intense selection pressure on weeds (Doole and Pannell, 2008). Livestock are the best long term solution to herbicide resistance when used to control weeds in combination with herbicides (Monjardino *et al.*, 2004). Furthermore, much of southern Australia has experienced dryland salinity because native vegetation has been replaced with annual crops and

pastures for agriculture (Hatton and Nulsen, 1999). Annual crops have shorter root systems which use less water than native vegetation causing the water table to rise (Asseng *et al.*, 2001). This rising of water tables brings salt deposits to the surface of soil profiles making the land saline and unsuitable for annual crops and pastures. In the cropping regions of Australia salinity was predicted to cost AU\$238 million in foregone profits (Kingwell, 2003). The best solution to prevent salinity is replacing annual crops and pastures with perennial pastures to be grazed by livestock (Cocks, 2003). Saltland pastures are also an option for slightly saline areas that are no longer suitable for annual crops and pastures. O'Connell *et al.* (2006) found that saltland pastures planted and grazed by sheep on moderately saline environments increased profit and reduced recharge of water. Therefore, livestock systems in Western Australia have been faced with declining livestock numbers but remain an important enterprise.

Finally, Darnhofer *et al.* (2014) state that farming systems need to be diverse to be resilient to environmental and economic changes. Therefore it is important for sheep enterprises to remain profitable for farmers to maintain a good enterprise mix. Additionally, all components of sheep enterprises, for example meat and wool, need to be viable to maintain resilience within the farming system. Therefore, it is important to find solutions to increase the profitability and viability of sheep production systems in Western Australia.

1.2 Aims of thesis

Resilience to variation in pasture growth is important for the farming system as well as sheep managed on the farming system. In addition to being resilient the farming system also has to be profitable across years regardless of variation in the production environment and prices. One way to improve resilience and profitability of farming systems is through breeding of sheep. Breeding sheep to be more profitable requires selecting the sheep that will make the most money in a production system. This selection of sheep can be easily integrated in the management of the flock and the annual genetic changes of sheep flock are cumulative and permanent. This permanent nature of genetic change means that farmers should ensure they are selecting the right sheep to breed for the longer term. Animal breeding aims to select the animals that will perform best in a given production system. Consequences of breeding for resilience can be investigated at the animal level, by selecting sheep that are resilient to variation in pasture growth, or at the farm system level, by selecting sheep that will lead to the most profitability at farm level.

In the last 20 years the Australian sheep industry has made significant genetic gains in production traits through its use of MERINOSELECT, a quantitative genetic evaluation system of Merino rams (Banks *et al.*, 2006). During the 1990s Australian farmers have selected sheep to decrease fibre diameter and increase fleece weight so sheep produce more fine wool (Taylor and Atkins, 1997). However, an increase in meat prices and a decrease in wool price and fibre diameter premium (Figure 1.4 and Figure 1.5) have shifted breeding emphasis more towards lamb production. These breeding goals have focused mostly on improving production in sheep. This production focus has reduced resilience in Merino sheep managed in Western Australia's Mediterranean regions (Adams *et al.*, 2006; Adams *et al.*, 2007).

The Mediterranean regions in Western Australia have large variations in pasture growth between years with the length and severity of drought periods between years hard to predict. There is limited information on how to identify the best type of sheep to breed in these environments when pasture growth and price variability may affect the optimal breeding scheme for farmers in these regions. This erratic feed supply between years is predicted to worsen due to the effects of climate change (IPCC, 2008). Therefore, farmers will become more reliant on grain supplements to fill the feed gap during summer and autumn (Purser, 1981) which impacts on whole farm profit (Kingwell, 2002; Kopke *et al.*, 2008). Therefore farmers should consider improving animal traits that make sheep more robust to periods of low nutrition and will require less supplementary feeding during summer and autumn.

The growth of green feed during winter and spring means that sheep generally have a positive energy balance during this period and a negative energy balance during summer and autumn. This negative energy balance in autumn is exaggerated as Merino ewes in Mediterranean environments are normally pregnant during autumn (Croker *et al.*, 2009). This means ewes generally lose weight during summer and autumn and regain weight during late winter and spring when their energy balance is positive (Adams and Briegel, 1998). Adams and Briegel (1998) recorded average live weight loss of 12 kg for Merino ewes during summer and autumn in Bakers Hill in Western Australia. This high weight loss significantly decreases the maternal performance of ewes and the survival of lambs (Kelly and Ralph, 1988; Kelly, 1992).

Therefore, live weight change may be an appropriate trait to represent sheep that require less supplementary feeding during drought periods. Live weight change in adult ewes could represent the performance of sheep under a fluctuating feed supply, with sheep losing less live weight during drought being more resilient. This approach is similar to the research for body condition score (Berry *et al.*, 2002;

Veerkamp *et al.*, 2001) as an indicator of energy balance in dairy cattle. Additionally, phenotypic correlations reported in other studies (Kelly and Ralph, 1988; Kelly, 1992) suggest that live weight change has important phenotypic correlations with reproduction in sheep. If there are significant genetic correlations between live weight change and reproduction, then this could have implications for optimal breeding strategies.

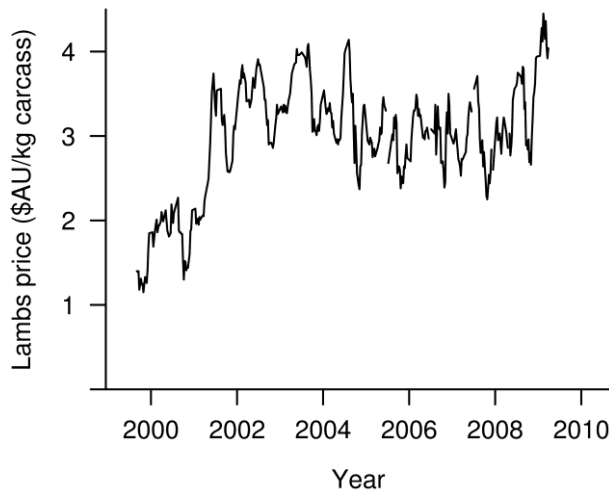


Figure 1.4 Over the hooks lamb price in Australia, for lambs with 20-22 kg carcass weight, fat score 2-4. (Meat and Livestock Australia).

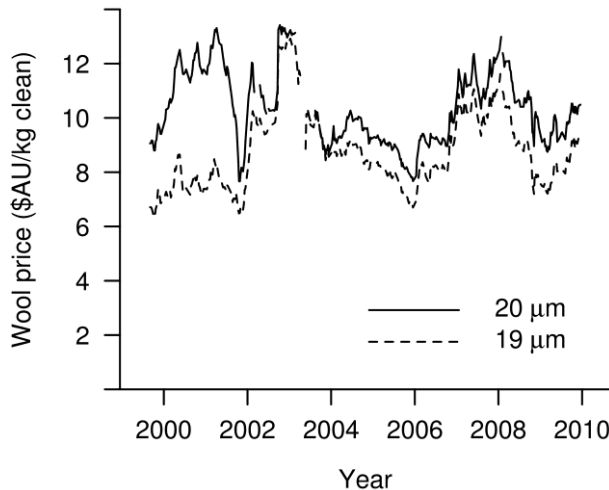


Figure 1.5 Wool price for clean wool with fibre diameter of 19 and 20 µm (Western Region micron price guide). (Wool Desk, Department of Agriculture and Food WA, and Australian Wool Exchange).

The current genetic evaluation system called MERINOSELECT provides selection indices to breeders of Merino sheep in Australia (Brown *et al.*, 2006). This system uses the SHEEPOBJECT software (Swan *et al.*, 2007) which does not consider the impact of variation in pasture growth and prices to estimate the economic values of different traits.

There are many studies on how farms can be managed to improve resilience to uncertain pasture (Olson and Mikesell, 1988; Kingwell *et al.*, 1993; Jacquet and Pluvinage, 1997; Kobayashi *et al.*, 2007) and prices (Lambert, 1989; Barbier and Bergeron, 1999; Lien and Hardaker, 2001; Ridier and Jacquet, 2002; Mosnier *et al.*, 2009; Mosnier *et al.*, 2011). These studies provide insights into how management can be optimised to increase profit under uncertainty but have not been applied to animal breeding. Therefore, these techniques can be applied to a breeding context and will help to bridge the gap in knowledge between economics and breeding.

Furthermore, in Western Australia's sheep growing area there are big differences between regions in the amount and variation of pasture growth within and between years (Rossiter, 1966; Schut *et al.*, 2010). These differences between regions in pasture growth can affect the optimal management of livestock in each system (Chapman *et al.*, 2009). These changes in management may also affect optimal breeding goals because changing each trait changes the energy requirements of sheep by different amounts and at different times of the year. Therefore, it is important to understand if different regions need adapted breeding goals, or if one breeding goal for all regions can be used.

Therefore, this thesis has two aims; 1. How to make sheep more resilient and 2. How to make farming systems more resilient. The first aim involved investigating live weight change as an indicator of resilience to drought periods. The second aim involved investigating how variation in pasture growth and prices affect optimal breeding goals for sheep farms in different regions and using different management. To investigate if live weight change can be included in breeding programs, I first estimated the heritability of live weight change in Chapter 2. In this chapter I tested the hypothesis that live weight loss during mating in summer and live weight gain during lactation in winter/spring are genetically different traits. I also tested the hypothesis that live weight change is a different trait in young ewes compared with mature ewes. I tested these hypotheses using 3 methods: live weight change traits, random regression analysis, and multivariate analysis. These three methods helped identify the suitability of each method when using composite traits such as live weight change. I also estimated the correlations between live weight change during mating and lactation.

In Chapter 3 I tested the hypothesis that increases in ewe live weight during the mating and pregnancy periods would have significant positive genetic correlations with reproduction traits. These correlations were important to estimate because live weight change has important phenotypic correlations with reproduction. I compared correlations estimated with and without correcting live weight for reproductive performance. I did this comparison to identify the best method of estimating correlations between live weight and reproduction which have high genetic and phenotypic correlations.

To identify if sheep breeding can be used to make farming systems more resilient, in Chapter 4 I tested the hypothesis that accounting for the variation in pasture growth and meat, wool and grain prices across years changes the relative economic value of traits in the breeding goal. I also tested whether the change in profit due to variation across years was affected by how much energy requirements change when traits are changed. To test these hypotheses I made a bio-economic model of a sheep farm with high variation in pasture growth and prices across years to calculate economic values of production traits. The model used dynamic recursive analysis to simulate a farmer that has to make decisions in each year in reaction to change in pasture growth and prices. I compared economic values using average pasture growth and prices and using varying pasture growth and prices across 5 years.

In Chapter 5 I tested the hypothesis that economic values and response to selection of sheep breeding goal traits change for different regions depending on how pasture growth is distributed across years. I tested this hypothesis by modifying the model from Chapter 4 to calculate economic values for 11 years, but assuming farmers keep sheep constant across all years. I also included 9 more regions with different reliability of pasture growth defined by the amount and variation across years. I also calculated the response to selection of each breeding program estimated for the 10 regions to compare the direction of change for each trait.

In the general discussion (Chapter 6) I combine the results of Chapters 2 to 5 to bring together breeding sheep for resilience and how breeding can be used to make sheep farms more resilient. Results from the four chapters are discussed and compared to gain insight into the how breeding can help production systems be more profitable and resilient to uncertain pasture growth and prices.

2

Merino ewes can be bred for live weight change to be more tolerant to uncertain feed supply

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¹ In this chapter alterations were made to the printed article, changing English from US to United Kingdom, replacing body weight with live weight and changing the format of headings and tables to make it consistent with the rest of the thesis.

Abstract

Sheep in Australia experience periods with different feed supply causing them to gain and lose live weight (LW) during the year. It is more efficient if ewes lose less LW during periods of poor nutrition and gain more LW during periods of good nutrition. We investigated whether LW loss during periods of poor nutrition and LW gain during periods of good nutrition are genetically different traits. We used LW measurements from 2,336 adult Merino ewes managed over 5 year in a Mediterranean climate in Katanning, Australia. Live weight loss is the difference between 2 LW measured 42 d apart during mating, a period of poor nutrition. Live weight gain is the difference between 2 LW measured 131 d apart during a period of good nutrition between prelambling and weaning. We used 3 methods to estimate variance components of LW change: 1) as a trait calculated by subtracting the first LW from the second, 2) multivariate analysis of LW traits, and 3) random regression analysis of LW. The h^2 and genetic correlations (r_g) estimated using the multivariate analysis of LW and the LW change trait were very similar whereas the random regression analysis estimated lower heritabilities and more extreme negative genetic correlations between LW loss and gain. The multivariate model fitted the data better than random regression based on Akaike and Bayesian information criterion so we considered the results of the multivariate model to be more reliable. The heritability of LW loss ($h^2 = 0.05\text{--}0.16$) was smaller than that of LW gain ($h^2 = 0.14\text{--}0.37$). Live weight loss and gain can be bred for independently at 2 and 4 year of age ($r_g = 0.03$ and -0.04) whereas at 3 year of age ewes that genetically lost more LW gained more LW ($r_g = -0.41$). Live weight loss is genetically not the same trait at different ages (r_g range $0.13\text{--}0.39$). Live weight gain at age 3 year is genetically the same trait at age 4 year ($r_g = 0.99$) but is different between age 2 year and the older ages ($r_g = 0.53$ and 0.51). These results suggest that as the ewes reach their mature LW, LW gain at different ages becomes the same trait. This does not apply to LW loss. We conclude that LW change could be included in breeding programs to breed adult Merino ewes that are more tolerant to variation in feed supply.

Keywords: climate change, heritability, live weight change, sheep

2.1 Introduction

The wool and lamb industry in Australia is mostly in the Mediterranean climate regions of southern Australia, using mostly Merino ewes. The rainfall patterns of these regions are expected to be more variable and less winter dominant (IPCC, 2007) with the length and severity of the annual periods of drought harder to predict. This erratic climate will make managing sheep more difficult as most Merino ewes lose live weight (LW) during summer and autumn and then regain LW during late winter and spring (Adams and Briegel, 1998). Farmers currently overcome some of the deficit in pasture feed by feeding grain, hay, or silage but this has major feed and labor costs (Young *et al.*, 2011b).

A possible solution is to breed sheep that can maintain LW during times of feed shortage and are therefore more resilient to variation in feed supply. Borg *et al.* (2009) and Rauw *et al.* (2010) estimated moderate heritabilities for LW loss and gain in adult ewes grazing in rangelands. However, these studies did not investigate if LW change is genetically different between periods of poor and good nutrition. They also did not compare LW change in younger ewes to older ewes, which could be genetically different traits.

Also, heritability of LW change can be calculated using the variance of each LW measurement and the covariance between them. These variances can be estimated treating each LW measurement as an individual trait in a multivariate analysis or treating LW as a repeated measure over time in a random regression model (Van der Werf *et al.*, 1998).

In this study we tested the hypothesis that LW loss during summer and LW gain during pasture growth are different traits. We also tested the hypothesis that LW change is a different trait in young ewes compared with mature ewes. We tested these hypotheses using 3 methods: LW change traits, random regression analysis, and multivariate analysis.

2.2 Materials and methods

The management of the ewes was approved by the Animal Ethics and Welfare Committee from the Department of Agriculture, Western Australia. More details about how the ewes were managed are in Greeff and Cox (2006)

Animals and their management

We used LW information from 2,336 fully pedigreed adult ewes from the Merino Resource flocks of the Department of Agriculture and Food Western Australia at Katanning (33°41' S, 117°35' E, and elevation 310 m). Katanning is in the

Mediterranean climate region with hot dry summers and mild wet winters. This combination of temperature and rainfall means there is a period when pasture does not grow during summer and autumn. All ewes were managed on 1 farm under conditions typical for commercial farms in that area. The ewes were fed two-thirds lupins and one-third oats. The amount fed varied between years but on average ewes were fed 100 g per animal per day in late December increasing gradually to 800 g per head per day at lambing. Hay was fed *ab libitum* during lambing. Lambing time was in July and ewes were shorn in October when the weight of greasy wool was recorded.

Live weight data

We used LW recorded from years 2000 to 2005. Ewes were weighed 4 times annually at approximately the same time each year (Table 2.1). The 4 LW were pre-mating LW (WT1), post-mating LW (WT2), pre-lamb LW (WT3), and weaning LW (WT4). There were 898 ewes with 1 year set, 715 with 2 year sets, and 723 with 3 year sets of all 4 LW, WT1, WT2, WT3, and WT4. There were 4,497 animal-age combinations of all 4 LW with on average 1.9 years data per ewe of which 1,868 were for 2-year-old ewes in their first parity, 1,501 for 3-year-old ewes, and 1,128 for 4-year-old ewes. The total pedigree file consisted of 29,300 sheep tracing back 10 generations, with 760 sires and 8,540 dams. One sire was mated with an average of 20 ewes with 1 paddock per ram.

Table 2.1 Timing of four live weight (WT) recordings in Katanning Resource Flock from 2000 to 2005.

Year	Traits			
	WT1	WT2	WT3	WT4
2000	10-Jan	23-Feb	30-May	27-Sep
2001	16-Jan	23-Feb	06-May	25-Sep
2002	15-Jan	26-Feb	03-Jun	08-Oct
2003	13-Jan	26-Feb	03-Jun	07-Oct
2004	13-Jan	23-Feb	17-May	07-Oct
2005	11-Jan	25-Feb	18-May	03-Oct
Average	13-Jan	24-Feb	23-May	02-Oct
Average days from start of year	13	55	143	274

2 Adult ewes can be bred for live weight change

We adjusted LW for wool weight, assuming constant wool growth during the year regardless of season and for conceptus weight using the equations from the GRAZPLAN model (Freer *et al.*, 1997). We estimated conceptus weight using actual birth weight of the lambs instead of standard birth weight used by Freer *et al.* (1997). Over the 6 years, 590 ewes gave birth to no lambs, 2,637 gave birth to 1 lamb, and 1,270 ewes gave birth to multiple lambs.

Genetic Analysis

To compare LW change at different times during the year and at different ages, we used 3 different methods to identify the best way to analyse LW change.

Live weight Change Trait Analysis. The first LW was subtracted from the second LW to define a LW change trait such as in Borg *et al.* (2009) and Rauw *et al.* (2010). Then we estimated the variance components of the LW change traits at each age and the genetic correlations between ages (e.g., between young ewes and mature ewes).

Multivariate Analysis of LW. Here we used the LW at each time point as different traits in a multivariate analysis to estimate genetic covariance or variance between each LW point during the year within each age group. Subsequently, these estimates were used to calculate heritabilities and genetic correlations for LW loss and gain using variance and covariance rules.

Random Regression Analysis of LW. Here we used random regression to model changes in variances and covariances of LW within a year using continuous polynomial functions. This allows the genetic variance to be estimated for LW change between any days within a year.

Variance components were estimated using ASReml (Gilmour *et al.*, 2006). Convergence was assumed if the REML log-likelihood changed less than $0.002 \times$ the previous log-likelihood and the variance parameter estimates changed less than 1% over 6 runs. Goodness of fit of the multivariate and random regression analysis of LW was determined using the Akaike's information criterion (AIC; Akaike, 1973) and the Bayesian-Schwarz information criterion (BIC; Schwarz, 1978). It was not possible to compare these analyses that use 4 LW to the LW change trait analysis that uses 2 LW change traits.

Fixed effects

We included fixed effects in all models for all traits for year (2000 to 2005), number of lambs born by each ewe in the year of LW measurement (0 to 2), number of lambs reared in the year of LW measurement (0 to 2), number of lambs born in the year before the LW measurements (0 to 2), and number of lambs weaned in the year before the LW measurements (0 to 2). In the random regression analyses we nested a fixed curve for average LW over time within these fixed effects.

Live weight Change Trait Analysis

To analyse LW loss and gain as 2 separate traits, we defined LW loss (LOSS) as $LOSS = WT2 - WT1$ and LW gain (GAIN) as $GAIN = WT4 - WT3$. This means that if LOSS or GAIN is negative, then the ewe lost LW, and if LOSS or GAIN is positive, then the ewe gained LW. The WT1 and WT2 were on average 42 d apart and recorded during a period of poor nutrition in January and February during mating. Live weights WT3 and WT4 were measured on average 131 d apart during a period of good nutrition period between May and October, during lactation.

We did multivariate analyses for LOSS and GAIN for ages 2, 3, and 4 years. The model used for age-specific LOSS and GAIN was

$$\begin{bmatrix} y_{age2} \\ y_{age3} \\ y_{age4} \end{bmatrix} = \begin{bmatrix} X_{age2} & 0 & 0 \\ 0 & X_{age3} & 0 \\ 0 & 0 & X_{age4} \end{bmatrix} \begin{bmatrix} b_{age2} \\ b_{age3} \\ b_{age4} \end{bmatrix} + \begin{bmatrix} Z_{age2} & 0 & 0 \\ 0 & Z_{age3} & 0 \\ 0 & 0 & Z_{age4} \end{bmatrix} \begin{bmatrix} a_{age2} \\ a_{age3} \\ a_{age4} \end{bmatrix} + \begin{bmatrix} e_{age2} \\ e_{age3} \\ e_{age4} \end{bmatrix}$$

in which y_{age2} , y_{age3} , and y_{age4} are the observations for LOSS or GAIN when ewes are 2, 3, and 4 years old, b_i is the vector of fixed effects, a_i is the vector of additive genetic effects, e_i is the vector of error effects, and X_i and Z_i are the incidence matrices (i = age 2, age 3, and age4 years).

$$\text{var} \begin{bmatrix} e_{age2} \\ e_{age3} \\ e_{age4} \end{bmatrix} = R \otimes I \text{ where } R = \begin{bmatrix} \sigma_{e \text{ age2}}^2 & \text{COV}_{e \text{ age2 age3}} & \text{COV}_{e \text{ age2 age4}} \\ \text{COV}_{e \text{ age3 age2}} & \sigma_{e \text{ age3}}^2 & \text{COV}_{e \text{ age3 age4}} \\ \text{COV}_{e \text{ age4 age2}} & \text{COV}_{e \text{ age4 age3}} & \sigma_{e \text{ age4}}^2 \end{bmatrix} \text{ and}$$

$$\text{var} \begin{bmatrix} a_{age2} \\ a_{age3} \\ a_{age4} \end{bmatrix} = G \otimes A \text{ where } G = \begin{bmatrix} \sigma_{a \text{ age2}}^2 & \text{COV}_{a \text{ age2 age3}} & \text{COV}_{a \text{ age2 age4}} \\ \text{COV}_{a \text{ age3 age2}} & \sigma_{a \text{ age3}}^2 & \text{COV}_{a \text{ age3 age4}} \\ \text{COV}_{a \text{ age4 age2}} & \text{COV}_{a \text{ age4 age3}} & \sigma_{a \text{ age4}}^2 \end{bmatrix},$$

in which I is the identity matrix, A is the additive genetic relationship matrix, and \otimes is the direct matrix product operator.

We used bivariate analyses to estimate genetic correlations between each LOSS and GAIN at each age, similarly as between ages.

Multivariate Analysis of LW

We estimated the covariance or variance components between the 4 LW measurements (WT1, WT2, WT3, and WT4) in each age group using a multivariate analysis:

$$\begin{bmatrix} \mathbf{y}_{WT1} \\ \mathbf{y}_{WT2} \\ \mathbf{y}_{WT3} \\ \mathbf{y}_{WT4} \end{bmatrix} = \begin{bmatrix} \mathbf{X}_{WT1} & 0 & 0 & 0 \\ 0 & \mathbf{X}_{WT2} & 0 & 0 \\ 0 & 0 & \mathbf{X}_{WT3} & 0 \\ 0 & 0 & 0 & \mathbf{X}_{WT4} \end{bmatrix} \begin{bmatrix} \mathbf{b}_{WT1} \\ \mathbf{b}_{WT2} \\ \mathbf{b}_{WT3} \\ \mathbf{b}_{WT4} \end{bmatrix} + \begin{bmatrix} \mathbf{Z}_{WT1} & 0 & 0 & 0 \\ 0 & \mathbf{Z}_{WT2} & 0 & 0 \\ 0 & 0 & \mathbf{Z}_{WT3} & 0 \\ 0 & 0 & 0 & \mathbf{Z}_{WT4} \end{bmatrix} \begin{bmatrix} \mathbf{a}_{WT1} \\ \mathbf{a}_{WT2} \\ \mathbf{a}_{WT3} \\ \mathbf{a}_{WT4} \end{bmatrix} + \begin{bmatrix} \mathbf{e}_{WT1} \\ \mathbf{e}_{WT2} \\ \mathbf{e}_{WT3} \\ \mathbf{e}_{WT4} \end{bmatrix}$$

where \mathbf{y}_{WT1} , \mathbf{y}_{WT2} , \mathbf{y}_{WT3} and \mathbf{y}_{WT4} are the observations for WT1, WT2, WT3 and WT4, \mathbf{b}_i is the vector of fixed effects, \mathbf{a}_i is the vector of additive genetic effects and \mathbf{e}_i is the vector of residuals. \mathbf{X}_i and \mathbf{Z}_i are the incidence matrices ($i = \text{WT1, WT2, WT3 and WT4}$).

$$\text{var} \begin{bmatrix} \mathbf{e}_{WT1} \\ \mathbf{e}_{WT2} \\ \mathbf{e}_{WT3} \\ \mathbf{e}_{WT4} \end{bmatrix} = \mathbf{R} \otimes \mathbf{I}, \mathbf{R} = \begin{bmatrix} \sigma_e^2 \text{WT1} & \text{COV}_e \text{WT1 WT2} & \text{COV}_e \text{WT1 WT3} & \text{COV}_e \text{WT1 WT4} \\ \text{COV}_e \text{WT2 WT1} & \sigma_e^2 \text{WT2} & \text{COV}_e \text{WT2 WT3} & \text{COV}_e \text{WT2 WT4} \\ \text{COV}_e \text{WT3 WT1} & \text{COV}_e \text{WT3 WT2} & \sigma_e^2 \text{WT3} & \text{COV}_e \text{WT3 WT4} \\ \text{COV}_e \text{WT4 WT1} & \text{COV}_e \text{WT4 WT2} & \text{COV}_e \text{WT4 WT3} & \sigma_e^2 \text{WT4} \end{bmatrix} \text{ and}$$

$$\text{var} \begin{bmatrix} \mathbf{a}_{WT1} \\ \mathbf{a}_{WT2} \\ \mathbf{a}_{WT3} \\ \mathbf{a}_{WT4} \end{bmatrix} = \mathbf{G} \otimes \mathbf{A}, \mathbf{G} = \begin{bmatrix} \sigma_a^2 \text{WT1} & \text{COV}_a \text{WT1 WT2} & \text{COV}_a \text{WT1 WT3} & \text{COV}_a \text{WT1 WT4} \\ \text{COV}_a \text{WT2 WT1} & \sigma_a^2 \text{WT2} & \text{COV}_a \text{WT2 WT3} & \text{COV}_a \text{WT2 WT4} \\ \text{COV}_a \text{WT3 WT1} & \text{COV}_a \text{WT3 WT2} & \sigma_a^2 \text{WT3} & \text{COV}_a \text{WT3 WT4} \\ \text{COV}_a \text{WT4 WT1} & \text{COV}_a \text{WT4 WT2} & \text{COV}_a \text{WT4 WT3} & \sigma_a^2 \text{WT4} \end{bmatrix}$$

Where \mathbf{I} is the identity matrix, \mathbf{A} is the relationship matrix.

Calculation of Genetic Parameters Using Multivariate Analysis of LW

We estimated the additive genetic and residual variance for LOSS and GAIN using the variances of the 2, involved LW and the covariance between them. For example, the additive genetic variance for LOSS (WT2 – WT1) was calculated using

$$\sigma_a^2 (\text{WT2-WT1}) = \sigma_a^2 \text{WT2} + \sigma_a^2 \text{WT1} - 2 * \text{cov}_a (\text{WT2, WT1})$$

in which $\sigma_a^2 \text{WT2}$ and $\sigma_a^2 \text{WT1}$ are the additive genetic variances of WT1 and WT2, respectively, and $\text{cov}_a (\text{WT2, WT1})$ is the additive genetic covariance between WT2 and WT1. This means that when the covariance between LW points is positive, variance in LW change exists only when twice the covariance between 2 points is lower than the variance of the 2 points. This means highly correlated points will have less variance for the LW change between them.

We calculated the genetic covariance between LOSS (WT2 – WT1) and GAIN (WT4 – WT3) using

$$\text{cov}_a(\text{WT2-WT1}, \text{WT4-WT3}) =$$

$$\text{cov}_a(\text{WT2}, \text{WT4}) - \text{cov}_a(\text{WT2}, \text{WT3}) - \text{cov}_a(\text{WT1}, \text{WT4}) + \text{cov}_a(\text{WT1}, \text{WT3})$$

in which cov_a is the additive genetic covariance between LW at each measurement time indicated in the parentheses.

Random Regression Analysis of LW

We used random regression to analyse LW change as a continuous function of time across the seasons (Henderson, 1982; Schaeffer, 2004). This random regression analysis was done separately for ages 2, 3, and 4 years.

$$\mathbf{y} = \mathbf{X}\mathbf{b} + \mathbf{\Phi}_a \mathbf{k}_a + \mathbf{\Phi}_p \mathbf{k}_p + \mathbf{e},$$

In which \mathbf{y} is a vector of observations for live weights of individual ewes; \mathbf{X} is the incidence matrix for the vector of the fixed effects \mathbf{b} ; $\mathbf{\Phi}_a$ and $\mathbf{\Phi}_p$ are the matrices with orthogonal polynomial coefficients of $j \times i$ dimensions in which j is the number of polynomial coefficients and i is the number of live weight points standardised to the first and last time points. $\mathbf{\Phi}_a$ and $\mathbf{\Phi}_p$ correspond to the matrices with additive genetic and permanent environmental random regression coefficients \mathbf{k}_a and \mathbf{k}_p , and \mathbf{e} is the random residual. Permanent environmental effects were estimated to account for non-genetic variance between the repeated live weight measurements. We fitted the fixed curve of average LW as a third order polynomial nested within year, number of lambs born by each ewe in the year of LW measurement (0 to 2), number of lambs reared in the year of LW measurement (0 to 2), number of lambs born in the year before the LW measurements (0 to 2), and number of lambs weaned in the year before the LW measurements (0 to 2). The third order was the greatest possible order using 4 data points and was the best fit based on F-tests. We then selected the order of fit for the random effects, additive genetic and permanent environmental, by comparing the 9 possible models for each age from order 1 to 3. The best fit of the 9 different models was based on the BIC. The optimum fit for all ages was the third order for additive genetic effects and the first order for permanent environmental effects.

We included 4 separate residual variance classes along the time x axis, 1 for each time point, because the residual variance for each separate LW measurement estimated using the multivariate analysis was different. Due to the small variation in measurement date between years, these classes were 10 to 16, 54 to 57, 126 to 154, and 268 to 281 d from the start of the year. We used these 4 time points because it maximised the number of individuals that could be included in the

analysis as most ewes were culled between weaning and the next mating, so most ewes had LW for the first 4 LW of the year.

The variances and covariances between the 4 LW points were calculated based on the random regression variance–covariance functions at 13, 55, 143, and 274 d from the start of the year.

The additive genetic variance and permanent environmental variance and covariance between LOSS and GAIN were calculated using the same equations as in the multivariate analysis of LW analysis. The only difference was that the phenotypic variance for LOSS and GAIN was estimated by adding the additive genetic and permanent environmental variances estimated from the random curves to the estimates for residual variance at the relevant time points. These residual estimates were assumed to be independent of each other because we estimated the permanent environmental effects to account for environmental covariances between time points.

2.3 Results

As ewes aged they got heavier and their LW varied less over the year (Table 2.2). The ewes were lighter at age 2 years at each point in the year and ewes aged 4 years were the heaviest. Additionally, the ewes on average lost LW between WT1 and WT2 (LOSS) and gained LW between WT3 and WT4 (GAIN) at all ages with younger ewes (age 2 years) losing and gaining more LW than older ewes (age 3 years and age 4 years). This suggests that ewes aged 2 years were still growing to maturity.

Variance of LW

The additive genetic variance of LW was mostly similar when estimated using multivariate analysis of LW and random regression (Figure 2.1). At age 3 years the additive variance of LW estimated using random regression as compared with multivariate analysis was greater for WT1 and WT2 and lower for WT4. The additive variance at age 4 years was greater for WT3 and lower for WT4 when estimated with random regression compared with multivariate analysis of LW. We used these variances and the covariance between each LW measurement to estimate the heritability of LW change.

Table 2.2 Mean and standard deviation (SD) of live weight 1 to 4, LOSS and GAIN of ewes aged 2, 3 and 4 years old.

Trait	Mean (kg)	SD (kg)
WT1 age = 2	50.2	6.24
WT1 age = 3	58.6	7.09
WT1 age = 4	61.7	7.30
WT2 age = 2	48.0	6.46
WT2 age = 3	58.0	6.45
WT2 age = 4	60.7	6.62
WT3 age = 2	50.3	6.04
WT3 age = 3	58.5	6.77
WT3 age = 4	60.9	7.13
WT4 age = 2	56.9	7.41
WT4 age = 3	61.7	8.13
WT4 age = 4	63.7	8.70
LOSS age = 2	-2.23	2.73
LOSS age = 3	-0.606	3.95
LOSS age = 4	-0.968	3.79
GAIN age = 2	6.55	7.20
GAIN age = 3	3.14	7.20
GAIN age = 4	2.83	7.41

Additive Genetic Variance, Phenotypic Variance, and Heritability

Estimates for LW loss

The multivariate analysis of LW fit the data better than random regression at all ages according to the BIC and AIC (Table 2.3). Table 2.4 shows estimates of the variance components for LOSS using the variance and covariance estimated with random regression and multivariate analyses of LW. The additive variance for LOSS was greater using multivariate whereas residual variance was greater using random regression. The heritability of LOSS calculated using random regression was lower than those calculated using multivariate (Table 2.5) analysis of LW and the LW change trait methods.

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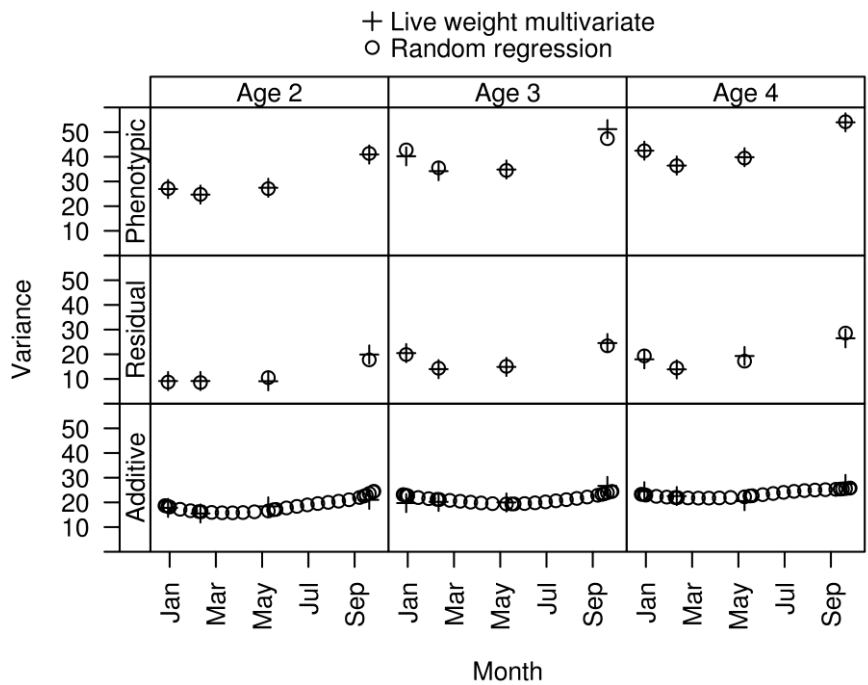


Figure 2.1 Variance components for LW estimated using multivariate analysis of LW and random regression analysis with third order polynomial for additive genetic variance and first order polynomial for permanent environmental effects. The residual for the random regression includes the permanent environmental and residual variance together. Plotted for age 2, 3, and 4 years.

Table 2.3 Akaike’s information criterion (AIC), and the Bayesian-Schwarz information criterion (BIC) for multivariate and random regression analysis of live weight at ages 2, 3 and 4.

Method	Age 2	Age 3	Age 4
AIC			
Multivariate	25713	22630	17389
Random Regression	25757	22685	17443
BIC			
Multivariate	25851	22764	17517
Random Regression	25875	22799	17552

Additive, Phenotypic, and Heritability Estimates for LW gain

The additive variance for GAIN estimated using multivariate analysis was greater than that estimated using random regression (Table 2.6). As a consequence, the heritability estimated using random regression was lower than the heritability estimated with the multivariate analysis of LW and LW change trait analyses (Table 2.7). Additionally, GAIN became less heritable as ewes aged using all 3 methods. At age 2 years, heritability of GAIN was greater compared with at age 3 years and age 4 years. The heritabilities for GAIN were always greater than LOSS.

Genetic Correlations between LW loss and LW gain

There was almost 0 genetic correlation between LOSS and GAIN except a medium negative correlation at age 3 years when correlations were estimated with multivariate analysis of LW and the LW change trait (Table 2.8). At age 2 and 4 years the genetic correlation between LOSS and GAIN was nearly 0 when estimated using the LW change trait and the multivariate analysis of LW (Table 2.8). Alternatively, these genetic correlations estimated using random regression were moderate and negative for age 2 and 4 years. The genetic correlations between LOSS and GAIN for age 3 years were greater than age 2 and 4 years for all 3 methods. For ewes aged 3 years, the genetic correlations estimated using LW change trait and multivariate analysis of LW were moderate and negative whereas the estimate using random regression analysis was very negative.

Genetic Correlations between Ages

The LOSS had low to moderate positive genetic correlations between ages (Table 2.9). The GAIN at age 2 years was moderately and positively correlated with GAIN at age 3 years whereas LW gain at age 3 years is the same trait as GAIN at age 4 years. The correlations between LOSS at age 2 years and LOSS at age 3 and 4 years are moderate whereas correlation between ages 3 and 4 years is low. This is not expected as ages 2 and 3 years or ages 3 and 4 years ought to have a greater genetic correlation than ages 2 and 4 years although the SE are high for these correlations. The genetic correlations for the GAIN traits were more in line with expectations, with age 3 and 4 years being highly correlated whereas there were lower correlations between age 2 and 3 years as well as ages 3 and 4 years. These results suggest that early growth to maturity at age 2 years is different to growth in adult Merino during periods of high nutrient availability.

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Table 2.4 Additive genetic ($\sigma_{a(WT2-WT1)}^2$) and residual plus permanent environmental ($\sigma_{e(WT2-WT1)}^2$) variance of LOSS calculated using the variance for each live weight and covariance between live weights estimated using multivariate analysis of live weight and random regression analyses. For example, the additive genetic variance was estimated using $\sigma_{a(WT2-WT1)}^2 = \sigma_{aWT2}^2 + \sigma_{aWT1}^2 - 2 \cdot \text{cov}_a(WT2, WT1)$. Permanent environmental variance was only estimated for the random regression.

Additive genetic	σ_{aWT1}^2	σ_{aWT2}^2	$\text{COV}_a(WT1, WT2)$	$\sigma_{a(WT2-WT1)}^2$
Age = 2				
Multivariate	17.7 (1.79)	15.5 (1.62)	16.2 (1.61)	0.89 (0.26)
Random regression	18.5 (1.73)	16.6 (1.65)	17.3 (1.68)	0.63 (0.23)
Age = 3				
Multivariate	19.7 (2.74)	20.2 (2.50)	19.1 (2.50)	1.69 (0.56)
Random regression	20.5 (2.64)	19.7 (.46)	19.7 (2.49)	0.79 (0.48)
Age = 4				
Multivariate	24.5 (3.64)	22.5 (3.13)	22.9 (3.21)	1.24 (0.65)
Random regression	23.2 (3.37)	22.1 (3.11)	22.4 (3.18)	0.42 (0.35)
Residual + Permanent environmental	σ_{eWT1}^2	σ_{eWT2}^2	$\text{COV}_e(WT1, WT2)$	$\sigma_{e(WT2-WT1)}^2$
Age = 2				
Multivariate	9.16 (1.17)	9.17 (1.08)	6.49 (1.05)	5.35 (0.28)
Random regression	8.74 (1.09)	8.54 (1.01)	5.83 (1.05)	5.62 (0.27)
Age = 3				
Multivariate	20.5 (2.11)	14.0 (1.78)	12.6 (1.81)	9.24 (0.58)
Random regression	20.0 (2.09)	14.7 (1.72)	12.4 (1.77)	9.81 (0.54)
Age = 4				
Multivariate	17.9 (2.75)	13.9 (2.30)	11.1 (2.34)	9.69 (0.72)
Random regression	19.4 (2.67)	14.6 (2.29)	11.8 (2.33)	10.3 (0.64)

Table 2.5 Estimates of additive ($\sigma_{a\text{LOSS}}^2$) and phenotypic variance ($\sigma_{p\text{LOSS}}^2$) and heritability (h^2) for LOSS with standard errors in brackets estimated using multivariate analysis of live weight, random regression and the live weight change trait analyses.

Method	Age	$\sigma_{a\text{LOSS}}^2$	$\sigma_{p\text{LOSS}}^2$ ¹	h^2
Multivariate	2	0.89 (0.26)	6.24 (0.20)	0.14 (0.04)
Random regression	2	0.63 (0.23)	6.06 (0.20)	0.07 (0.03)
Live weight change trait	2	0.86 (0.26)	6.24 (0.21)	0.14 (0.04)
Multivariate	3	1.69 (0.56)	10.9 (0.41)	0.15 (0.05)
Random regression	3	0.79 (0.48)	10.6 (0.40)	0.07 (0.03)
Live weight change trait	3	1.51 (0.55)	10.8 (0.41)	0.14 (0.05)
Multivariate	4	1.24 (0.65)	10.9 (0.47)	0.11 (0.06)
Random regression	4	0.42 (0.35)	10.7 (0.48)	0.04 (0.03)
Live weight change trait	4	1.23 (0.65)	10.9 (0.47)	0.11 (0.06)

¹ the phenotypic variance of LOSS by adding the additive, residual and permanent environmental variances from Table 2.4.

Table 2.6 Additive genetic ($\sigma_a^2_{(WT4-WT3)}$) and residual plus permanent environmental ($\sigma_e^2_{(WT4-WT3)}$) variance of GAIN calculated using the variance for each live weight and covariance between live weights estimated using multivariate analysis of live weight and random regression. For example, the additive genetic variance was estimated using $\sigma_a^2_{(WT4-WT3)} = \sigma_a^2_{WT4} + \sigma_a^2_{WT3} - 2 \cdot \text{cov}_a(WT4, WT3)$. Permanent environmental variance was only estimated for the random regression.

Additive genetic	$\sigma_a^2_{WT3}$	$\sigma_a^2_{WT4}$	$\text{COV}_a(WT3, WT4)$	$\sigma_a^2_{(WT4-WT3)}$
Age = 2				
Multivariate	18.4 (1.81)	21.0 (2.59)	15.8 (1.88)	7.73 (1.31)
Random regression	15.9 (1.60)	19.9 (2.01)	16.0 (1.68)	3.62 (0.83)
Age = 3				
Multivariate	19.8 (2.48)	26.7 (3.67)	20.4 (2.67)	5.95 (1.55)
Random regression	19.6 (2.35)	23.5 (2.85)	20.3 (2.44)	2.63 (1.13)
Age = 4				
Multivariate	20.5 (3.27)	27.5 (4.42)	21.4 (3.38)	5.24 (1.78)
Random regression	21.8 (3.07)	24.5 (3.70)	21.2 (3.12)	3.87 (1.42)
Residual + Permanent environmental	$\sigma_e^2_{WT3}$	$\sigma_e^2_{WT4}$	$\text{COV}_e(WT3, WT4)$	$\sigma_e^2_{(WT4-WT3)}$
Age = 2				
Multivariate	9.08 (1.17)	19.9 (1.87)	6.61 (1.25)	15.8 (1.11)
Random regression	10.5 (1.08)	17.5 (1.78)	6.03 (1.09)	15.9 (1.09)
Age = 3				
Multivariate	14.9 (1.80)	24.5 (2.76)	8.78 (1.90)	21.9 (1.51)
Random regression	15.7 (1.60)	24.3 (2.51)	8.91 (1.71)	22.2 (1.51)
Age = 4				
Multivariate	19.3 (2.57)	26.5 (3.48)	11.0 (2.58)	5.24 (1.78)
Random regression	17.3 (2.33)	28.5 (3.14)	10.9 (2.32)	3.87 (1.42)

Table 2.7 Estimates of additive genetic ($\sigma_a^2_{\text{GAIN}}$) and phenotypic variance ($\sigma_p^2_{\text{GAIN}}$) and heritability (h^2) for GAIN with standard errors in brackets estimated with multivariate analysis of live weight, random regression and the live weight change trait methods.

Method	Age	$\sigma_a^2_{\text{GAIN}}$	$\sigma_p^2_{\text{GAIN}}$ ¹	h^2
Multivariate	2	7.73 (1.31)	23.5 (0.83)	0.33 (0.05)
Random regression	2	3.62 (0.83)	19.5 (1.24)	0.18 (0.04)
Live weight change trait	2	7.92 (1.32)	23.5 (0.84)	0.33 (0.05)
Multivariate	3	5.95 (1.55)	27.8 (1.05)	0.21 (0.05)
Random regression	3	2.63 (1.13)	24.9 (1.75)	0.11 (0.04)
Live weight change trait	3	4.89 (1.37)	27.6 (1.03)	0.18 (0.05)
Multivariate	4	5.24 (1.78)	29.1 (1.25)	0.18 (0.06)
Random regression	4	3.87 (1.42)	27.8 (2.1)	0.14 (0.05)
Live weight change trait	4	5.71 (1.68)	29.3 (1.26)	0.19 (0.05)

¹ the phenotypic variance of GAIN by adding the additive, residual and permanent environmental variances from Table 2.6.

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Table 2.8 Estimates of genetic correlations between LOSS and GAIN ($r_{g \text{ LOSS GAIN}}$) with standard errors in brackets estimated with multivariate analysis of live weight, random regression and the live weight change trait analyses.

Method	Age	cov(LOSS,GAIN) ¹	$r_{g \text{ LOSS GAIN}}$
Multivariate	2	-0.00 (0.42) ¹	-0.00 (0.16)
Random regression	2	-0.59 (0.25) ¹	-0.47 (0.13)
Live weight change trait	2	0.08 (0.43)	0.03 (0.16)
Multivariate	3	-1.32 (0.66) ¹	-0.42 (0.19)
Random regression	3	-1.27 (0.42) ¹	-0.87 (0.21)
Live weight change trait	3	-1.33 (0.66)	-0.42 (0.20)
Multivariate	4	-0.09 (0.76) ¹	-0.03 (0.30)
Random regression	4	-0.75 (0.50) ¹	-0.57 (0.24)
Live weight change trait	4	-0.06 (0.75)	-0.02 (0.30)

¹ estimated using; $\text{cov}_a(\text{WT2-WT1}, \text{WT4-WT3})$

$$= \text{cov}_a(\text{WT1}, \text{WT3}) + \text{cov}_a(\text{WT2}, \text{WT4}) - \text{cov}_a(\text{WT1}, \text{WT4}) - \text{cov}_a(\text{WT2}, \text{WT3})$$

Table 2.9 Genetic correlations between ages for live weight loss and gain (\pm s.e. in brackets). LOSS = live weight loss and GAIN = live weight gain.

Age	LOSS		GAIN	
	Age 3	Age 4	Age 3	Age 4
Age 2	0.34 (0.24)	0.39 (0.30)	0.53 (0.14)	0.51 (0.15)
Age 3		0.13 (0.32)		0.99 (0.15)

2.4 Discussion

Our study found that LW loss during periods of poor nutrition and LW gain during periods of good nutrition are genetically different traits. Additionally, LW loss and gain are genetically different in young ewes compared with old ewes. The estimates of heritability and correlations for LW change were different depending on the method used.

Comparison of Methods

In this paper we used 3 methods for estimating genetic parameters. The estimates from the random regression analysis were clearly different from the estimates from the 2 other methods. The preferred method of the 3 is either the multivariate analysis of LW or LW change trait analyses because the multivariate analysis fit the data better than random regression according to the AIC and BIC. The LW change analysis cannot be directly compared with the multivariate and random regression analyses based on AIC and BIC but yields very similar results as the multivariate analyses. The random regression approach has a number of theoretical advantages but in our case was not an appropriate method. In our research, genetic

correlations between LW at different time points were greater with random regression than with multivariate analysis of LW. This makes the heritability of LW change lower because there is less genetic variation in the difference between LW when they are highly correlated. This is different to the analysis by Huisman *et al.* (2002) who found that the correlations between 5 LW points in growing pigs had a similar correlation using both multivariate and random regression analysis. With our data with only 4 LW points, multivariate analysis uses 20 parameters compared with the random regression, which uses 17, so there is not a major disadvantage for using the multivariate analysis whereas the multivariate analysis fits the data better than the random regression analysis.

Random regression could however be useful when data has more time points during the year because fewer parameters are required to predict variance and covariance using curves compared with multivariate analysis between many time points (van der Werf *et al.*, 1998). Additionally, if the measurements are recorded on different days for each individual making it harder to define specific traits or there are many missing values, random regression would be preferred. This is because multi-trait models become over parameterised as the model tries to estimate variance and covariance for time points with few records (Veerkamp *et al.*, 2001). In our study however, the LW points were well clustered together making 4 distinct traits so there is no clear advantage of using random regression. Therefore, the multivariate analysis or the LW change analysis is preferred.

The multivariate analysis of LW change and the LW change trait were very similar in terms of heritabilities of LW change and the genetic correlations between loss and gain. The preferred method of the 2 is the multivariate analysis because fixed effects can be allocated to each LW separately. For example, the number of lambs born would affect weight at lambing more than at the start of mating. Therefore, the fixed effect of number of lambs born can be better modeled for each LW trait separately.

An important conclusion from our analysis is the difficulty in estimating variances and correlations between LW change traits. To estimate the correlation between LOSS and GAIN using multivariate and random regression, 4 estimated variances and 6 estimated covariances were used. Although the differences between the random regression and the multivariate estimates are not large in terms of model fit and variance components, differences in estimates accumulate in calculating genetic correlations between LW changes resulting in very different outcomes between random regression and multivariate analysis.

Heritability Estimates

Our analysis revealed that LOSS and GAIN are genetically different traits with LOSS less heritable than GAIN. This can be partly explained by the difference in periods over which GAIN and LOSS were calculated. The trait LOSS was LW change during mating on poor quality pasture and GAIN was LW change during lactation on good quality pasture. Therefore, the physiological process of the LW change would be different between the 2 periods. Also, GAIN was estimated from LW 131 d apart compared with the LOSS LW, which were 42 d apart. We did not divide LW change by the number of days of each period because there was little variation in number of days between animals for each period. Longer time between points allows bigger genetic differences to accumulate. Our study is in line with the previous studies showing that genetic variation exists in farmed animal populations to breed for increased tolerance against climate change (Ravagnolo and Miszal, 2000; Borg *et al.*, 2009; Hayes *et al.*, 2009; Rauw *et al.*, 2010; Bloemhof *et al.*, 2012).

Our estimates of heritability were different from other studies with Rauw *et al.* (2010) estimating greater heritability for LW loss and Borg *et al.* (2009) estimating a lower heritability. Also, Borg *et al.* (2009) estimated a lower heritability for LW gain. Both of these studies were done in a semi-arid environment and used different breeds. Additionally, our heritabilities were estimated at each age independently, which makes a difference compared with pooling information from all ages together. For example, Vehviläinen *et al.* (2008) estimated lower heritability for survival with pooled generations compared with individual generations. Furthermore, we found genetic correlations between ages for LOSS and GAIN mostly less than 1. Therefore, LOSS and GAIN are not the same traits when ewes are maturing compared with when ewes are mature. The combination of different method, breed, environment, and timing of measurements may explain the different heritabilities between our study and the research by Borg *et al.* (2009) and Rauw *et al.* (2010).

Genetic Correlations between LOSS and GAIN

The genetic correlations suggest that LOSS and GAIN can be bred for independently and that LOSS and GAIN are different traits at different ages. There was close to 0 genetic correlation between LOSS and GAIN at ages 2 and 4 years whereas there was a moderate negative (-0.42) correlation at age 3 years when estimated with the multivariate analysis of LW and the LW change trait methods. Therefore, ewes can be selected to lose less LW potentially requiring less supplementary feeding and to gain more LW during spring and use more of the cheap feed supply, increasing their reserves before summer and autumn. The negative correlation at

age 3 years means that ewes that lose more LW also gain more LW, but the negative genetic correlation may have been due to sampling given the large standard errors.

Live weight loss appears to be lowly heritable at all ages, with little association across ages. Live weight gain appears to be moderately heritable, particularly among 2-year-old ewes. The genetics of gain therefore resembles that of a growth trait. In contrast, loss behaves more like a physiological trait with less genetic variation. Live weight LOSS is genetically a different trait at different ages and is a different trait at age 2 years compared with age 3 and 4 years and GAIN at age 3 and 4 years are genetically the same. This is probably because ewes at age 2 years are still growing to mature size whereas ewes at age 3 and 4 years are mature. Although GAIN is the same trait at age 3 and 4 years, it is recommended to consider LOSS and GAIN at different ages as different traits in genetic evaluation as well as in a selection index.

Implications for Breeding

The heritability estimates in this study show that it is feasible to breed adult Merino ewes that gain more LW. Live weight loss can also be selected for although the response to selection will be lower than for LW gain due to the lower heritability. Additionally, genetic correlations between LOSS and GAIN are mostly low, indicating that selection can be directed to one of them without affecting the other much. This means that sheep can be bred to lose less LW during periods of poor nutrition and gain more LW during periods of good nutrition. The implications of this depend on the role of LW change in the breeding goal and selection index of Merino sheep breeders.

Live weight change does not have a direct economic value in a selection index. However, it may be used in a selection index if it is genetically correlated to feed intake or efficiency. For example, LW loss could be used to represent breeding goal traits to reduce energy requirements for maintenance or increase intake when grazing poor quality feed (Fogarty *et al.*, 2009; Silanikove, 2000). A study by Young *et al.* (2011a) calculated that reducing maintenance costs or increasing intake on poor pasture had a high economic value. The increase in profit was because farmers could manage more ewes on each hectare of land if they are more efficient. If ewes are, however, able to maintain or gain LW during summer due to reallocating resources from other competing body functions such as fertility or immunity (van der Waaij, 2004), then LW change does not represent efficiency within the breeding goal and is less valuable. Therefore, it will be useful to understand if ewes lose or gain more LW because they allocate their resources

differently to wool, pregnancy, or lactation. This means that the genetic correlations between LW change and other production traits are needed before LW change can be used as an index trait.

Although all ewes had access to the same feed, the grazing behavior and actual intake by each ewe is not known. Therefore, it is possible that some ewes were more efficient at grazing or had first access to supplementary feed. To get better insight why some ewes lose less weight or gain more LW, individual feed intake data would be required.

2.5 Conclusion

In conclusion it is possible to breed adult ewes that lose less LW during periods of poor nutrition and gain LW during periods of good nutrition. More research is required to see if LW change can be used as an indicator trait for breeding goal traits such as feed intake or efficiency. If LW change is included in a breeding program, breeders need to consider the age of ewes and the timing of measurements. This research would benefit from a dataset with more measurements during the year that represents the trajectory of the LW curve better.

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3

Genetic correlations between live weight change and reproduction traits in Merino ewes depend on age

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² In this chapter alterations were made to the printed article, changing English from US to United Kingdom, replacing body weight with live weight and changing the format of headings and tables to make it consistent with the rest of the thesis.

Abstract

Merino sheep in Australia experience periods of variable feed supply. Merino sheep can be bred to be more resilient to this variation by losing less live weight when grazing poor quality pasture and gaining more live weight when grazing good quality pasture. Therefore, selection on live weight change might be economically attractive but correlations with other traits in the breeding objective need to be known. The genetic correlations (r_g) between live weight, live weight change, and reproduction were estimated using records from ~7350 fully pedigreed Merino ewes managed at Katanning in Western Australia. Number of lambs and total weight of lambs born and weaned were measured on ~5300 2-year-old ewes, ~4900 3-year-old ewes and ~3600 4-year-old ewes. On a proportion of these ewes live weight change was measured: ~1950 two-year-old ewes, ~1500 three old ewes and ~1100 four-year-old ewes. The live weight measurements were for three periods. The first period was during mating period over 42 days on poor pasture. The second period was during pregnancy over 90 days for ewes that got pregnant on poor and medium quality pasture. The third period was during lactation over 130 days for ewes that weaned a lamb on good quality pasture. Genetic correlations between weight change and reproduction were estimated within age classes. Genetic correlations were tested to be significantly greater magnitude than zero using likelihood ratio tests. Nearly all live weights had significant positive genetic correlations with all reproduction traits. In two-year old ewes, live weight change during the mating period had a positive genetic correlation with number of lambs weaned ($r_g = 0.58$); live weight change during pregnancy had a positive genetic correlation with total weight of lambs born ($r_g = 0.33$) and a negative genetic correlation with number of lambs weaned ($r_g = -0.49$). All other genetic correlations were not significantly greater magnitude than zero but estimates of genetic correlations for three-year-old ewes were generally consistent with these findings. The direction of the genetic correlations mostly coincided with the energy requirements of the ewes, and the stage of maturity of the ewes. In conclusion, optimised selection strategies on live weight changes to increase resilience will depend on the genetic correlations with reproduction, and are dependent on age.

Keywords: live weight change; genetic correlations, Merino ewes, reproduction

3.1 Introduction

Most Merino sheep in Australia are farmed in Mediterranean climate regions and they generally lose live weight during summer and autumn and regain live weight during late winter and spring (Adams and Briegel, 1998). Managing the extent and timing of live weight loss and gain in relation to pasture supply and animal requirements can affect whole farm profit (Young *et al.*, 2011b). Management of live weight of ewes will become more difficult if length of annual periods of drought during summer and winter become longer and harder to predict (IPCC, 2007). One way to make sheep production systems more resilient to uncertain pasture supply is to select sheep that lose less live weight when the supply and quality of paddock feed is low (Rose *et al.*, 2013).

Phenotypically, Merino ewes that are heavier at mating have a higher reproductive rate (Ferguson *et al.*, 2011). Additionally, there are positive phenotypic correlations between live weight gain during pregnancy and birth and weaning weight in lambs, with heavier lambs more likely to survive both prior to and after weaning (Oldham *et al.*, 2011; Thompson *et al.*, 2011).

Genetic correlations between live weight change and reproduction depend on correlations between live weight at all times during the reproductive cycle and reproduction traits. Therefore it is important to know the genetic correlations between live weight at key times during the reproductive cycle and reproduction traits. Ewe live weight prior to mating has a positive genetic correlation with fertility (Owen *et al.*, 1986; Cloete and Heydenrych, 1987). Borg *et al.* (2009) estimated positive genetic correlations between number of lambs born and live weight change during late lactation but correlations during the mating period and pregnancy are still unknown. Based on these correlations the hypothesis that increases in ewe live weight during the mating and pregnancy periods would have significant positive genetic correlations with reproduction traits was tested.

3.2 Materials and methods

Records from 7,346 Merino ewes were used from 697 sires and 4,724 dams using pedigree records from 17,836 sheep over 10 generations. These sheep were from the Merino Resource flocks of the Department of Agriculture and Food Western Australia located at Katanning (33°41'S, 117°35'E, elevation 310m). Katanning is in a Mediterranean climatic region with hot dry summers and mild wet winters. This combination of temperature and rainfall means that there is a period of no pasture growth during summer and autumn, typically extending from November to May each year. All ewes were managed on one farm under conditions typical for

commercial farms in the area. The amount of supplement fed varied between years but on average ewes were fed 100 grams of an oats and lupin grain mixture per head per day in late December increasing gradually to 800 grams per head per day at lambing in July. Hay was fed *ad libitum* during lambing. More information about how the flock was managed can be found in Greeff and Cox (2006).

Live weight change

To estimate change in live weight of ewes live weight data from ewes aged 2, 3 and 4 years old was used and live weight at each age was treated as different traits, using the same data as used by Rose *et al.* (2013). The age groups were 2, 3, and 4 years old at lambing in July. The ewes were weighed 4 times during the year. The average dates for each live weight were: 13th of January for pre-mating weight (WT1), 24th of February for post-mating weight (WT2), 23rd May for pre-lambing weight (WT3) and 2nd of October for weaning weight (WT4). The timing of measurements varied between years with WT1, WT2 and WT4 all measured within a week of each other while WT3 was measured within a month. Live weights were corrected for wool weight by estimating wool growth from shearing to the day the live weight was measured. These estimates were based on the greasy fleece weight of ewes, and assumed that wool growth was linear across the year. Conceptus weight was estimated using equations from the GRAZPLAN model (Freer *et al.*, 1997) and subtracted from WT2 and WT3.

Live weight change was then split into three parts of the reproduction cycle; mating, pregnancy and lactation. For live weight change during the mating period all ewes that were mated were included, for pregnancy only ewes that gave birth to lambs were included, and for lactation only ewes that weaned at least one lamb were included. Therefore, new live weight traits were created that only included the relevant ewes. These traits were for mating, WT1mate and WT2mate, for pregnancy WT2preg and WT3preg, and for lactation WT3lact and WT4lact. These three groups were derived because ewes that did not bear or rear lambs have different energy and protein requirements compared with ewes that were pregnant and lactating. Therefore, live weight change in ewes that do not bear or rear lambs may be genetically different than live weight change in ewes that do bear or rear lambs.

Using these new live weights the genetic parameters for live weight change during mating period ($\Delta\text{WT}_{\text{mate}} = \text{WT2}_{\text{mate}} - \text{WT1}_{\text{mate}}$), during pregnancy ($\Delta\text{WT}_{\text{preg}} = \text{WT3}_{\text{preg}} - \text{WT2}_{\text{preg}}$) and during lactation ($\Delta\text{WT}_{\text{lact}} = \text{WT4}_{\text{lact}} - \text{WT3}_{\text{lact}}$) could be estimated. Live weight change during mating period ($\Delta\text{WT}_{\text{mate}}$) was measured in summer when pasture was dry, $\Delta\text{WT}_{\text{preg}}$ was measured in autumn when pasture

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was dry and the start of winter when pasture started growing, and ΔW_{lact} was measured during winter and spring when pasture growth was most rapid.

The variance components of these live weight change traits were calculated by estimating the covariance between both live weights. The additive genetic variance of change in live weight ΔW ($\sigma^2_{a(\Delta W)}$) is;

$$\sigma^2_{a(\Delta W)} = \sigma^2_{a_{WT2}} + \sigma^2_{a_{WT1}} - 2 \times \text{cov}_a(WT2, WT1)$$

where $\sigma^2_{a_{WT2}}$ is the additive genetic variance of WT2, $\sigma^2_{a_{WT1}}$ is the additive genetic variance of WT1 and $\text{cov}_a(WT2, WT1)$ is the additive genetic covariance between WT2 and WT1.

Live weights were used instead of calculating live weight change because the number of records for the four traits was different. Therefore, only including records from animals with both traits would bias the estimates for live weight change. Additionally, the fixed effects can be fitted to each live weight trait separately.

Reproduction data

Reproduction traits at 2 (first lambing opportunity), 3 (second lambing opportunity) and 4 years of age (third lambing opportunity) were used. These traits were total weight of lambs born (TBW) and total weight of lambs weaned (TWW) in each age group. These traits incorporate most of the aspects of reproduction such as fecundity, mothering ability and ease of birth into one composite trait (Snowder and Fogarty, 2009). Variances and covariances for total number of lambs born in each year (NLB) and total number of lambs weaned in each year (NLW) were also estimated. Both NLB and NLW were estimated as linear traits including ewes that had no lambs born or weaned. Traits TBW and TWW were only measured in ewes that gave birth to or weaned lambs. The genetic correlations between live weight change and reproduction traits were estimated in the same year at the same age.

Genetic correlations between number of lambs born and weaned with live weight change

The genetic correlations (r_g) between live weights during the mating, pregnancy and lactation periods, and NLB and NLW were calculated by estimating the genetic covariance between the two live weights and each reproduction trait using equation 2. This equation was used to estimate the genetic correlations between live weight change during pregnancy and lactation and NLB and NLW. Equation 2 is

$$\begin{bmatrix} \mathbf{y}_{\text{trait}} \\ \mathbf{y}_{\text{wt}_a} \\ \mathbf{y}_{\text{wt}_b} \end{bmatrix} = \begin{bmatrix} \mathbf{x}_{\text{trait}} & 0 & 0 \\ 0 & \mathbf{x}_{\text{wt}_a} & 0 \\ 0 & 0 & \mathbf{x}_{\text{wt}_b} \end{bmatrix} \begin{bmatrix} \mathbf{b}_{\text{trait}} \\ \mathbf{b}_{\text{wt}_a} \\ \mathbf{b}_{\text{wt}_b} \end{bmatrix} + \begin{bmatrix} \mathbf{z}_{\text{trait}} & 0 & 0 \\ 0 & \mathbf{z}_{\text{wt}_a} & 0 \\ 0 & 0 & \mathbf{z}_{\text{wt}_b} \end{bmatrix} \begin{bmatrix} \mathbf{a}_{\text{trait}} \\ \mathbf{a}_{\text{wt}_a} \\ \mathbf{a}_{\text{wt}_b} \end{bmatrix} + \begin{bmatrix} \mathbf{e}_{\text{trait}} \\ \mathbf{e}_{\text{wt}_a} \\ \mathbf{e}_{\text{wt}_b} \end{bmatrix} \quad \text{Eq. 2}$$

where $\mathbf{y}_{\text{trait}}$ are the observations for NLB and NLW, \mathbf{y}_{wt_a} are the observations for the first live weight used to calculate live weight change and \mathbf{y}_{wt_b} are the observations for the second live weight used to calculate live weight change, \mathbf{b}_i is the vector of fixed effects, \mathbf{a}_i is the vector of additive genetic effects and \mathbf{e}_i is the vector of error effects. \mathbf{X}_i and \mathbf{Z}_i are the incidence matrices ($i = \text{trait}, \text{wt}_a$ and wt_b). The random effects \mathbf{a}_i and \mathbf{e}_i are trivariate normally distributed with mean zero and variance:

$$\text{var} \begin{bmatrix} \mathbf{e}_{\text{trait}} \\ \mathbf{e}_{\text{wt}_a} \\ \mathbf{e}_{\text{wt}_b} \end{bmatrix} = \mathbf{R} \otimes \mathbf{I} \text{ where } \mathbf{R} = \begin{bmatrix} \sigma_{\mathbf{e} \text{ trait}}^2 & \sigma_{\mathbf{e} \text{ trait wt}_a} & \sigma_{\mathbf{e} \text{ trait wt}_b} \\ \sigma_{\mathbf{e} \text{ wt}_a \text{ trait}} & \sigma_{\mathbf{e} \text{ wt}_a}^2 & \sigma_{\mathbf{e} \text{ wt}_a \text{ wt}_b} \\ \sigma_{\mathbf{e} \text{ wt}_b \text{ trait}} & \sigma_{\mathbf{e} \text{ wt}_b \text{ wt}_a} & \sigma_{\mathbf{e} \text{ wt}_b}^2 \end{bmatrix} \text{ and}$$

$$\text{var} \begin{bmatrix} \mathbf{a}_{\text{trait}} \\ \mathbf{a}_{\text{wt}_a} \\ \mathbf{a}_{\text{wt}_b} \end{bmatrix} = \mathbf{G} \otimes \mathbf{A} \text{ where } \mathbf{G} = \begin{bmatrix} \sigma_{\mathbf{a} \text{ trait}}^2 & \sigma_{\mathbf{a} \text{ trait wt}_a} & \sigma_{\mathbf{a} \text{ trait wt}_b} \\ \sigma_{\mathbf{a} \text{ wt}_a \text{ trait}} & \sigma_{\mathbf{a} \text{ wt}_a}^2 & \sigma_{\mathbf{a} \text{ wt}_a \text{ wt}_b} \\ \sigma_{\mathbf{a} \text{ wt}_b \text{ trait}} & \sigma_{\mathbf{a} \text{ wt}_b \text{ wt}_a} & \sigma_{\mathbf{a} \text{ wt}_b}^2 \end{bmatrix}$$

\mathbf{I} is the identity matrix and \mathbf{A} is the additive genetic relationship matrix between ewes.

Variance components and their standard errors were estimated using ASReml (Gilmour et al., 2006). For all traits fixed effects were for year (1982-2005), the age of the dam of the ewe (years), birth and rearing type of the ewe (single or multiple) and birthdate as a fixed covariate.

Reproductive performance of a ewe affects live weight change during pregnancy and lactation, as more lambs will cause a higher foetal and lactation burden. Ewes that produce larger litters are expected to lose more live weight during pregnancy and lactation. Therefore, correlations between live weight change during pregnancy and lactation and reproduction were calculated with and without fixed effects fitted for number of lambs born and reared by the ewes in the year of measurement. Differences in correlations using both methods are in Appendix A for number of lambs born and weaned and Appendix B for total weaning weight and total birth weight.

The genetic correlations between live weight change and reproduction traits were calculated from the covariances between the two live weights and the reproduction trait and the variances of all three traits. For example, the genetic correlation between live weight change and NLB ($r_{g \Delta \text{WT}, \text{NLB}}$) is;

$$r_{g \Delta \text{WT}, \text{NLB}} = \frac{\text{cov}_a(\text{WT2}, \text{NLB}) - \text{cov}_a(\text{WT1}, \text{NLB})}{\sigma_{\mathbf{a} \text{ NLB}} \times \sqrt{\sigma_{\mathbf{a} \text{ WT2}}^2 + \sigma_{\mathbf{a} \text{ WT1}}^2 - 2 \times \text{cov}_a(\text{WT1}, \text{WT2})}} \quad \text{Eq. 3}$$

To test if this genetic correlation was significantly greater magnitude than zero a likelihood ratio test was used to compare the fit of two models. The first model was with no restrictions on the estimates for variance and covariance and the second model required the covariance between WT2 and NLB to be equal to the

covariance between WT1 and NLB. Making the covariances between each live weight and NLB equal makes the numerator for the correlation zero. The second model therefore reflects our null hypothesis that the genetic correlation is equal to zero.

Genetic correlations between total birth and weaning weights with live weight change

Removing the ewes that did not give birth to or weaned a lamb from the analysis would bias the estimates for variance of TBW and TWW and the covariance between these traits and other traits (Thompson, 1973). Therefore when TBW was analysed a binary trait was included for ewes that were mated and did (1) or did not (0) give birth to any lambs (HAVELAMB). When TWW was analysed a binary trait was included for ewes that were mated and did (1) or did not (0) wean any lambs (WEANLAMB). These binary traits were included in multivariate analyses with reproduction traits (TBW or TWW) and the two live weight traits used to estimate the live weight change trait at ages 2, 3 and 4 using equation 4.

$$\begin{bmatrix} \mathbf{y}_{bin} \\ \mathbf{y}_{repro} \\ \mathbf{y}_{wt_a} \\ \mathbf{y}_{wt_b} \end{bmatrix} = \begin{bmatrix} \mathbf{X}_{bin} & 0 & 0 & 0 \\ 0 & \mathbf{X}_{repro} & 0 & 0 \\ 0 & 0 & \mathbf{X}_{wt_a} & 0 \\ 0 & 0 & 0 & \mathbf{X}_{wt_b} \end{bmatrix} \begin{bmatrix} \mathbf{b}_{bin} \\ \mathbf{b}_{repro} \\ \mathbf{b}_{wt_a} \\ \mathbf{b}_{wt_b} \end{bmatrix} + \begin{bmatrix} \mathbf{Z}_{bin} & 0 & 0 & 0 \\ 0 & \mathbf{Z}_{repro} & 0 & 0 \\ 0 & 0 & \mathbf{Z}_{wt_a} & 0 \\ 0 & 0 & 0 & \mathbf{Z}_{wt_b} \end{bmatrix} \begin{bmatrix} \mathbf{a}_{bin} \\ \mathbf{a}_{repro} \\ \mathbf{a}_{wt_a} \\ \mathbf{a}_{wt_b} \end{bmatrix} + \begin{bmatrix} \mathbf{e}_{bin} \\ \mathbf{e}_{repro} \\ \mathbf{e}_{wt_a} \\ \mathbf{e}_{wt_b} \end{bmatrix} \quad \text{Eq. 4}$$

where \mathbf{y}_{bin} are the observations for the binary reproduction traits HAVELAMB or WEANLAMB, \mathbf{y}_{repro} are the observations for the reproduction traits TBW or TWW, \mathbf{y}_{wt_a} are the observations for the first live weight used to calculate live weight change, \mathbf{y}_{wt_b} are the observations for the second live weight used to calculate live weight change, \mathbf{b}_i is the vector of fixed effects, \mathbf{a}_i is the vector of additive genetic effects and \mathbf{e}_i is the vector of error effects. \mathbf{X}_i and \mathbf{Z}_i are the incidence matrices ($i = bin, repro, wt_a$ and wt_b). The random effects \mathbf{a}_i and \mathbf{e}_i are multivariate normally distributed with mean zero and variance:

$$\text{var} \begin{bmatrix} \mathbf{e}_{bin} \\ \mathbf{e}_{repro} \\ \mathbf{e}_{wt_a} \\ \mathbf{e}_{wt_b} \end{bmatrix} = \mathbf{R} \otimes \mathbf{I} \quad \text{where } \mathbf{R} = \begin{bmatrix} 1 & 0 & \sigma_{e \text{ bin } wt_a} & \sigma_{e \text{ bin } wt_b} \\ 0 & \sigma_{e \text{ repro}}^2 & \sigma_{e \text{ repro } wt_a} & \sigma_{e \text{ repro } wt_b} \\ \sigma_{e \text{ wt}_a \text{ bin}} & \sigma_{e \text{ wt}_a \text{ repro}} & \sigma_{e \text{ wt}_a}^2 & \sigma_{e \text{ wt}_a \text{ wt}_b} \\ \sigma_{e \text{ wt}_b \text{ bin}} & \sigma_{e \text{ wt}_b \text{ repro}} & \sigma_{e \text{ wt}_b \text{ wt}_a} & \sigma_{e \text{ wt}_b}^2 \end{bmatrix} \quad \text{and}$$

$$\text{var} \begin{bmatrix} \mathbf{a}_{\text{bin}} \\ \mathbf{a}_{\text{repro}} \\ \mathbf{a}_{\text{wt}_a} \\ \mathbf{a}_{\text{wt}_b} \end{bmatrix} = \mathbf{G} \otimes \mathbf{A} \text{ where } \mathbf{G} = \begin{bmatrix} \sigma_a^2 \text{ bin} & \sigma_a \text{ bin repro} & \sigma_a \text{ bin wt}_a & \sigma_a \text{ bin wt}_b \\ \sigma_a \text{ repro bin} & \sigma_a^2 \text{ repro} & \sigma_a \text{ repro wt}_a & \sigma_a \text{ repro wt}_b \\ \sigma_a \text{ wt}_a \text{ bin} & \sigma_a \text{ wt}_a \text{ repro} & \sigma_a^2 \text{ wt}_a & \sigma_a \text{ wt}_a \text{ wt}_b \\ \sigma_a \text{ wt}_b \text{ bin} & \sigma_a \text{ wt}_b \text{ repro} & \sigma_a \text{ wt}_b \text{ wt}_a & \sigma_a^2 \text{ wt}_b \end{bmatrix}$$

For HAVELAMB and WEANLAMB traits a LOGIT link function was used and the residual variance was set to one. The residual covariance between the binary and reproduction traits was set to zero. The implicit residual variance on the underlying scale for the logit link is $\pi^2/3 \sim 3.3$ (Gilmour *et al.*, 2006). The genetic correlations between live weight change and the reproduction traits (TWW and TBW) were calculated using equation 3.

3.3 Results

Trait information and heritability

Two-year-old ewes had the lowest live weights and live weight increased as ewes got older (Table 3.1). Two-year-old ewes were still growing to maturity and gained the most live weight between lambing and weaning (Table 3.1). At all ages ewes were on average heaviest at weaning (WT2lact). Weight differences between ages were significant ($P < 0.05$). The heritability of live weight was moderate to high (0.47 to 0.72) and decreased with age (Table 3.1). Within each age group the heritability of live weight at different weight measurements were different (Table 3.1). For ewes aged 2 years, heritabilities were highest for prelambling weights (WT3preg and WT3lact) while for older ewes (aged 3 and 4 years) heritabilities were highest for postmating weights (WT2mate and WT2preg) (Table 3.1). For ewes aged 2 and 3 years, heritability was lowest for weaning weight (WT4lact) while for ewes aged 4 years, heritability was lowest for prelambling weights (WT3preg and WT3lact) (Table 3.1).

At all ages ewes on average lost live weight during mating period (ΔWTMATE) and gained weight during lactation (ΔWTlact ; Table 3.2). During pregnancy (ΔWTpreg), 2-year-old pregnant ewes gained weight, 3-year-old ewes slightly gained weight and 4-year-old ewes slightly lost weight (Table 3.2). Differences in changes in body weight between ages were significant ($P < 0.05$). The heritability of live weight change was highest at all ages for lactating ewes (ΔWTlact ; Table 3.2). For ewes aged 2 years the heritability of live weight change was lowest for pregnant ewes (ΔWTpreg), while for ewes aged 3 and 4 years old heritability of live weight change during mating period was lowest (Table 3.2).

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Ewes gave birth to more lambs (NLB) as they aged and the total weight of those lambs at birth (TBW) increased ($p < 0.05$) (Table 3.3). In addition, as ewes aged they weaned more lambs (NLW) and the total weight of those lambs at weaning (TWW) increased ($p < 0.05$) (Table 3.3). The heritability of reproduction traits NLB, NLW, TBW, and TWW was low to moderate (0.08-0.17; Table 3.3). Heritabilities of birth traits (NLB and TBW) decreased when age of ewes increased while heritabilities of weaning traits (NLW and TWW) were highest at age 2 years and lowest at age 3 years (Table 3.3). Although some differences in heritability were substantial, they were generally not statistically significant due to the relatively large approximated standard errors.

Table 3.1 Weight measurements by age, number of observations, mean, phenotypic variance (σ_p^2) and heritability (h^2) (standard errors)

Weight traits ¹	Records	Mean (kg)	σ_p^2 (kg)	h^2
Age 2				
WT1mate	1940	50.4	8.64	0.70 (0.05)
WT2mate	1940	48.2	25.10	0.68 (0.05)
WT2preg	1540	48.7	21.53	0.68 (0.06)
WT3preg	1540	50.7	33.33	0.72 (0.05)
WT3lact	1290	50.8	20.19	0.72 (0.06)
WT4lact	1280	55.3	34.54	0.60 (0.07)
Age 3				
WT1mate	1520	58.8	7.89	0.52 (0.06)
WT2mate	1520	58.2	20.20	0.63 (0.06)
WT2preg	1330	58.5	21.70	0.58 (0.06)
WT3preg	1330	58.7	26.35	0.57 (0.06)
WT3lact	1150	58.5	22.06	0.53 (0.07)
WT4lact	1140	61.2	25.69	0.52 (0.07)
Age 4				
WT1mate	1110	62.1	8.03	0.56 (0.07)
WT2mate	1110	61.2	15.70	0.58 (0.07)
WT2preg	960	61.4	21.59	0.59 (0.08)
WT3preg	960	61.1	24.25	0.47 (0.08)
WT3lact	850	61.1	22.75	0.47 (0.08)
WT4lact	840	62.5	25.77	0.53 (0.09)

¹Weight traits: WT1mate = live weight pre-mating of all ewes that were mated; WT2mate = live weight post-mating of all ewes that were mated; WT2preg = live weight post-mating for ewes that got pregnant; WT3preg = live weight pre-lambing for all ewes that got pregnant; WT3lact = live weight pre-lambing for ewes that weaned lambs; WT4lact = live weight at weaning for ewes that weaned lambs.

Table 3.2 Live weight change measurements by age, mean, phenotypic variance (σ_p^2) and heritability (h^2) (standard errors).

Weight change traits ¹	Mean (kg)	σ_p^2 (kg)	h^2
Age 2			
ΔWTmate	-2.20	6.43	0.14 (0.04)
ΔWTpreg	2.00	8.82	0.13 (0.04)
ΔWTlact	4.60	22.8	0.36 (0.06)
Age 3			
ΔWTmate	-0.50	11.5	0.15 (0.05)
ΔWTpreg	0.20	9.14	0.16 (0.06)
ΔWTlact	2.70	29.5	0.24 (0.06)
Age 4			
ΔWTmate	-0.90	10.8	0.12 (0.06)
ΔWTpreg	-0.3	11.1	0.18 (0.07)
ΔWTlact	1.4	32.1	0.24 (0.07)

¹Weight change traits: ΔWTmate = change in live weight during mating for all ewes that were mated; ΔWTpreg = change in live weight during pregnancy for ewes that got pregnant; ΔWTlact = change in live weight lactation for ewes that reared lambs.

Table 3.3 Reproduction trait measurements by age, mean, phenotypic variance (σ_p^2) and heritability (h^2) (standard errors).

Traits ¹	Units	Age	Number	Mean	σ_p^2	h^2
NLB	lambs	2	6756	0.78	0.26	0.15 (0.02)
NLB	lambs	3	5585	1.05	0.33	0.12 (0.02)
NLB	lambs	4	4360	1.11	0.41	0.10 (0.02)
TBW	kg	2	4699	4.85	0.75	0.17 (0.02)
TBW	kg	3	4609	5.13	1.07	0.15 (0.02)
TBW	kg	4	3551	5.36	1.32	0.12 (0.03)
NLW	lambs	2	4699	0.64	0.27	0.11 (0.02)
NLW	lambs	3	4609	0.87	0.36	0.08 (0.02)
NLW	lambs	4	3551	0.94	0.41	0.09 (0.02)
TWW	kg	2	4092	26.5	22.2	0.17 (0.03)
TWW	kg	3	4089	27.6	29.7	0.13 (0.03)
TWW	kg	4	3363	28.10	36.3	0.15 (0.03)

¹Reproduction traits: NLB = number of lambs born; TBW = total weight of lambs born; NLW = total number of lambs weaned; TWW = total weight of lambs weaned.

Genetic correlations live weights and reproduction

All genetic correlations between all live weights and reproduction traits were positive. The highest genetic correlations were between live weights and total weaning weight (TWW; Table 3.4). At age 2 TBW and TWW had the highest genetic correlation with WT1mate while NLB and NLW had the highest genetic correlation with WT2preg (Table 3.4). At age 3 TBW had the highest genetic correlation with WT1mate while TWW and NLW had the highest genetic correlation with WT3wean,

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and NLB had the highest genetic correlation with WT2mean (Table 3.4). For 4-year-old ewes TBW had the highest genetic correlation with WT3preg while TWW, NLB, and NLW had the highest genetic correlation with WT3wean (Table 3.4). All reproduction traits had lowest genetic correlations with WT4wean at all ages except for TWW at age 3, which had the lowest genetic correlation with WTmate (Table 3.4).

Table 3.4 Genetic correlations between live weights and reproduction traits at ages 2, 3 and 4 with standard errors in brackets. Correlations in bold are significantly larger than zero.

Weight traits ²	Reproduction traits ¹			
	TBW	TWW	NLB	NLW
Age 2				
WT1mate	0.40 (0.09)	0.76 (0.09)	0.36 (0.09)	0.29 (0.11)
WT2mate	0.37 (0.09)	0.75 (0.09)	0.46 (0.09)	0.46 (0.11)
WT2preg	0.27 (0.10)	0.65 (0.10)	0.48 (0.09)	0.47 (0.11)
WT3preg	0.33 (0.09)	0.64 (0.10)	0.37 (0.10)	0.31 (0.11)
WT3wean	0.37 (0.10)	0.63 (0.10)	0.32 (0.10)	0.26 (0.12)
WT4wean	0.24 (0.11)	0.50 (0.11)	0.28 (0.12)	0.29 (0.13)
Age 3				
WT1mate	0.34 (0.11)	0.39 (0.12)	0.36 (0.13)	0.27 (0.16)
WT2mate	0.31 (0.10)	0.45 (0.11)	0.49 (0.11)	0.41 (0.15)
WT2preg	0.21 (0.11)	0.46 (0.13)	0.43 (0.12)	0.36 (0.16)
WT3preg	0.24 (0.11)	0.49 (0.13)	0.40 (0.13)	0.45 (0.16)
WT3wean	0.24 (0.12)	0.55 (0.14)	0.40 (0.13)	0.52 (0.16)
WT4wean	0.15 (0.12)	0.52 (0.14)	0.19 (0.15)	0.24 (0.18)
Age 4				
WT1mate	0.39 (0.14)	0.66 (0.14)	0.23 (0.16)	0.29 (0.16)
WT2mate	0.48 (0.13)	0.73 (0.13)	0.33 (0.15)	0.41 (0.15)
WT2preg	0.52 (0.14)	0.76 (0.14)	0.35 (0.16)	0.37 (0.16)
WT3preg	0.53 (0.16)	0.75 (0.15)	0.32 (0.18)	0.33 (0.18)
WT3wean	0.47 (0.16)	0.78 (0.16)	0.42 (0.18)	0.49 (0.18)
WT4wean	0.12 (0.16)	0.60 (0.16)	0.19 (0.19)	0.26 (0.19)

¹Reproduction traits: NLB = number of lambs born; TBW = total weight of lambs born; NLW = total number of lambs weaned; TWW = total weight of lambs weaned.

²Weight traits: WT1mate = live weight pre-mating of all ewes that were mated; WT2mate = live weight post-mating of all ewes that were mated; WT2preg = live weight post-mating for ewes that got pregnant; WT3preg = live weight pre-lambing for all ewes that got pregnant; WT3lact = live weight pre-lambing for ewes that weaned lambs; WT4lact = live weight at weaning for ewes that weaned lambs.

Genetic correlations live weight change and reproduction

The genetic correlations between live weight change and reproduction traits ranged between -0.49 and 0.58 (Table 3.5) but only four out of 26 were significantly greater magnitude from zero. These significant genetic correlations were at age 2 between NLW and Δ WTmate (0.58), between NLW and Δ WTpreg (-0.49), and between TBW and Δ WTpreg (0.33; Table 3.5). The other genetic correlation significantly different from zero was at age 4 between TBW and Δ WTlact (-0.42; Table 3.5). For 3-year-old ewes some correlations were close to significance with a p-value less than 0.10. These were between Δ WTmate, and NLB, between Δ WTmate and NLW, between Δ WTpreg and NLW, between Δ WTlact, and NLW, and between Δ WTlact and NLB (Table 3.5).

Table 3.5 Genetic correlations between live weight change and reproduction traits at ages 2, 3 and 4 with standard errors in brackets. Correlations in bold are significantly larger than zero.

Weight change trait ²	Reproduction traits ¹			
	TBW	TWW	NLB	NLW
Age 2				
Δ WTmate	-0.26 (0.16)	-0.20 (0.17)	0.27 (0.17)	0.58 (0.17)
Δ WTpreg	0.33 (0.17)	0.24 (0.20)	-0.34 (0.17)	-0.49 (0.19)
Δ WTlact	-0.15 (0.13)	-0.1 (0.14)	-0.08 (0.14)	0.00 (0.16)
Age 3				
Δ WTmate	-0.1 (0.16)	0.24 (0.19)	0.39 (0.20)	0.48 (0.23)
Δ WTpreg	0.21 (0.19)	0.16 (0.21)	0.15 (0.24)	0.53 (0.27)
Δ WTlact	-0.09 (0.16)	0.06 (0.18)	-0.35 (0.18)	-0.46 (0.20)
Age 4				
Δ WTmate	0.26 (0.24)	0.13 (0.23)	0.27 (0.29)	0.33 (0.29)
Δ WTpreg	-0.07 (0.22)	-0.22 (0.21)	-0.15 (0.25)	-0.21 (0.25)
Δ WTlact	-0.42 (0.20)	0.00 (0.20)	-0.21 (0.22)	-0.20 (0.22)

¹Reproduction traits: NLB = number of lambs born; TBW = total weight of lambs born; NLW = total number of lambs weaned; TWW = total weight of lambs weaned.

²Weight change traits: Δ WTmate = change in live weight during mating for all ewes that were mated; Δ WTpreg = change in live weight during pregnancy for ewes that got pregnant; Δ WTlact = change in live weight lactation for ewes that reared lambs.

3.4 Discussion

In this study, the genetic correlations between live weight change during mating and pregnancy and reproduction traits in Merino ewes varied. The only significant positive genetic correlations estimated were between live weight change during mating period and number of lambs weaned and between live weight change during pregnancy and total birth weight for two-year-old ewes. Moreover, there was a significant negative genetic correlation between live weight change during pregnancy and number of lambs weaned in two-year-old ewes. However, there were suggestive positive genetic correlations between live weight change during mating period and number of lambs born and weaned and between live weight change during pregnancy and number of lambs weaned in three-year-old ewes. Overall, the hypothesis that live weight change during mating and pregnancy would have significant positive genetic correlations with reproduction traits in Merino ewes was rejected.

For two-year-old and three-year-old mated ewes, number of lambs weaned had a larger genetic correlation with live weight postmating than live weight premating. These correlations made the genetic correlation between live weight change during mating period and number of lambs weaned positive, and significantly greater than zero for two-year-old ewes. Live weight during the mating period and energy balance affects fertility (Forcada and Abecia, 2006). Therefore, ewes that gain weight during mating period would be expected to wean more lambs because they have a positive energy balance.

For pregnant ewes, the correlations were not as clear as for mated ewes, with two-year-old ewes having different correlations than three-year-old ewes. For two-year-old pregnant ewes, number of lambs weaned had a larger genetic correlation with live weight postmating than live weight prelambing. For three-year-old pregnant ewes, number of lambs weaned had a larger genetic correlation with live weight prelambing than with live weight postmating. These correlations meant that for two-year-old ewes, total birth weight had a genetic correlation with live weight change during pregnancy significantly less than zero, while for three-year-old ewes the correlation was in the opposite direction. Additionally, for two-year-old ewes, total birth weight had a larger genetic correlation with live weight prelambing than live weight postmating. These correlations made the genetic correlation between live weight change during pregnancy and total birth weight significantly greater than zero. These genetic correlations meant that two-year-old ewes that gained weight during pregnancy gave birth to a higher total birth weight but weaned fewer lambs while three year old ewes that gained more weight during pregnancy

weaned more lambs. These different correlations between ages are perhaps due to differences in physiology between young and older ewes.

There were differences in live weight and reproductive performance between two and three-years-old ewes that could affect the physiology of the two age groups. Two-year-old ewes were still growing to maturity and were 10-12 kg lighter at the start of mating than 3 and 4-year-old ewes. Additionally, three-year-old ewes gave birth to and weaned more twin lambs than two-year-old ewes. This may explain why weight change during pregnancy for pregnant two-year-old ewes had a positive genetic correlation with total birth weight but a negative correlation with number of lambs weaned. Because two-year-old ewes mostly had 1 lamb, number of lambs weaned indicates if the ewes got pregnant. The total birth weight indicates how big the lamb was at lambing. Getting pregnant is probably more related to energy balance during mating period while lamb growth is probably related to energy balance during pregnancy. Therefore, if two-year-old ewes are selected to gain live weight during mating and pregnancy periods, the correlated response will be to wean a lamb which has a higher birth weight. In three-year-olds, more ewes weaned multiple lambs than two-year-old ewes. This was because two lambs require more resources from the ewe for successful weaning of lambs, with resources requirements peaking after lambing. Therefore, three-year-old ewes require positive energy balance during mating, and during pregnancy, to ensure that lambs can survive to weaning. So despite the differences in physiology and genetic correlations between two and three-year-old ewes, selecting ewes to gain weight during mating and pregnancy periods will have a favourable correlated response in number of lambs weaned.

For four-year-old lactating ewes, total birth weight had a larger genetic correlation with live weight prelambling than live weight at weaning. This was also the case for three-year-old ewes with number of lambs born and number of lambs weaned both having larger genetic correlations with live weight prelambling than live weight at weaning. These genetic correlations suggest that these ewes needed to be heavier at lambing to have enough energy for milk production but then lose that weight during lactation. Therefore, losing live weight during lactation period will increase the number of lambs born and weaned in three-year-old ewes, and increase total birth weight in four-year-old ewes. These genetic correlations are supported by three and four-year-old lactating ewes weaning more lambs than young ewes.

Including fixed effects for lambs born and reared for live weight change during pregnancy and lactation changed the interpretation of the live weight traits. Our results showed that ewes that gained live weight during pregnancy gave birth to a

higher total birth weight but weaned less lambs. When live weight change during pregnancy was corrected for number of lambs born and reared, the genetic correlation with number of lambs weaned became less negative and not greater magnitude than zero. This change means that correcting for number of lambs weaned reduces the importance of the correlation. The correlation became less negative because of a reduced covariance between live weight change and number of lambs weaned. Therefore, correcting live weight change for number of lambs weaned reduced the influence of live weight change on number of lamb weaned. Additionally, including number of lambs born and weaned had more effect on the correlations between live weight change with number of lambs weaned and born, than the correlations with total birth and weaning weight. To best test the hypothesis that live weight change during pregnancy and lactation is genetically correlated with reproduction traits, live weight change uncorrected for reproduction provides the best interpretation of the trait to account for changes in reproduction. This is the best interpretation because the covariance between live weight change and reproduction is not altered by correcting live weight for reproduction at the same time.

The genetic correlations between live weight change during all periods and both total weaning weight, and number of lambs born were not significant. Genetic correlations between total weaning weight and live weights and most of the genetic correlations between total birth weight and live weights were all similar during mating period, pregnancy and lactation. When the genetic correlations between two live weights and reproduction are similar, then the covariance between live weight change and reproduction will tend towards zero. This meant that the genetic correlations between total weaning weight, and total birth weight and live weight change were near zero because heavy ewes at any time during the reproductive cycle weaned a higher total weight of lambs. Ewes that weaned multiple lambs had a higher total weaning weight ($p < 0.05$) than ewes that weaned one lamb, but the weight of each lamb was lower ($p < 0.05$). Therefore, the positive genetic correlations between live weight and total weaning weight are mainly due to higher number of lambs weaned. Furthermore, maternal genetic effects might be confounded with direct genetic effects on weaning weight of each lamb. Separation of these effects is difficult because each ewe has one record for weaning weight at each age. Additionally, ewes on average did not lose a lot of weight during mating and pregnancy periods. Mating period was short, and pregnancy period was perhaps too long to accurately describe changes in live weight. The pregnancy period perhaps should be split into two periods, early pregnancy and late pregnancy, as ewes generally lose weight during early

pregnancy and gain weight during late pregnancy in Mediterranean environments (Ferguson *et al.*, 2011). Therefore, the physiology of the animals would be different during these periods, as animals that lose weight during early pregnancy and gain weight during late pregnancy would be treated the same as those that did not lose or gain any weight during pregnancy.

The heritability of traits estimated in our study are similar to those estimated in previous studies and range from 0.47 to 0.72 for live weight, 0.10 to 0.15 for number of lambs born and 0.08 to 0.11 for number of lambs weaned. Huisman *et al.* (2008) estimated a heritability of 0.44 for live weight, 0.09 for number of lambs born and 0.07 for number of lambs weaned for 2-year-old Merino ewes. Cloete *et al.* (2002) estimated a heritability of 0.04 for total weaning weight which was much smaller than the range found in this study 0.13-0.17. Additionally, Owen *et al.* (1986) estimated a positive genetic correlation (0.40) between live weight pre-mating and prolificacy in Cambridge sheep, similar to our estimates between live weights pre and post-mating and number of lambs born. Cloete and Heydenrych (1987) estimated low positive genetic correlations between live weight pre-mating and number of lambs born (0.24) and number of lambs weaned (0.20) in two-year-old Tygerhoek Merino ewes. These estimates had higher error than our estimates which were higher and significantly greater than zero. Borg *et al.* (2009) estimated a low positive genetic correlation (0.12) between adult live weight post weaning and number of lambs born. These estimates were smaller than our estimates between weaning live weight and number of lambs born. It is reasonable to conclude that our heritabilities are in the range of other studies, suggesting our dataset is appropriate to study correlations between live weight change and reproduction.

These results are important because ewes on sheep farms in Mediterranean regions of Australia are mated during periods of low nutrition availability (Pitta *et al.*, 2005; Demmers *et al.*, 2011; Ferguson *et al.*, 2011). This means farmers put a high emphasis on nutrition of ewes during the mating period to increase ovulation rate and during pregnancy to increase lamb survival. Selecting for ewes that lose less weight during pregnancy will have mostly favourable correlated responses in reproductive traits. Therefore, the advantage of breeding two and three-year-old ewes to be robust to this low nutrition is that they are both easier to manage during the mating period and are genetically more fertile.

Optimal selection strategies on live weight changes to increase resilience depend on the genetic correlations with reproduction, and are dependent on age. Index selection could be used to minimise undesired effects on total weaning weight and number of lambs born. This means that Australian sheep farmers and breeders can

select for live weight change to make adult ewes more robust to uncertain feed supply and increase reproduction simultaneously.

3.5 Conclusion

Live weight change during mating period, pregnancy and lactation had significant genetic correlations with number of lambs weaned and total birth weight. These genetic correlations are caused by different strengths of genetic correlations between live weights and reproduction. The interpretation of the genetic correlations implies gaining weight during certain stages of reproduction will affect how many lambs are weaned and the total weight of lambs born.

The direction of the genetic correlations mostly coincided with the energy requirements of the ewes, and the stage of maturity of the ewes. Live weight change during mating period was most important for two year old ewes which were still growing to maturity and required energy during mating period to get pregnant. Live weight change during pregnancy was more important for three-year-old ewes which gave birth to and weaned more lambs and required more energy at the end of pregnancy and during lactation.

Therefore, optimised selection strategies on live weight changes to increase resilience will depend on the genetic correlations with reproduction, and are dependent on age.

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Appendix A. Comparing genetic correlations between live weight change and birth and wean weight traits with and without fixed effects for number lambs born and reared in current year and previous year. Correlations are for ages 2, 3 and 4 with standard errors in brackets. Correlations in bold are significantly larger than zero.

Weight change traits ²	Birth and wean weight traits ¹			
	TBW		TWW	
	Without	With	Without	With
Age 2				
ΔWTpreg	0.33 (0.17)	0.34 (0.17)	0.24 (0.20)	0.26 (0.20)
ΔWTlact	-0.15 (0.13)	-0.15 (0.13)	-0.10 (0.14)	-0.10 (0.14)
Age 3				
ΔWTpreg	0.21 (0.19)	0.27 (0.19)	0.16 (0.21)	0.15 (0.21)
ΔWTlact	-0.09 (0.16)	0.01 (0.17)	0.06 (0.18)	0.05 (0.19)
Age 4				
ΔWTpreg	-0.07 (0.22)	-0.07 (0.23)	-0.22 (0.21)	-0.21 (0.22)
ΔWTlact	-0.42 (0.20)	-0.33 (0.19)	0.00 (0.20)	0.05 (0.19)

¹Birth and wean weight traits: TBW = total weight of lambs born; TWW = total weight of lambs weaned.

²Weight change traits: ΔWTmate = change in live weight during mating for all ewes that were mated; ΔWTpreg = change in live weight during pregnancy for ewes that got pregnant; ΔWTlact = change in live weight lactation for ewes that reared lambs

Appendix B. Comparing genetic correlations between live weight change and number lambs born and weaned traits with and without fixed effects for number lambs born and reared in current year and previous year. Correlations are for ages 2, 3 and 4 with standard errors in brackets. Correlations in bold are significantly larger than zero.

Weight change traits ²	Number born and weaned traits ¹			
	NLB		NLW	
	Without	With	Without	With
Age 2				
ΔWTpreg	-0.34 (0.17)	-0.22 (0.19)	-0.49 (0.19)	-0.42 (0.19)
ΔWTlact	-0.08 (0.14)	-0.09 (0.14)	0.00 (0.16)	0.09 (0.16)
Age 3				
ΔWTpreg	0.15 (0.24)	0.25 (0.24)	0.53 (0.27)	0.53 (0.26)
ΔWTlact	-0.35 (0.18)	-0.32 (0.19)	-0.46 (0.20)	-0.37 (0.24)
Age 4				
ΔWTpreg	-0.15 (0.25)	-0.02 (0.27)	-0.21 (0.25)	-0.13 (0.26)
ΔWTlact	-0.21 (0.22)	0.06 (0.23)	-0.20 (0.22)	0.06 (0.22)

¹Number born and weaned traits: NLB = number of lambs born; NLW = total number of lambs weaned;

²Weight change traits: ΔWTmate = change in live weight during mating for all ewes that were mated; ΔWTpreg = change in live weight during pregnancy for ewes that got pregnant; ΔWTlact = change in live weight lactation for ewes that reared lambs

4

Varying pasture growth and commodity prices change the value of traits in sheep breeding objectives

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³ In this chapter alterations were made to the printed article changing the format of headings and tables to make it consistent with the rest of the thesis.

Abstract

Breeding programs for livestock require economic weights for traits that reflect the most profitable animal in a given production system. Economic weights are commonly based on average conditions. In pasture based livestock production systems the cost of feed is an important profit driver, but availability of feed from pasture can vary greatly within and between years. Additionally, the price of supplementary feed during periods of feed shortage and the prices for meat and wool vary between years. Varying prices and pasture growth can change the optimal management of the flock affecting profitability. This paper investigates how variation in commodity prices and pasture growth affect the economic values of traits in the breeding objective. We modelled a sheep farm with a self-replacing Merino flock bred for wool and meat in a Mediterranean environment. We optimised management decisions across 5 years using dynamic recursive analysis to maximise profit when commodity prices and pasture growth varied annually. Actual pasture growth and wool, meat, and grain prices from 2005-2009 were used. Management could adapt to varying pasture growth and commodity prices by changing sheep numbers, age structure of the flock and amount of grain fed to sheep. The economic value of seven traits in the breeding objective were compared for a scenario with average pasture growth and commodity prices over years and a scenario with varying pasture growth and commodity prices over years. Variation in pasture growth and commodity prices decreased average profit and increased the economic value of all breeding goal traits compared to the average scenario. The order of importance of traits stayed the same between varying and average scenarios but the relative importance of traits changed. The economic values that increased the most were for traits that had increased profit with the smallest impact on energy requirements such as yearling live weight, longevity and fibre diameter. Our results showed that it is important to account for variation in feed availability and commodity prices when determining the expected profit and economic values for traits. The results also suggest that whereas variation in pasture growth and commodity prices between years makes farming operations less profitable, these changing conditions increase the genetic variation in profitability of sheep. Therefore, genetic improvement has more value relative to scenarios where pasture feed supply and prices are constant.

Keywords: uncertainty, management, breeding, economic values

4.1 Introduction

Breeding programs for livestock require clearly defined breeding objectives that select the animals that are most profitable in a given production system. To calculate the economic value of changing traits in animals, changes in optimal management need to be accounted for before calculating the change in profit (Groen, 1989; Amer, 1994). Economic weights used to optimise selection on multiple traits can be derived from profit models of such systems and those models are usually based on average conditions (Byrne *et al.*, 2010; Conington *et al.*, 2004; Wolfova *et al.*, 2009). However, many livestock production systems have high levels of variability in pasture growth and commodity prices across years. For example, periods of drought in summer and autumn in Mediterranean climates require farmers to feed grain, which is more expensive than feeding pasture (Purser, 1981, p 181). Additionally, the length and severity of these drought periods varies between years (Thompson *et al.*, 1994; Kingwell, 2002; Kopke *et al.*, 2008). Farmers manage variation in pasture growth by altering the grain feeding and the number of sheep managed from year to year (Saul and Kearney, 2002; Young *et al.*, 2011b). Despite the influence on varying prices and pasture growth, little attention has been paid to how variation across years affects the importance of traits within breeding objectives.

Changes in management depend largely on the energy requirements of the flock, and since the energy requirements of sheep change when most traits in the breeding objective are altered, uncertainty in pasture growth and prices may also affect the economic value of traits in the breeding objective. These changes in energy are not always at the same time of the year. For example, energy requirements for reproduction peak around lambing time, whereas the energy requirements for wool growth are distributed evenly across the whole year and changing the diameter of wool fibres has no impact on energy requirements. Therefore, the economic values of traits may respond differently to varying pasture growth and commodity prices across years.

The effect of variation in commodity prices and pasture growth on breeding objectives can be simulated in bio-economic models that optimise management to adapt to such changes. Recursive dynamic models can be used to optimise farmer decisions in response to variation in commodity prices and pasture growth between years where the management of the current year depends on the optimal management of previous years (Mosnier *et al.*, 2009). Many models have investigated the impact of pasture (Olson and Mikesell, 1988; Kingwell *et al.*, 1993; Jacquet and Pluvillage, 1997; Kobayashi *et al.*, 2007) and price (Lambert, 1989;

Barbier and Bergeron, 1999; Lien and Hardaker, 2001; Ridier and Jacquet, 2002; Mosnier *et.al.*, 2009; Mosnier *et.al.*, 2011) uncertainty, providing insights into optimal management of farming systems under uncertainty. There are limited studies, however, into how variability in pasture growth and commodity prices across years affects the relative economic value of changing breeding goal traits.

In this study, we tested the hypothesis that accounting for the variation in pasture growth and meat, wool and grain prices across years changes the relative economic value of traits in the breeding goal. We also tested whether the change in profit due to variation across years was affected by how much energy requirements change when traits are changed.

4.2 Materials and methods

Testing the hypotheses that economic values of breeding goal traits are affected by variation in prices and pasture growth across years required three steps:

1. Model – model a sheep farm that can optimise farm profit across years for the purpose of calculating economic values for sheep.
2. Scenarios – define scenarios for different pasture growth and prices across years.
3. Economic values – calculate the economic values for each pasture growth and price scenario for individual years and across years. We calculated economic values for seven breeding goal traits: weaning weight, yearling weight, fleece weight, fibre diameter, longevity, and number of lambs weaned.

Model description

We modelled monthly production decisions for a sheep farm in an environment which experiences significant variation in pasture growth and wool, meat, and grain prices between years. The modelled farm had a self-replacing Merino sheep flock bred for wool and meat. The parameters of the farm and sheep represent a typical sheep enterprise in South Western Australia with one lambing per year in July and lambs weaned at 3 months old. There was no allowance for buying and selling of livestock additional to those bred on the farm. We based pasture growth on the Katanning region (33°41'S, 117°35'E, elevation 310m). Katanning is located in a Mediterranean climatic region with hot dry summers and mild wet winters. This combination of temperature and rainfall means that there is a period of no pasture growth during summer and autumn, typically extending from November to May each year.

Profit from wool and sheep sales was maximised for the sheep farm per hectare (ha) by optimising sheep sales and grain feeding based on pasture availability and prices of grain, wool and meat. We maximised profit per ha because pasture growth (pgr) per ha affects how many sheep can be managed on the farm and the number of sheep managed mostly determines farm profit (Warn *et al.*, 2006; Young *et al.*, 2011b). Therefore, we optimised management of sheep sales and grain feeding per ha using the General Algebraic Modelling System with the linear programming solver BDMLP (Brooke, Drud, and Meeraus linear program) Brooke *et al.*, (2013).

The optimisation included five groups of equations, profit (objective function), flock structure, pasture, energy requirements and intake. Profit depended on the number of sheep (via wool sales and variable costs), sheep sold and grain intake. The amount of pasture available affected how much pasture could be eaten by sheep which also affected how much was available in the next period. The number of sheep depended on energy requirements, potential intake, and the number of sheep sold. The amount of pasture and grain eaten was constrained by the potential intake of the sheep, whilst pasture and grain eaten had to match the energy requirements of the sheep. Figure 4.1 shows that all the relevant interactions between price, pasture growth, flock structure, energy requirements and intake were in the model, and how the variables and parameters interacted in the optimisation of profit.

The model optimised profit for five years using dynamic recursive programming to simulate the sequential decision-making of farmers based on changes in prices and pasture growth from year to year. The first year had the current prices and pasture growth whilst years 2-5 used average prices and pasture growth. This simulates a farm where decisions have to be made in the current year without knowledge of pasture growth or prices in the following years. Average pasture growth and prices are used as the best source of information to make decision in the current year, considering the long term profit of the farm. The profit from the first year was recorded and the optimised values from the first year used as the starting point for the next analysis, with new prices or pasture growth values for the first year of analysis. We used prices and pasture growth from years 2005-2009. The starting points for variables in the first optimisation step for 2005 were taken from the equilibrium from average prices and pasture growth. The optimised variables from the first analysis of 2005 was used as starting values for the first month of the first year to optimise management for 2006, again assuming the following four years had average prices and pasture growth. This was done until all years up until 2009 were optimised. Predictions for each year were optimal for the five year planning horizon and different to optimising years 2005-2009 together. This is because the

modelled farmer could adjust management based on anticipated sudden changes in prices and pasture growth across the 5 years.

It was assumed that ewes were kept up to an age of 78 months and litter size varied between 0 and 2 lambs. This resulted in 79 categories for age-months ($a = \{0,1,2,3,\dots,78\}$), 3 categories for litter size at birth ($b = \{0,1,2\}$), and litter size at weaning ($r = \{0,1,2\}$), and two categories for sex ($s = \{\text{wether (castrated male) or ewe (female)}\}$). Ewes were first mated at 20 months old. There were 6 categories for litter size at birth and litter size at weaning: 0 born and 0 weaned, 1 and 0, 1 and 1, 2 and 0, 2 and 1, and 2 and 2. In total there were $78 (\text{age}) \times 2 (\text{sex}) \times 6 (\text{litter size at birth and weaning}) = 936$ categories of sheep. Energy requirements and potential intake were calculated for the 936 categories, whilst grain and pasture intake, and sheep numbers were optimised for the 936 categories.

The parameters, variables and optimisation equations for prices and pasture were for years ($y = \{1,2,3,4,5\}$) and months ($m = \{1,2,3,\dots,12\}$). There were two types of pasture ($p = \{\text{green, dry}\}$). All parameters and variables were calculated for monthly periods. Parameters that varied within a month, such as foetus growth and milk production, were estimated daily and averaged over each month. Lupins and oats could be used as supplements in any month. These monthly categories were linked to the sheep age categories based on the age of each sheep in each month of the year, with lambs born in July.

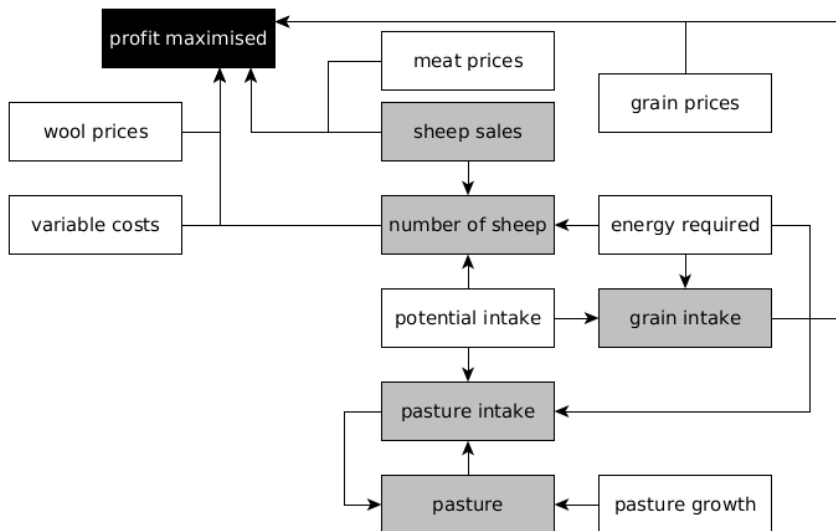


Figure 4.1 interactions between parameters (white boxes) and variables (grey boxes) and how they affect profit (black box).

Profit equation. The production system was optimised by maximising the net present value of profit over a five year period to simulate a farmer's long term decision horizon. The profit was the gross margin for each year ($GROSSMARGIN_y$) summed across the five years and discounted at 4% per year (Lence 2000). The gross margin was the income minus variable costs. To terminate the five years ($y = 5$ and $m = 12$) and ensure that all the sheep were not sold, we included the value of selling sheep for meat in the final month ($ENDVAL$), discounted for five years ($disc =$ discount rate). This allowed the five year period to be evaluated assuming that the farmer will continue farming after 5 years.

$$PROFIT = \sum_{y=0}^Y ((1-disc)^{y-1} \times GROSSMARGIN_y) + (1-disc)^Y \times ENDVAL$$

The gross margin in each year was income from meat and wool sales minus variable and grain costs. Meat sales were the product of number of sheep sold, live weight, price per kg carcass and carcass dressing percentage. Sheep sales were split into mutton (over 20 months old) and hoggets (less than 20 months old) with different prices for both classes. We assumed the minimum carcass weight that sheep can be sold was 16kg. Wool income was the product of number of sheep in November (shearing month), wool weight, and wool price minus shearing costs. Variable costs were the product of sheep number and variable costs per sheep. Variable costs included crutching, drenching, pregnancy scanning, fly control, and marking lambs including all additional labour associated with these activities (DAFWA 2005). Grain costs were a product of grain intake and grain prices. We assumed that labour costs for the farmer were constant and we did not consider fixed costs. We did not include costs for labour despite the high labour requirements for grain feeding sheep (Rose *et al.*, 2009) and assumed that farmers work longer hours in periods that require more grain feeding. Live weights, wool information and variable costs are in Additional Files 4.A and 4.B. The profit equation therefore included all the relevant incomes and costs to calculate the impact of varying prices and pasture growth on profit.

Flock equations. The flock equations were recursive functions that calculated the number of sheep based on deaths and sales. Number of sheep in each category for age, sex, birth and rear category ($NSHEEP_{a,s,b,r}$) for each month m of year y depended on the number of sheep ($NSHEEP_{a-1,s,b,r}$), survival ($surv_{a-1,s,b,r}$), and sheep sold ($SALES_{a-1,s,b,r}$) one month earlier.

$$NSHEEP_{a,s,b,r} = NSHEEP_{a-1,s,b,r} \times surv_{a-1,s,b,r} - SALES_{a-1,s,b,r}$$

We assumed that sheep died and were sold on the last day of the month. Survival was calculated for each age assuming that ewes had the same probability of surviving in each month. Survival rates are in Additional files 4.A, Table A4.4.

The number of lambs born in each sex and litter size at birth category was equal to the number of mated ewes in each birth category in July multiplied by the number of lambs in each category. The number of lambs weaned in each sex, litter size at birth and litter size at weaning was the number of mated ewes in each litter and birth category in October (weaning month) multiplied by the number of lambs in each category. The proportion of ewes in each litter size at birth and litter size at weaning category was deducted from Figure A4.3 in the additional files, with the proportion of ewes with 0, 1 and 2 lambs changing as the average number of lambs weaned changed. The birth and rear categories for a ewe in different years were assumed independent. New categories were made for each year.

Starting values for sheep numbers for $m = 1$ and $y = 1$ were taken from the equilibrium of optimal production for a year with average prices and pasture growth. This equilibrium was calculated by cycling through the flock function for one year. These starting numbers simulated a farmer that has had a series of average years and has adjusted stocking rate ready for another average year.

We constrained the model to sell all sheep before they reached 78 months old. Pregnant and lactating ewes could not be sold during pregnancy and lactation, from February to September. Non pregnant ewes could be sold in April after pregnancy scanning. This is a common practice for farmers that want to reduce stock numbers, particularly in years with low pasture growth. Ewe numbers could increase or decrease by adjusting the number of sheep sold either through culling of hogget ewes before first mating, selling of ewes during the year and selling ewes after their 5th parity. Changing the number of ewes sold affected the number of lambs born which subsequently affected the number of ewes that could be selected for the first mating two years later. So the cycling of sheep numbers made the flock structure dynamic through selling or retaining sheep for future years.

Sheep characteristics. The sheep were medium fibre diameter Merinos bred for wool and meat. A detailed description of the sheep is in Appendix A. The sheep had a mature body weight of 50kg. The weights of sheep from birth till 20 months of age depended on the sex and birth and rear category. Wethers grew faster than ewes, whilst lambs born into a higher litter size initially had lower growth rate until 12 months of age. Live weights were assumed the same by 20 months of age independent on litter size based on Thompson *et al.* (2011). Live weights of sheep above 20 months of age were assumed to be managed the same regardless of how

4 Varying pasture and breeding objectives

many lambs the ewes gave birth to or reared. These weights were based on Young *et al.*, (2011b). Average fibre diameter across all ages was 20.9 and average clean fleece weight was 3.35 kg. The diameter of wool increased with age and the weight of wool increased until 5 years old and then decreased as the ewes got older (Cloete *et al.*, 2003). The average number of lambs weaned per ewe mated across all age groups was 0.87. With increasing age of ewes, litter size increased with a maximum at their fourth mating and decreased thereafter (Cloete *et al.*, 2003). Mortality of ewes decreased with age until 5 years of age and then increased in the oldest age groups (Turner and Young, 1969). The characteristics of sheep at each age has implications for the optimum flock structure, with older ewes weaning more lambs and growing more wool but the diameter of the wool increases. Therefore, changes in the structure of flock age changed the income from the total flock.

Pasture equations. The pasture equations were recursive functions that calculated the amount of green and dry (p) pasture ($PASTURE_{y,m,p}$) in each month (m) of each year (y) based on proportion of pasture decay ($decay_{y,m-1,p}$), growth ($pgr_{y,m,p}$), intake ($PASTUREINT_{y,m,g}$) and proportion of trampling ($trample_{y,m,p}$).

$PASTURE_{y,m,p} =$

$$PASTURE_{y,m-1,p} \times (1 - decay_{y,m-1,p}) + 30.4(pgr_{y,m,p} - PASTUREINT_{y,m,g}(1 + trample_{y,m,p}))$$

The pasture intake variable for each sheep class was assigned to a month based on the age of each sheep in each class. For example, ages of sheep in the lambing month July were $a_{m=7} = \{0, 12, 24, 36, 48, 60, 72\}$. The pasture intake is the total intake for all sheep in each class. We fixed green pasture to 0 kg DM/ha in months when pasture did not grow ($pgr = 0$) and dry pasture to 0 kg DM/ha when pasture grew ($pgr > 0$) except for the first month of pasture growth. Additionally, in months when no pasture grew we fixed dry pasture greater or equal to 700 kgDM/ha. This lower limit prevented pasture being grazed too low which causes soil erosion (Moore *et al.* 2009). The assumptions for pasture are in Additional files 4.C. Therefore the pasture equations included the interactions between pasture intake and pasture available that could be used to optimise the number of sheep managed on the farm.

Energy equations. Energy equations made sure sheep from each age, sex, litter size at birth and litter size at weaning category consumed at least the energy they required. Energy was required for maintenance (main), live weight gain (growth), wool growth (wool), pregnancy (preg), and lactation (lact), whilst energy was

available for other functions from losing live weight (loss) ($e = \{\text{main, growth, wool, preg, lact, loss}\}$; $e = \text{main} + \text{growth} + \text{wool} + \text{preg} + \text{lact} - \text{loss}$). Live weight loss and gain were the difference between live weight in the following month and the current month. We assumed sheep gained or lost the same amount of weight on each day of the month, i.e. linear growth. The net energy required from pasture and grain was the total energy required (equations in Additional files 4.D) minus the energy available from losing live weight. All energy equations were from Freer *et al.* (1997) and Freer *et al.* (2007).

Sheep convert metabolisable energy into net energy with different efficiencies (equations in Additional files 4.E) depending on quality of the diet. Lupins and oats had higher digestibility than pasture, so the efficiency of using metabolisable energy from lupins and oats was higher. Therefore, we split the energy equation into two sets of equations. The first set of equations constrained the net energy provided by pasture (NEPASTURE_p) and grain (NEGRAIN_g) for each sex (s), age (a), birth (b) and rear (r) category and each energy type (e) to be more than the net energy (ne) minus net energy available from weight loss ($ne_{e-\text{loss}}$).

$$\text{NSHEEP}_{s,a,b,r} \times \left(\sum_e ne_{e,s,a,b,r} - ne_{e-\text{loss},s,a,b,r} \right) \leq \sum_e (\text{NEPASTURE}_{p,e,s,a,b,r} + \text{NEGRAIN}_{g,e,s,a,b,r})$$

We included number of sheep in this equation to calculate the total metabolisable energy eaten by all sheep in that class. The second set of energy equations calculated the optimum amount of pasture and grain that had to be eaten to match the metabolisable energy requirements. There were two equations for this step, one for pasture and one for grain.

$$\text{mepasture}_p \times \text{PASTUREINT}_{p,s,a,b,r} \geq \frac{\text{NEPASTURE}_{e,p,s,a,b,r}}{kp_{e,p}}$$

$$\text{megrain}_g \times \text{GRAININT}_{g,s,a,b,r} \geq \frac{\text{NEGRAIN}_{e,g,s,a,b,r}}{kg_{e,g}}$$

here mepasture_p is the metabolisable energy available in pasture (MJ/kg),

$kp_{e,g}$ was the efficiency of transferring net energy into metabolisable energy for each pasture type,

megrain_g is the metabolisable energy available in grain (MJ/kg),

$kg_{e,g}$ was the efficiency of transferring net energy into metabolisable energy for each grain type and

$\text{GRAININT}_{g,s,a,b,r}$ is the grain intake by each sex, age, birth and rear type.

These energy equations had an important link with the pasture equation through pasture intake. The equations also optimised grain feeding depending on energy requirements how much pasture can be eaten. Splitting the energy equation into

4 Varying pasture and breeding objectives

pasture and grain meant that the efficiency of transferring net energy into metabolisable energy for grain and pasture could be correctly allocated to the relevant intake type.

Intake equations. Sheep in each age, sex, litter size at birth and litter size at weaning had a maximum daily intake. This maximum had to be equal or less than total pasture and grain intake of each sheep. The digestibility and amount of pasture affected the maximum intake because poor quality pasture took longer to digest and low amounts of pasture were harder to graze. Therefore, the intake equation included parameters maximum intake (maxint), limit in intake due to digestibility (limdm) and limit in intake due to amount of pasture (limpasture) and variables pasture intake (PASTUREINT), grain intake (GRAININT) and number of sheep (NSHEEP). We included number of sheep to sum the total requirements of sheep in each category.

$$\frac{\text{PASTUREINT}_{s,a,b,r}}{\text{limdm} \times \text{limpasture}} + \text{GRAININT}_{s,a,b,r} \leq \text{maxint}_{s,a,b,r} \times \text{NSHEEP}_{s,a,b,r}$$

The limit in pasture intake due to digestibility and amount of pasture was different for green and dry pasture. The parameter limpasture depended on the variable PASTURE. In linear programming it is not possible to divide a variable (PASTUREINT) by another variable (PASTURE), which would require non-linear programming. Therefore, we calculated limpasture by estimating amount of pasture without the variables PASTUREINT and NSHEEP, as if no pasture was eaten. Equations for intake are in Additional files 4.F.

Scenarios

We optimised profit for two scenarios: average pasture growth and average prices and varying pasture growth and varying prices. These pasture growth and prices were from 2005-2009 (Figure 4.2). We selected these years because they had typical pasture growth and prices. Pasture growth was very high in 2005 and very low in 2006, grain prices were low in 2005 and high in 2007 and 2008, wool prices were low in 2005 and high in 2007, and meat prices were very high in 2009. Average pasture growth and prices were monthly averages across the five years and are at the right of Figure 4.2. We included monthly averages to keep the seasonality of pasture growth and prices. We fixed wool prices to the prices of wool in November, when the sheep were shorn.

Pasture growth was estimated from “Pastures from Space” (Hill *et al.*, 1999) recorded at Katanning Western Australia (www.pasturesfromspace.csiro.au). Wool prices were taken from the Western region micron price guide from the Wool Desk,

Department of Agriculture and Food WA and Australian Wool Exchange (DAFWA, 2009). Meat prices were hogget and mutton prices from Meat and Livestock Australia's National Livestock Reporting Service (MLA, 2009). Grain prices were based on Co-operative Bulk Handling (CBH, 2009).

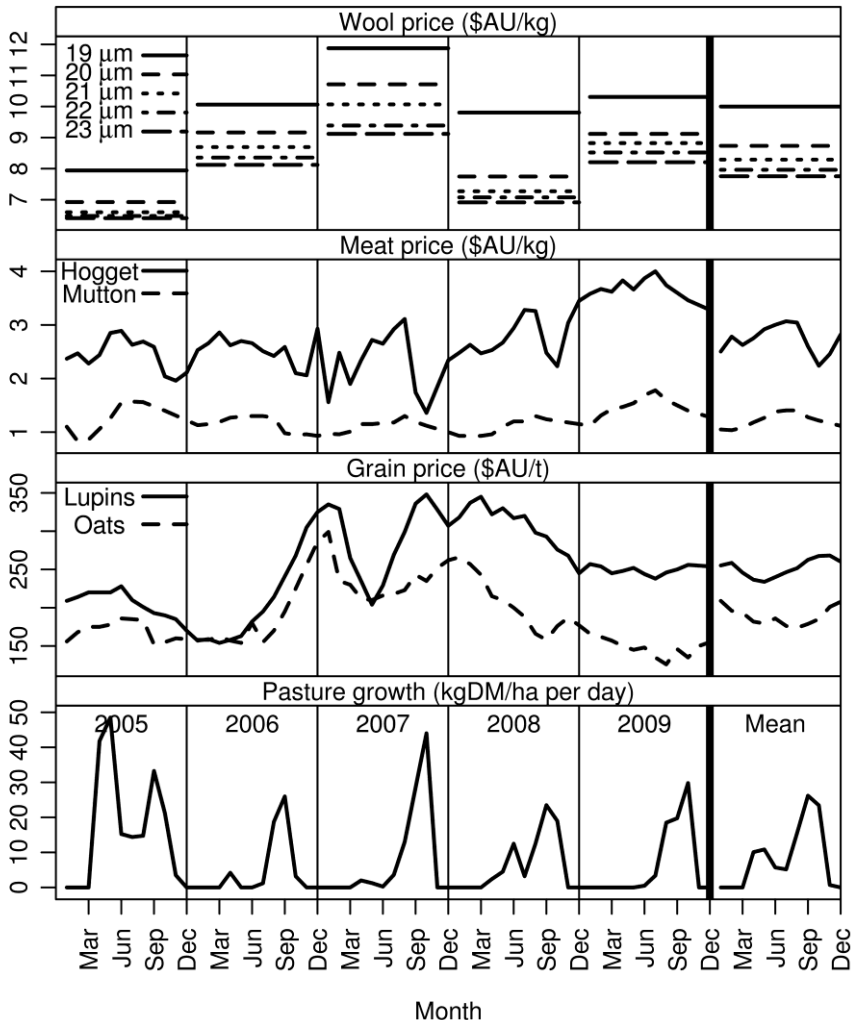


Figure 4.2 Prices for wool, meat and grain, and pasture growth for the 5 years used. The average is the average price for the total period and the average pasture is the average for each month.

Economic values

Breeding programs aim to increase profit per animal by genetic improvement of traits that affect profit. Therefore, running a breeding program starts with specifying the traits affecting profit and quantifying the economic values for each trait, i.e. the change in profit when the trait is genetically improved by one unit keeping all other traits constant. All other traits are kept constant to avoid double counting the value of changing traits when the economic values are used in a breeding index. Mathematically, the breeding goal can be represented as a linear equation in which breeding values for each trait are multiplied with economic values (Hazel, 1943). We calculated the economic value for 7 traits: weaning live weight, yearling live weight, adult live weight, adult fleece weight, adult fibre diameter, adult longevity, and number of lambs weaned (Table 4.1). We chose these traits because they are used in various industry indexes in Australia.

We calculated economic values by increasing each trait by one genetic standard deviation (Table 4.1) because a genetic standard deviation is a measure of how easy it is to select for each trait and makes economic values more comparable between traits. For adult live weight we increased all live weights and the standard reference weight of sheep above 20 months. A change in weaning or yearling live weight implied an alteration of the growth curve from birth to 20 months of age depending on the age of the live weight measurement (Additional files 4.A, Figure A4.2). The economic value of longevity was estimated by altering the probability of surviving each year (surv). For example, changing the survival from age 20 months to 70 months from 0.85 to 0.90 is equivalent to adding an extra 115 productive days. The economic value for longevity was then calculated by multiplying the associated change in profit by a factor $304/115$, where 304 is the value (in days) of one genetic standard deviation for longevity. This procedure is similar to Fuerst-Waltl and Baumung (2009). The economic value for fibre diameter is the value of decreasing the diameter of wool. We decreased fibre diameter because finer wool is more profitable than broad wool. The value of increasing number of lambs weaned was calculated from the change in proportion of ewes with 0, 1, and 2 lambs born and weaned. We calculated economic values per ha and expressed them as economic values per ewe. We calculated the economic values per ha because the farm area is the main limitation of production. We presented the economic values per sheep (\$AU/genetic standard deviation) because in selection index theory, it is easier to interpret the economic values as the extra value obtained per ewe mating.

Table 4.1 Definition of traits with genetic standard deviations (σ_g) and the equations each trait affects.

Variable	Unit	σ_g	Flock	Energy	Intake
weaning weight	kg	3.6 ¹		✓	✓
yearling weight	kg	3.4 ¹		✓	✓
adult live weight	kg	3.56 ¹		✓	✓
fleece weight	kg	0.36 ¹		✓	
fibre diameter	µm	0.95 ¹			
longevity	days	304 ^{3,4}	✓		
lambs weaned	lambs	0.124 ²	✓	✓	

¹Huisman et al. (2008)

²Cloete et al. (2004)

³Fuerst-Waltl and Baumung (2009)

⁴changing reducing death% by 1% in adult ewes was equivalent to 115 extra days of productive life. Therefore, the economic values for longevity were scaled by 304/115

Economic values were calculated by maximising profit after traits were increased by one genetic standard deviation (Table 4.1) and subtracting the maximised profit using mean trait values. The economic value per ha was the profit optimised with the average genotype subtracted from the re-optimised profit after changing the trait. We then divided the economic value per ha by the number of ewes mated to calculate the economic value per sheep. We also calculated the economic value for each trait relative to the economic value of number of lambs weaned. This indicates the relative importance of each trait.

With changes in trait mean due to genetic change, the optimal management changes for the scenario with average prices and pasture growth. Therefore we calculated new equilibrium values for the number of sheep and pasture with average prices and pasture growth after each trait was changed. These equilibrium values were used as the starting values for $y=1$ and $m=1$ when analysed with prices and pasture growth varying.

Table 4.2 Variables green and dry pasture, lupins and oats fed and number of wether and ewe sheep from average pasture growth, prices and genotype. Totals are bold.

Variable	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
pasture (kgDM/ha)												
Green	-	-	-	306	384	296	296	534	1108	1490	1047	-
Dry	904	795	700	-	-	-	-	-	-	-	-	1027
grain (kg/month)												
lupins	145	55	73	5	0	30	0	0	1	0	1	132
oats	18	0	0	0	0	0	0	0	0	0	0	14
total	163	55	73	5	0	30	0	0	1	0	1	146
number for each age class in months for ewes (ewes/ha)												
0-5	-	-	-	-	-	-	3.00	3.00	2.42	2.42	2.4	2.38
6-17	2.37	2.35	2.33	2.31	2.29	1.26	1.25	1.25	1.24	1.24	1.23	1.23
18-29	1.22	1.21	1.21	1.2	1.2	1.19	1.19	1.19	1.18	1.18	1.17	1.17
30-41	1.17	1.16	1.16	1.16	1.15	1.15	1.15	1.14	1.14	1.14	1.13	1.13
42-53	1.13	1.12	1.12	1.12	1.12	1.11	1.11	1.11	1.1	1.1	1.1	1.1
54-65	1.1	1.09	1.09	1.09	1.09	1.08	1.08	1.08	1.08	1.07	1.07	1.07
66-77	1.07	1.06	1.06	1.06	1.06	1.05	1.05	0.9	0.9	0.89	0.89	0
number for each age class (wethers/ha)												
1-6	-	-	-	-	-	-	3	3	2.42	2.42	2.4	2.38
7-18	2.37	2.35	2.33	2.31	2.29	2.28	1.09	0.92	0	0	0	0
total¹	10.43	10.34	10.3	10.25	10.2	9.12	13.92	13.59	11.48	11.46	11.39	10.46

¹total for wethers and ewes

4.3 Results

Average scenario

For the average scenario with no fluctuations in prices or pasture growth across years, pasture started growing in April and peaked in October at 1407 kg DM/ha (Table 4.2). After the pasture dried off in December, the amount of pasture decreased until April and the amount of grain fed was highest during these months. Almost no grain was fed from July to October.

The number of sheep was highest in July when the lambs were born. The drop in sheep numbers in the 0-5 month old category from August to September was from lamb deaths between birth and weaning. The drop in ewes in the 6-17 month old category from May to June was from culling hogget ewes. The drop in ewes in the 66-77 month old category was from selling ewes that did not give birth to any lambs. All ewes were sold by 76 months old. Most of the wether hoggets were sold at the end of May when they were 11 months old with the remainder sold when they were 14 months old in August. These hoggets were sold in August because they were born and reared in a litter size of 2 and grew slower.

Comparing average scenario to varying pasture and price

Varying pasture growth and prices decreased the average profit from 2005-2009 by 12% compared to the average scenario (Table 4.3). Profit decreased because grain costs increased by 40% compared to the average scenario. This increase in grain feeding was partly attributed to an 11% increase in ewes mated. This increase in ewes mated increased hogget income by 9%, mutton income by 16% and wool income by 10% compared to the average scenario, but this was not enough to offset the higher grain costs. The decrease in average profit across the five years was due mostly to large decreases in profit in 2005, 2006, and 2008, which were not offset by the large increase in profit in 2009.

In 2005 profit decreased by 26% compared to the average scenario because of low wool prices and low grain prices. Additionally, high mutton prices meant no ewe hoggets were sold in 2005 because it was optimal to sell 5 year old ewes and retain extra hogget ewes to be mated in 2006. More ewes were mated in 2006 because high pasture growth reduced grain requirements for managing a high number of ewes into 2006, which was anticipated to be an average year. The increase in ewes mated in 2006, in combination with low pasture growth and high grain prices at the end of 2006, decreased profit by 70% compared to the average scenario. Additionally the number of ewes mated in 2007 decreased because high grain prices and low pasture growth towards the end of the year made it unprofitable to

carry high ewe numbers into 2007. Carrying over more ewes from 2005 to 2006 in anticipation of an average year was the main cause of the profit decrease in 2006 and made the farm vulnerable to a poor year like 2006, where pasture growth was low and grain prices were high. High wool prices in 2007 offset the low pasture growth at the end of 2007 and profit increased by 2% compared to the average scenario. High pasture growth and high wool prices meant it was optimal to increase the number of ewes mated in 2008 because it was cheap to maintain the ewes and shear them at the end of 2007. High grain prices, lower than average pasture growth and more ewes mated in 2008 decreased profit by 33% compared to the average scenario. In response to these high grain prices and high meat prices at the end of 2008 more adult ewes were sold decreasing the number of ewes mated in 2009. High meat prices in 2009, high pasture growth at the end of 2009 and an increase in lambs born in 2008 increased profit by 69% in 2009 compared to the average scenario.

In summary, profit was lower with varying prices and pasture growth mainly due to changes in management in reaction to changes in pasture growth and prices. These changes in management, in particular, changing the number of ewes mated, made farm profit vulnerable to unfavourable changes in pasture growth and commodity prices. Additionally, positive deviations of prices and pasture growth did not compensate the impacts of their negative variations.

Comparing economic values between average and varying scenarios

The economic value for lambs weaned had the highest economic value per head per genetic standard deviation for both average and varying scenarios (Table 4.4). The order of importance of the other traits was fleece weight, fibre diameter, longevity, yearling weight, weaning weight and adult weight. This order did not change between the average and varying scenarios. Additionally, the economic values were all higher per mated ewe for the varying scenario compared to the average scenario. Although the order of importance of traits did not change, the relative contribution of each trait changed. Yearling weight increased the most when pasture growth and commodity prices were varied, followed by longevity, fibre diameter, lambs weaned and fleece weight. Weaning weight increased from a small negative to a small positive economic value whereas adult live weight became slightly less negative.

Table 4.3 Profit, ewes mated, sheep sales, age of ewes (months), lambs weaned, hogget, mutton, and wool income and grain costs for 2005-2010 for average, varying prices and varying pasture scenarios.

Variable	Scenario	Year					Mean
		2005	2006	2007	2008	2009	
profit (\$AU/ha)	Average	184	184	184	184	184	184
	Varying	136	55.9	188	123	311	162
ewes mated (ewes/ha)	Average	5.27	5.27	5.27	5.27	5.27	5.27
	Varying	5.27	6.18	5.71	6.34	5.72	5.84
ewe hoggets sold /ha	Average	0.95	0.95	0.95	0.95	0.95	0.95
	Varying	0.00	1.06	0.74	1.17	1.49	0.89
wether hoggets sold /ha	Average	2.10	2.10	2.10	2.10	2.10	2.10
	Varying	2.10	2.10	2.38	2.27	2.52	2.23
adult ewes sold /ha	Average	0.97	0.97	0.97	0.97	0.97	0.97
	Varying	1.06	1.30	0.79	1.51	0.94	1.12
average age of ewes	Average	32.2	32.2	32.2	32.2	32.2	32.2
	Varying	31.2	29.4	30.4	29.9	31.7	30.5
hogget income (\$AU/ha)	Average	151	151	151	151	151	151
	Varying	99	136	147	188	254	164
mutton income (\$AU/ha)	Average	23.7	23.7	23.7	23.7	23.7	23.7
	Varying	25.6	32.8	16.8	36.5	25.3	27.4
wool income (\$AU/ha)	Average	201	201	201	201	201	201
	Varying	151	210	310	182	254	221
grain costs (\$AU/ha)	Average	136	136	136	136	136	136
	Varying	85	262	224	220	160	190

The economic values were higher when prices and pastures varied because optimisation caused changes of trait means to have more effect on profit when prices varied. This resulted in higher economic values for the varying scenario than the average scenario, even though the profit per ha was lower (Appendix A). When prices and pasture growth were average, it was optimal to manage high stocking rates because there was no consequence in following years. Therefore, the number of ewes mated increased more for each trait for the average scenario compared to the varying scenario. For the varying scenario, stocking rate was re-optimised each year based on the new pasture growth and prices. These adjustments could either capitalise on favourable prices or avoid high costs (see Appendix B). That is why the grain costs increased more for the average scenario when traits changed compared to the varying scenario. Therefore, it can be concluded that varying prices and pasture growth changed economic values substantially.

The economic value of traits was different between the average and varying scenario depending on how much each trait changed the energy requirements of the sheep. For example, increasing the productive life of ewes did not increase the energy requirements but changed the flock structure which increased the number of lambs weaned, the number of ewes shorn and the number of ewes sold at the end of their productive life. Decreasing fibre diameter improved the quality of wool without requiring extra energy. Increasing the number of lambs weaned increased the energy requirements of ewes, but it was optimal to manage fewer ewes, decreasing maintenance costs and increasing hogget income. Alternatively, increasing clean fleece weight and adult live weight increased energy costs for the whole year, making the farm relatively more vulnerable to variation in pasture growth compared to other traits, which meant its economic value did not increase as much as other traits. Weaning weight increased energy requirements for a short period only on a small proportion of the flock so it did not decrease profit as much as adult live weight. Increasing weaning weight did not coincide with sale time and had a low not impact on hogget income. The increase in live weight for yearling live weight is expressed as increased income from selling heavier hoggets. Yearling live weight had the biggest increase in value when pasture growth and commodity prices varied because more income from selling hoggets was not offset by the increase in energy requirements, which increased on a relative small proportion of the flock.

Table 4.4 Comparing economic values (\$AU per ewe mated per genetic standard deviation), economic values relative to number of lambs weaned, and ewes mated for each trait for the average and varying scenario.

Variable	Trait	Mean	Varying	Change
Economic value	Lambs weaned	2.61	4.84	2.23
	Fleece weight	2.33	3.59	1.26
	Fibre diameter	1.77	3.46	1.69
	Longevity	1.06	3.11	2.04
	Yearling weight	0.59	1.86	1.28
	Weaning weight	-0.01	0.1	0.11
	Adult weight	-0.35	-0.25	0.11
Economic value relative to lambs weaned	Lambs weaned	1	1	0
	Fleece weight	0.89	0.74	-0.15
	Fibre diameter	0.68	0.71	0.04
	Longevity	0.41	0.64	0.23
	Yearling weight	0.23	0.39	0.16
	Weaning weight	0	0.02	0.03
	Adult weight	-0.14	-0.05	0.08
Ewes mated/ha	Lambs weaned	5.36	5.37	0.01
	Fleece weight	5.59	6.08	0.49
	Fibre diameter	5.66	6.07	0.41
	Longevity	5.64	6.05	0.41
	Yearling weight	5.44	5.9	0.46
	Weaning weight	5.3	5.88	0.58
	Adult weight	5.1	5.66	0.56

4.4 Discussion

The economic values of wool, carcass and reproduction traits in the breeding objective of a self-replacing Merino flock increased when commodity prices and pasture growth varied between years. The relative importance of each trait also changed, with longevity and yearling weight becoming more important when commodity prices and pasture growth varied. These changes in traits were caused by differences in management between average scenarios and scenarios where pasture growth and prices varied. When pasture growth and prices varied, profit decreased compared to the average scenario because optimum management of the flock in previous years was not optimal when new prices and pasture growth were introduced. This decrease in profit between the average and varying scenario created more potential to improve profit when traits changed. Additionally, when prices and pasture growth favoured a particular trait, management could be

optimised in that year. Therefore, we accepted our hypothesis that accounting for uncertainty in pasture growth and commodity prices across years changes the economic value of breeding goal traits.

Our model is, to our knowledge, the first analysis of the effects of fluctuations in prices and feed availability on the economic values of breeding goal traits. We showed how breeding goals should be adapted to a production system with uncertain pasture growth and prices. For example, breeding goals for wool should aim less at production volume, such as fleece weight, but more on quality traits, such as fibre diameter. This is an important result because previous breeding programs have put high emphasis on fleece weight (Taylor and Atkins, 1997) and our results suggest that fleece weight has less importance.

The estimation of economic values using dynamic programming to optimise management across years when future pasture growth and prices are unknown captured the effects of pasture and price uncertainty. Optimising management in each year meant that management could be adapted based on current pasture growth and prices. This had both advantages and disadvantages for the economic value of traits. For example, when wool price was high, more ewes could be carried over to the next year to increase the amount of wool sold. This management option, however, was disadvantageous when pasture growth or wool price was low, or grain prices were high, in the following year, particularly if energy requirements increased when traits changed. Therefore, traits that caused bigger changes in management in favourable years, in particular, increasing sheep numbers, made the farming system more vulnerable to variation in pasture growth and prices. This vulnerability was further increased when changing traits increased energy requirements. Therefore, it is important to account for variation across years when calculating economic values for breeding goal traits.

We used historic pasture growth and prices similar to Kulak *et al.* (2003) which indicate variation in those specific years. Animal breeding should anticipate future prices and pasture growth which is difficult, although the mean and variation of historic pasture growth and prices give a good guideline for which parameters vary the most. Annual pasture growth and the distribution of pasture growth across the year are expected to become more variable and harder to predict due to changes in the climate (IPCC, 2007). Future research could include more variation in pasture growth to investigate how economic values are affected by extreme variation in pasture growth across years.

It was optimal to manage more ewes when prices and pasture varied compared to the average scenario. Australian farmers generally reduce sheep numbers to avoid having too many sheep in years with low pasture growth or low prices (Austen *et*

et al., 2002; Robertson and Wimalasuriya, 2004). Many studies have shown that climate variability decreases the number of livestock managed per unit of land (Olson and Mikesell, 1988; Kingwell *et al.*, 1993; Kobayashi *et al.*, 2007). Kobayashi *et al.* (2007) found that several drought years are required to significantly reduce stocking rate. We used average pasture growth as the estimate of future pasture growth, whilst most years pasture growth was below average. Therefore, maintaining or increase sheep numbers in years with high pasture growth was not optimal when the following year had below average pasture growth. The actual optimal number of sheep across all years may be lower than estimated in our study. If we had optimised sheep numbers across all years of pasture growth, then the traits that made the farming system more vulnerable to changes in pasture growth would potentially have more value, and differences between scenarios would be less obvious. We believe, however, that we represented the paradox that farmers experience every year when deciding how many ewes to mate when the years events are unknown, and the temptation to manage more sheep in years when pasture growth is favourable.

Uncertain pasture growth and prices make it difficult for farmers to anticipate conditions in the following year. We assumed farmers use average pasture growth and prices to guide their decisions for the future. Farmers' decisions, however, may not be based on average years and could be affected by the current years pasture growth and prices. Mosnier *et al.* (2009), for example, included current anticipation for future prices, with a weighting for future prices based on the current years prices. This anticipation for future prices may be beneficial for the start of the following year, however, the price information we used had large variation in prices within years. Therefore, modelling farmers anticipation for future pasture growth and prices is difficult, particularly when this anticipation may be different depending on each farmer's experiences in previous seasons. Despite these differences in anticipation, using average pasture growth and prices still captures the uncertainty of managing sheep because management decision based on pasture growth can not be made until pasture starts growing in Autumn and early winter.

Our results show that longevity, fibre diameter and yearling weight would be undervalued if varying prices and pasture growth were not considered. Changes in the relative importance of traits will affect the expected response of the traits resulting from the breeding program. Previous research on economic values has shown that reproduction and weaning weight are important for meat flocks (Conington *et al.*, 2004; Wolfova *et al.*, 2009; Byrne *et al.*, 2010). This is in agreement with our results. In addition our results show that for a mixed meat and

wool breeding program, wool, and survival traits are also important. Our results can be used as a guideline for how to manage a sheep flock when pasture growth and prices are uncertain. Therefore, our model is a valuable tool to support management and breeding decisions for farms in environments with uncertain pasture growth and prices.

Conclusions

Our study gives a comprehensive description of how management and breeding goals for a sheep farm change when prices and pasture growth vary across years. Varying prices and pasture growth decreased average profit but increased the economic value of all breeding goal traits compared to a scenario with no variation. The economic values increased most for traits that had increases in profit for a small increase in energy requirements such as yearling live weight, longevity and wool quality. This suggests that traits that make production systems less vulnerable to changes in pasture and prices are those that increase profit with small changes in energy requirements. Our results show that varying pasture growth and prices across years should be considered when estimating the economic value of breeding goal traits.

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Appendix A. Profit, Hogget income, mutton income, wool income, and grain costs for each trait in each year for the varying pasture growth and prices and average pasture growth and prices scenarios.

Variable	Trait	Varying						Average
		Years					Mean	
		2005	2006	2007	2008	2009		
profit (\$AU/ha)	Weaning weight	96.9	101	190	119	309	163	184
	Yearling weight	141	71.5	208	130	318	173	187
	Adult weight	97.1	99	180	121	310	161	182
	Fleece weight	155	73.6	225	130	339	184	198
	Fibre diameter	152	76.7	229	133	327	183	194
	Longevity	148	74.3	222	144	319	181	190
	Lambs weaned	191	85	210	159	297	188	198
hogget Income (\$AU/ha)	Weaning weight	62.2	188	148	187	255	168	150
	Yearling weight	108	153	184	203	273	184	167
	Adult weight	59.5	181	138	182	248	162	147
	Fleece weight	105	149	159	199	262	175	159
	Fibre diameter	106	154	166	196	257	176	162
	Longevity	108	157	174	198	265	180	167
	Lambs weaned	164	159	196	195	260	195	188
mutton income (\$AU/ha)	Weaning weight	25.8	33.1	16.9	36.4	23.5	27.1	23.9
	Yearling weight	26.4	33.9	17.4	36.6	26.1	28.1	24.5
	Adult weight	26.6	34.2	17.5	39.3	27.2	29.0	24.6
	Fleece weight	27.2	34.1	18.2	39.3	28.1	29.4	24.8
	Fibre diameter	27.5	36.8	18	36.4	30.5	29.8	25.5
	Longevity	28.2	40.6	18.4	39.1	29.2	31.1	26.2
	Lambs weaned	20.5	51	15.4	40.6	15.8	28.7	27.4
wool Income (\$AU/ha)	Weaning weight	152	211	311	183	255	222	203
	Yearling weight	156	216	317	180	246	223	208
	Adult weight	146	202	299	175	247	214	195
	Fleece weight	173	241	350	203	277	249	231
	Fibre diameter	170	234	344	195	265	242	227
	Longevity	163	224	330	182	254	231	217
	Lambs weaned	163	203	288	171	230	211	211
grain costs (\$AU/ha)	Weaning weight	87.5	270	224	223	162	193	137
	Yearling weight	92.4	269	249	227	167	201	155
	Adult weight	81.7	259	216	213	153	185	131
	Fleece weight	91.4	285	239	246	165	205	159
	Fibre diameter	92	282	236	229	163	200	160
	Longevity	92.1	282	236	210	167	197	160
	Lambs weaned	94.2	263	227	186	149	184	166

4 Varying pasture and breeding objectives

Appendix B. Economic values and ewes mated for each trait for each year for varying pasture growth and prices scenario.

Variable	Trait	Year					Mean
		2005	2006	2007	2008	2009	
Economic value (\$AU/ha)	Weaning weight	-38.6	44.8	1.7	-3.1	-1.6	0.6
	Yearling weight	5.8	15.7	19.3	7.2	7.1	11.0
	Adult weight	-38.4	43.2	-8.9	-2.0	-0.9	-1.4
	Fleece weight	19.7	17.7	36.4	7.1	28.0	21.8
	Fibre diameter	16.6	20.8	40.3	10.8	16.6	21.0
	Longevity	12.0	18.5	33.5	21.8	8.4	18.8
	Lambs weaned	55.7	29.1	21.9	36.3	-13.2	26.0
Ewes mated/ha	Weaning weight	5.3	6.22	5.74	6.36	5.76	5.88
	Yearling weight	5.44	6.38	5.81	6.23	5.62	5.9
	Adult weight	5.1	5.98	5.5	6.2	5.52	5.66
	Fleece weight	5.59	6.56	5.95	6.53	5.76	6.08
	Fibre diameter	5.66	6.64	5.88	6.39	5.77	6.07
	Longevity	5.64	6.69	5.85	6.37	5.71	6.05
	Lambs weaned	5.36	5.92	5.09	5.55	4.91	5.37

Additional files Chapter 4

Additional files 4.A – sheep parameters

Live weight We assumed that adult females were managed to have the same live weight regardless of their litter size at birth and litter size at weaning. The adult live weights are the live weights recommended for sheep farmers managing sheep in Mediterranean climate zones of Australia (Figure A4.1) (Young *et al.*, 2011b). Live weight in sheep younger than 20 months old depended on the sex, age and litter size which they were born and raised in (Figure A4.2). All sheep of the same sex weighed the same at 20 months old, the age of first mating for females. We made sheep the same weight based on results from Thompson *et al.* (2011).

Monthly live weight change ($\Delta\text{liveweight}_a$) at each age was the difference between live weight in the next month (liveweight_{a+1}) and live weight in the current month (liveweight_a)

$$\Delta\text{liveweight}_a = \text{liveweight}_{a+1} - \text{liveweight}_a$$

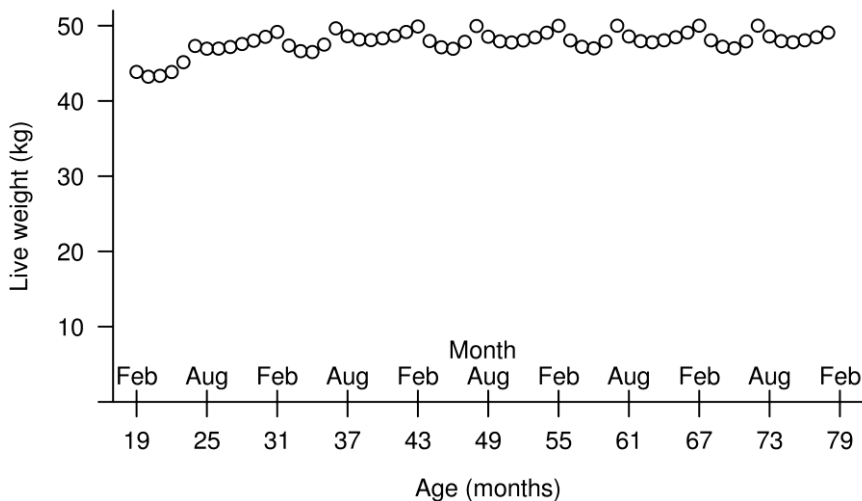


Figure A4.1 live weight of female sheep from 20 months til 80 months old with the month that each age corresponds to. These live weights are the same for all litter size at birth and litter size at weaning categories.

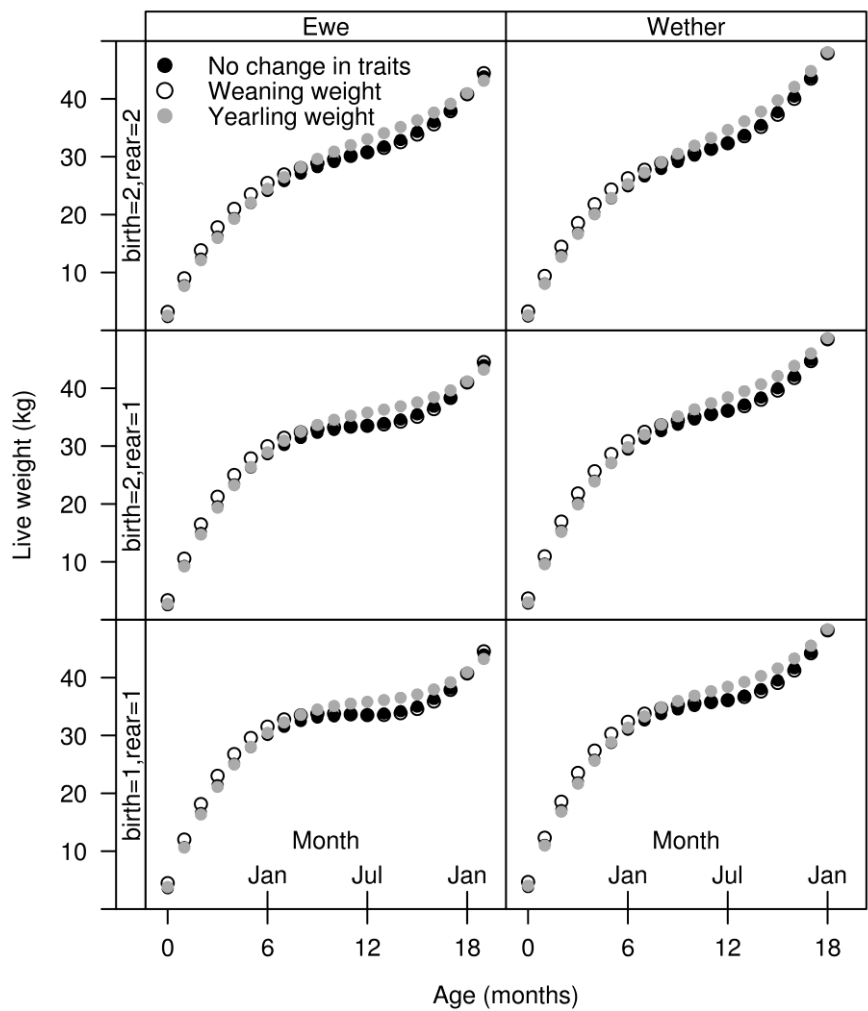


Figure A4.2 weight of young sheep depending on how they were born and raised and the alterations for calculating economic values for weaning weight and yearling weight.

Wool parameters Wool weight of all age groups was based on Cloete *et al.* (2003). The diameter of wool increased as ewes got older and wool weight increased till four years old and then decreased (Table A4.1). The proportion of wool grown in each month was seasonal and based on Adams and Briegel (1998) (Table A4.2).

Table A4.1 Parameters for each age group of the females for wool, number of lambs weaned and deaths at each yearly age group.

Wool parameter	Age (months)						
	0-11	12-23	24-35	36-47	48-51	52-63	64-71
wool weight (kg/sheep)	2.0	3.0	3.54	3.72	3.78	3.74	3.67
fibre diameter(μm)	19	20	20.5	21.0	21.5	22.0	22.5

Table A4.2 Proportion of wool grown in each month.

Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
11	9	8	6	5	5	6	8	9	10	10	11

Reproduction Ewes weaned on average more lambs as they got older until their last parity when number of lambs weaned decreases (Table A4.3) (Cloete *et al.*, 2003). The number of ewes in each of the 6 birth and wean categories was estimated from the reproduction of 8 information nucleus flocks (Sheep CRC) from Australia over 3 years. We fitted curves to these points and estimated the number of sheep in the 6 litter size at birth and litter size at weaning category (Figure A4.3).

Table A4.3 proportion of females in each litter size at birth and litter size at weaning categories at each lambing age for the average genotype.

lambing age	NLW	litter size birth	litter size weaning		
			0	1	2
20-31	0.65	0	0.31	NV	NV
		1	0.10	0.41	NV
		2	0.04	0.05	0.10
32-43	0.86	0	0.19	NV	NV
		1	0.08	0.47	NV
		2	0.03	0.06	0.16
44-55	0.97	0	0.16	NV	NV
		1	0.07	0.45	NV
		2	0.03	0.08	0.22
56-67	0.98	0	0.15	NV	NV
		1	0.07	0.45	NV
		2	0.03	0.08	0.23
68-79	0.90	0	0.18	NV	NV
		1	0.08	0.47	NV
		2	0.03	0.07	0.18

NV means no value.

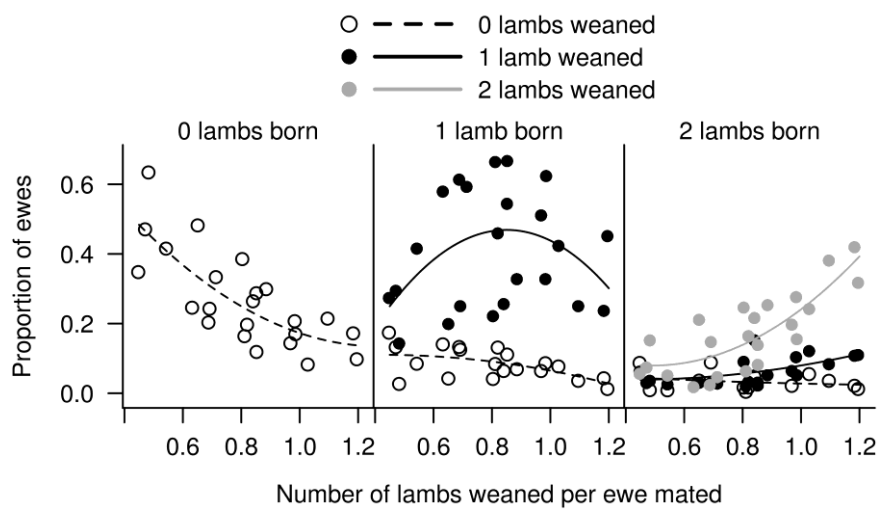


Figure A4.3. The proportion of ewes that give birth to and wean lambs based the average number of lambs weaned per ewe mated. The dots are the values recorded in the information nucleus flocks and the lines are the predicted values used in the model.

Flock The survival rates of ewes at each age based on Turner and Young (1969) p 235 are in Table A4.4.

Table A4.4 The survival rates of each age group.

Age (months)	0-11	12-23	24-35	36-47	48-51	52-63	64-71
surv	0.960	0.965	0.924	0.926	0.850	0.790	0.760

Additional files 4.B – variable costs

Variable costs are in Table A4.5.

Table A4.5 Variable costs for sheep at each age (\$AU)

Age (months)	Crutching	Health	Marking
1	0	0	3
8	1	3	0
20	1	3	0
32	1	3	0
44	1	3	0
56	1	3	0
68	1	3	0
80	1	3	0

Additional files 4.C – pasture

The dry matter digestibility (dmd) of dry and green pasture was estimated from Schut *et al.* (2010) (Table A4.6).

Table A4.6 green pasture information each month.

month	dmd%	clover%	decay%
January	75	40	3
February	75	40	3
March	75	23	3
April	75	20	4
May	75	20	5
June	75	18	6
July	75	25	7
August	75	37	8
September	75	43	9
October	75	47	10
November	64	42	12
December	52	42	12

The metabolisable energy from green and dry pasture (mepast) included dry matter digestibility (dmd).

$$\text{mepast} = 0.172 \times (\text{dmd}/100) - 1.707$$

(Freer *et al.*, 2007, p 9)

The limit in pasture intake (limdm) due to dry matter digestibility included dry matter digestibility and clover.

$$\text{limdm} = \min(1, 1 - 1.7 \times (0.8 - \text{dmd}) + 0.17 \times (\text{clover}/100))$$

(Freer *et al.*, 2007, p 220)

The limit in pasture intake due to the amount of pasture (limpasture) included the estimate of pasture available based on the pasture equation excluding pasture intake and sheep number (pasture).

$$\text{limpasture} = \max(0.1, (1 - \exp(-1.4(\text{pasture}/1000))) \times (1 + 0.6 \times \exp(-1.4(\text{pasture}/1000)^2)))$$

Additional files 4.D – Net energy requirements

The net energy requirements (netenergy) were used in the energy equation. The following equations were used to calculate net energy requirements before being divided by the efficiency of converting maintenance energy into net energy. Net energy requirements for maintenance included live weight and standard reference weight (SRW). Additionally, 9% of total metabolisable energy requirements was included in metabolisable energy requirements for maintenance.

$$\text{netenergy}_m = 0.28 \text{ liveweight}^{0.75} \exp(-0.03 \text{ SRW})$$

(Freer *et al.*, 2007, p19)

The net energy required for weight change at each age (netenergy_{live weight change}) included the change in live weight, live weight and standard reference weight. If sheep lost weight then net energy required was negative, if sheep gained weight then the net energy requirements were positive.

$$\text{netenergy}_{\text{live weight change}} = (\Delta \text{liveweight}) \times (5.7 - 17.3 / (1 + \exp(-6 \times (0.4 (\text{liveweight} / \text{SRW}))))$$

(Freer *et al.*, 2007, p 36)

Net energy requirements for required for wool growth at each age (netenergy_{wool}) included wool growth at each age (wool) above 6 grams/day. Wool growth up to 6 grams/day is assumed to be included in maintenance energy requirements. Parameter woolper is the percentage of wool that grew in each month (Table A4.2).

$$(\text{netenergy}_{\text{wool}}) = \max(0, 0.13((\text{wool}_a \times (\text{woolper}/100) \times 1000)/30.4 - 6))$$

(Freer *et al.*, 2007, p 46)

Net energy for pregnancy included the number of lambs born (lb), standard birth weight (sbr), and day of pregnancy (dop). We calculated pregnancy requirements for each day of pregnancy and averaged them for each month of pregnancy.

$$\text{nepreg} = \text{lb} \times \text{sbr} \exp(7.64 - 11.46(\exp(-0.000643 \times \text{dop})))$$

(Freer *et al.*, 2007, p 32)

where lb is the number of lambs born (0,1 or 2)

The maximum amount net energy available from milk included a lactation parameter, standard reference weight, day of lactation (dol), and live weight of the sheep.

$$\text{maxmilk} = \min(\text{lactp} \times \text{srw}^{0.75} (\text{dol}/22) \exp(1-\text{dol}/22), 4.5 \text{ lwt}^{0.75} 0.3 + 0.41 \exp(-0.071 \times \text{dol}))$$

(Freer *et al.*, 1997)

lactp was 0.48 for sheep that wean one lamb and 0.78 for sheep that wean two lambs.

If the net energy required by lambs was less than maximum amount energy a ewe can produce in milk then the net energy of lactation equaled maxmilk, otherwise the energy required from lactation equalled net energy required by lambs (nereqlamb). Net energy required by lambs included the net energy required for live weight change, maintenance and wool

$$\text{netereqlamb} = (1.1 \text{ ne}\Delta\text{lwt})/0.763 + \text{netenergy}_m/0.85 + \text{netenergy}_{\text{wool}}$$

(Freer *et al.*, 1997)

Additional files 4.E - Efficiency of using metabolisable energy

The efficiency that metabolisable energy was converted to net energy for maintenance, lactation, and live weight gain included the energy available from green grass, dry grass, lupins and oats. Efficiency of using net energy for live weight gain when sheep were eating pasture also included the proportion of clover, latitude (lat), and day of the year (doy).

$$\text{km} = 0.02 \text{ mef} + 0.5$$

(Freer *et al.*, 2007, p 20)

$$\text{klact} = 0.02 \text{ mef} + 0.4$$

(Freer *et al.*, 2007, p 47)

$$\text{kg}^* = 0.035 \text{ mef} (1 + 0.33(\text{clover}/100))(1 + 0.12 (\text{lat} \times \sin(0.0172 \text{ doy}))/40)$$

(Freer *et al.*, 2007, p 43)

* for grain kg = 0.43xmef

4 Varying pasture and breeding objectives

Additional files 4.F - Intake equations

The potential intake of dry matter included standard reference weight (srw) and normal weight (nwt).

$$\text{pint} = 0.04 \text{ srw} \times (\text{nwt}/\text{srw}) \times (1.7 - \text{nwt}/\text{srw})$$

(Freer *et al.*, 2007, p 9)

Normal weight included standard reference weight and standard birth weight (sbw)

$$\text{nwt} = \text{srw} - (\text{srw} - \text{sbw}) \times \exp(-0.47 \times \text{age} \times \text{srw}^{0.27})$$

(Freer *et al.*, 2007, p 207)

Potential intake of non milk diets for lambs before they were weaned included the age of the lamb (ageindays)

$$\text{pintnm} = (1 / (1 + \exp(-0.5 \times (\text{ageindays} - 25))))$$

(Freer *et al.*, 2007, p 211)

Potential intake of sheep when lactating included the time from parturition (T)

$$\text{potintlact} = 1.0 + 0.025 \times n \times T^{1.4} \exp(-0.05T)$$

(Freer *et al.*, 2007, p 210)

Where $n = 1.0$ for a sheep with 1 lamb suckling and a value of 1.35 for a sheep with two lambs suckling

5

Breeding objectives for sheep should be customised depending on variation in pasture growth across years

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Abstract

Breeding programs for livestock require economic weights for traits that reflect the most profitable animal in a given production system, which affect the response in each trait after selection. The profitability of sheep production systems is affected by changes in pasture growth and grain, meat and wool prices between seasons and across years. Annual pasture growth varies between regions within Australia's Mediterranean climate zone from low growth with long periods of drought to high growth with shorter periods of drought. Therefore, the objective of this study was to assess if breeding objectives need to be adapted for regions depending on how reliable pasture growth is across years. We modelled farms with Merino sheep bred for wool and meat for 10 regions in Western Australia. Across these 10 regions mean annual pasture growth decreased and the coefficient of variation of annual pasture growth increased as pasture growth for regions became less reliable. We calculated economic values for nine traits optimising management across 11 years including variation for pasture growth and wool, meat, and grain prices between and within years from 2002-2012. These economic values were used to calculate responses to selection for each trait for the 10 regions. We identified two potential breeding objectives, one for regions with low or high reliability and one for regions with medium reliability of pasture growth. Breeding objectives for high or low pasture growth reliability had more emphasis on live weight traits and number of lambs weaned. Breeding objectives for medium reliability of pasture growth had more emphasis on decreasing fibre diameter. Relative economic weights for fleece weight did not change across the regions. Regions with low or high pasture reliability had similar breeding objectives and response to selection because the relationship between the economic values and coefficient of variation pasture growth were not linear for live weight traits and number of lambs weaned. This non-linearity was caused by differences in distribution of pasture growth between regions, particularly during summer and autumn when ewes were pregnant, with increases in energy requirements affecting the value of lambs weaned. Additionally, increasing live weight increased the intake capacity of sheep which meant more poor quality pasture could be eaten during summer and autumn which had more value in regions with low and high pasture reliability. We concluded that breeding values for sheep production systems should be customised depending on the reliability of pasture growth between years.

Keywords: Pasture growth uncertainty, Price uncertainty, Sheep, Breeding objectives, Economic values

5.1 Introduction

Breeding programs for livestock require clearly defined breeding objectives that enable the selection of animals that will make the most money per hectare in a given production system. Changes in optimal management need to be accounted for when calculating how the profitability of a farm is influenced by changing traits of animals (Groen, 1989; Amer, 1994). In areas where sheep are produced in Western Australia there are big differences between regions in the amount and variation of pasture growth within and between years (Rossiter, 1966; Schut *et al.*, 2010). These differences between regions in pasture growth can affect the optimal management of livestock (Chapman *et al.*, 2009; Young *et al.*, 2011b). These changes in management may also affect optimal breeding objectives because changing each trait can change the energy requirements of sheep by different amounts and at different times of the year. It is not known if different regions require different breeding objectives, or if one breeding objective will maximise profitability for all regions.

Farming systems become more vulnerable when pasture growth and prices vary across years, because the optimal stocking rate is different in each year (Rose *et al.*, 2014). Many modelling studies have shown that increased climate variability decreases the number of livestock that can be managed per unit of land (Kingwell *et al.*, 1993; Kobayashi *et al.*, 2007; Olson and Mikesell, 1988). This modelling is supported by surveys of farmers that suggest most Australian farmers manage the stocking system at a fixed, manageable number of ewes to avoid having too many sheep in years with low pasture growth (Doyle *et al.*, 1993; Austen *et al.*, 2002; Robertson and Wimalasuriya, 2004).

Rose *et al.* (2014) used actual pasture growth information for one region to show that variation in pasture growth across years changes the economic value of traits in the breeding objective. That study used a management perspective where farmers were willing to change flock structure in response to variability in pasture growth and prices. This perspective is different to farmers that prefer to keep the flock size constant at more conservative numbers to reduce the risk of overstocking in poor years. It is important to understand how different strategies to manage risk affect breeding objectives across regions with different degrees of reliability in pasture growth.

Changing the perspective of breeding objectives to constant stocking rates compared to optimising management and adjusting stocking rates in each year may change the optimal breeding program. Brascamp *et al.* (1985) found that different perspectives of management for pigs have different optimal breeding programs and Rose *et al.* (2014) also found that traits that affect energy requirements the most had lower economic values when pasture growth varies between years. This was because managing sheep at high stocking rates in years with favourable pasture growth and grain prices created problems when the following year had unfavourable pasture growth and grain prices. These problems led to a larger decrease in profit, especially with traits that increase energy requirements such as wool weight. Therefore, optimising management across all years should yield higher economic values for traits with high energy requirements compared to optimising management in each year.

Finally, traits that have a greater effect on energy requirements are likely to have more value in regions that vary less across each year, because drought periods are less common. Therefore, we tested the hypothesis that economic values and responses to selection of sheep breeding objective traits change for different regions depending on how pasture growth varies across years.

5.2 Material and methods

Testing the hypothesis that economic values and optimal response to selection in sheep depend on climatic region required four steps:

1. Define climatic zones - pasture growth and meat, wool, and grain prices defined for regions with different reliability of pasture growth.
2. Model – develop a bio-economic model of a sheep farm with interactions between pasture growth, sheep production and commodity prices.
3. Economic values – calculate economic values for each trait using this bio-economic model, and vary assumptions about pasture variability and associated price changes for grain, wool and meat.
4. Response to selection – calculate optimal responses to selection for each trait for each climatic zone, given the genetic parameters and economic values of traits.

Climatic zones

We used ten climatic zones that represent the range of sheep farming areas of Western Australia (Figure 5.1, Table 5.1). These regions are characterised by warm/hot dry summers and cool/mild wet winters and have different amounts and distribution of pasture growth across the year (see Figure A5.1a and A5.1b for total

5 Breeding objectives for different regions

pasture growth in additional material). The mean annual pasture growth decreases and standard deviation of annual pasture growth increases the further north and east the regions are from the ocean (Table 5.1). The length of the pasture growth season also decreases and becomes more variable across years the further the regions are away from the ocean. Therefore, the coefficient of variation (CV) of pasture growth increases and the reliability of pasture growth decreases when moving further from the ocean. This decrease in reliability makes these 10 regions ideal to investigate if breeding programs are affected by the variability in pasture growth.

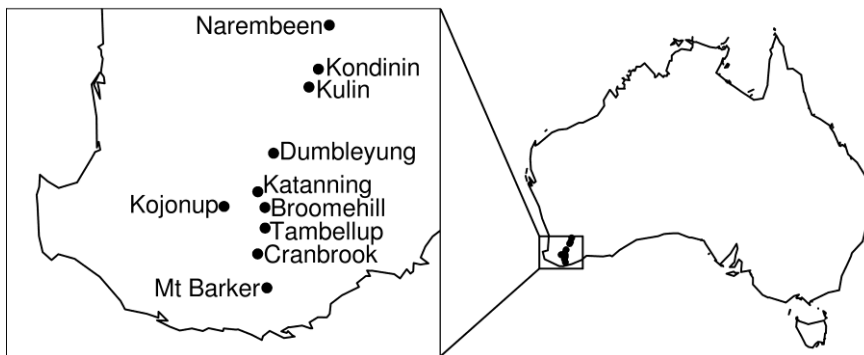


Figure 5.1 location of sheep regions of Western Australia used in this study.

Table 5.1 longitude, latitude, mean annual pasture growth and mean length of growing season (months) from 2002-2012 for the 10 study regions. The standard deviation (SD) and coefficient of variation (CV) of annual pasture growth and standard deviation of length of growing season across the 11 years are also shown.

Region	Latitude	Longitude	Pasture growth (kgDM/day)			Growing season	
			Mean	SD	CV	Mean	SD
Kulin	-32.67°S	118.16°E	4.65	3.16	0.68	5.10	1.73
Kondinin	-32.49°S	118.27°E	3.54	2.27	0.64	4.40	1.17
Narembeen	-32.07°S	118.39°E	3.85	2.45	0.64	4.09	1.58
Dumbleyung	-33.31°S	117.74°E	5.5	3.23	0.59	5.09	1.70
Katanning	-33.69°S	117.56°E	8.23	4.36	0.53	5.82	1.60
Tambellup	-34.04°S	117.64°E	10.6	5.55	0.52	6.55	1.44
Broomehill	-33.84°S	117.64°E	10.3	5.12	0.50	6.36	1.57
Cranbrook	-34.3°S	117.55°E	16.6	5.25	0.32	7.64	1.29
Kojonup	-33.83°S	117.16°E	16.7	4.75	0.29	7.55	1.13
Mt Barker	-34.63°S	117.66°E	19.5	5.07	0.26	7.82	1.47

We used 11 years of pasture growth (Figure A5.1a and A5.1b in additional material) and prices (Figure A5.2) from 2002-2012. We included the actual prices for grain, meat and wool in Figure A5.2 so any correlations between pasture growth and prices are included in the calculations for economic values. We assumed that all regions had the same prices, since sheep producers in these regions have access to the same markets for sheep and wool sales. The fluctuation of prices reflects the supply and demand of each commodity over time which is affected by many factors including the amount of pasture growth in all regions of the state. Therefore, including different pasture growth for each region but the same prices will include all of the relevant correlations between prices and pasture growth in each region. Pasture growth rates were used from Pastures from Space (Hill *et al.*, 1999) (<http://www.pasturesfromspace.csiro.au/index.asp>). Wool prices used were from the Western region micron price guide from the Wool Desk, Department of Agriculture and Food WA and Australian Wool Exchange (DAFWA, 2012). Meat prices used were hogget and mutton prices from Meat and Livestock Australia's National Livestock Reporting Service (MLA, 2012). Grain prices used were from Co-operative Bulk Handling (CBH, 2012).

Model

We modelled monthly production decisions for sheep farms with self-replacing Merino flocks bred for wool and meat using an adapted version of the model described by Rose *et al.* (2014). This model maximised profit from wool and sheep sales per hectare (ha) by optimising sheep numbers, sheep sales and grain feeding based on pasture availability and prices of grain, wool and meat. We maximised profit per ha because pasture growth per ha affects how many sheep can be managed on the farm and the number of sheep per ha mostly determines farm profit (Warn *et al.*, 2006; Young *et al.*, 2011b). Therefore, we optimised management of sheep sales and grain feeding per ha using the General Algebraic Modelling System with the linear programming solver BDMPLP (Brooke *et al.*, 2013). The model of Rose *et al.* (2014) optimised management decisions across five years using dynamic recursive analysis to maximise profit when commodity prices and pasture growth varied annually. Actual pasture growth and wool, meat, and grain prices from 2005-2009 were used. Management could adapt to varying pasture growth and commodity prices by changing sheep numbers, age structure of the flock and amount of grain fed to sheep. In this study, however, we optimised management across all years to find the most profitable long term stocking rate rather than optimising stocking rate every year, representing farmers trying to avoid managing high sheep numbers in unfavourable years. Additionally, we

maximised profit across 11 years to provide a better long term indication of the effect of pasture growth on profit and the economic values of traits.

The optimisation included five groups of equations, profit (objective function), flock structure, pasture, energy and intake. Profit depended on the number of sheep, sheep sold and grain intake. The amount of pasture available affected how much pasture could be eaten by sheep, which also affected how much is available in the next period. The number of sheep depended on energy requirements, potential intake, and the number of sheep sold. The amount of pasture and grain eaten was constrained by the potential intake of the sheep, while pasture and grain eaten had to match the energy requirements of the sheep.

Profit was derived from income from meat and wool sales minus variable and grain costs. Meat sales were the product of number of sheep sold, live weight, price per kg carcass and carcass dressing percentage. Sheep sales were split into mutton (over 20 months old) and hoggets (less than 20 months old) with different prices for both classes. We assumed that the minimum carcass weight that sheep can be sold was 16 kg. Wool income was the product of number of sheep in November (shearing month), wool weight, and wool price minus shearing costs. The profit equation therefore included all the relevant incomes and costs to calculate the impact of varying prices and pasture growth on breeding objectives.

We maximised profit across 11 years by optimising each year in a sequence, fixing the number of sheep across years and carrying over the amount of pasture from one year to the next. We found the optimal flock size by fixing the number of ewes mated and increasing the number by small increments until we found the maximum profit for the 11 study years. An example of how optimal profit was found is in Figure A5.3 for Narembeen in the additional material. The flock structure was optimised for each climatic region and each trait using average pasture growth and prices. Using these methods, we were able to optimise management of sheep across 11 years to estimate economic values for traits. In this way, we could account for optimal management across years with respect to changes in number of sheep and flock structure.

We limited the amount of pasture in December to be at least 800 kg/ha. This lower limit prevented pasture being grazed too low which causes soil erosion (Moore *et al.* 2009). In years when pasture growth was not enough to have 800 kgDM/ha in December, we lowered the lower limit of pasture in December by 10 kgDM/ha increments until the program became feasible. We did not include any consequences for future pasture growth when the pasture limit was lowered. The final amount of Pasture in December became the starting amount for the next year's analysis.

Economic values

Breeding programs aim to increase profit per animal through genetic improvement of traits that affect profit. Therefore, running a breeding program starts with specifying the traits affecting profit. The next step is to estimate the economic values for each trait, i.e. the change in profit when the trait is genetically improved by one unit keeping all other traits constant. Mathematically, the breeding objective can be represented as a linear equation in which breeding values for each trait are multiplied with economic values (Hazel, 1943). We calculated the economic value for nine traits shown in Table 5.2. These traits represent the economically important traits in current Merino breeding programs in Australia (Swan *et al.*, 2007), with live weight and number of lambs weaned important for meat income and clean fleece weight and fibre diameter important for wool income.

Table 5.2 phenotypic variance, and heritability of traits used to calculate economic values and responses to selection from MERINOSELECT database (Brown *et al.* 2006).

Traits	Heritability	Phenotypic variance
Weaning weight (kg)	0.40	18.6
Yearling live weight (kg)	0.43	28.3
Hogget live weight (kg)	0.39	35.1
Adult live weight (kg)	0.44	28.8
Hogget clean fleece weight (kg)	0.36	0.18
Adult clean fleece weight (kg)	0.50	0.26
Hogget fibre diameter (μm)	0.62	1.68
Adult fibre diameter (μm)	0.67	1.35
Number lambs weaned	0.07	0.27

We calculated the economic values for each trait as the difference in profit when increasing the trait by one genetic standard deviation compared to when the trait was not improved, while keeping all other traits constant. We changed the traits by one genetic standard deviation because this represents how easy traits change under selection. When we changed the traits, the energy requirements and potential feed intake of all animals changed. Increasing live weight, clean fleece weight and number of lambs weaned increased the metabolisable energy requirements. Increasing live weight increased the potential intake of sheep because bigger sheep can eat more. Neither energy requirements nor potential intake changed when we changed fibre diameter.

For adult live weight we increased live weights and standard reference weight of sheep older than 20 months but did not change the live weight change at any other age. For weaning, yearling and hogget live weight we changed the live weight at the relevant age and adapted the curves from birth to 20 months old (Figure A5.4).

5 Breeding objectives for different regions

These adaptations meant that the weights before and after each measurement were also altered. For example, when weaning weight increased by one genetic standard deviation, we adjusted the curve so that there was a higher growth rate up to weaning. Therefore growth rate after weaning was lower so that weights at older ages were not altered. Increasing number of lambs weaned changed the proportion of ewes with 0, 1, and 2 lambs born and weaned based on Figure A5.5, the same as described in Rose *et al.* (2014). Using the relationships in Figure A5.5, we estimated the number of ewes in each birth and wean class based on number of lambs weaned per ewe in the flock. Increasing the number of lambs weaned increased the proportion of ewes that gave birth to and weaned 2 lambs and decreased the proportion of ewes that gave birth to and weaned no lambs. Ewes that give birth to and wean two lambs have higher energy requirements for pregnancy and lactation than ewes that give birth and wean one lamb. Additionally, the flock structure changed when the number of lambs weaned increased. For more details, see Rose *et al.* (2014).

We used the economic values per unit of the trait (\mathbf{v}) to calculate the relative contribution (c_x^2) of each trait (x) to the genetic variance ($\sigma_H^2 = \mathbf{v}^T \mathbf{G} \mathbf{v}$) of the breeding objective (H) using the equation;

$$c_x^2 = \frac{\mathbf{V} \times \mathbf{G} \times \mathbf{v}}{\mathbf{v}^T \times \mathbf{G} \times \mathbf{v}}$$

Where \mathbf{V} is a matrix with economic values on the diagonal, \mathbf{G} is the genetic variance-covariance matrix and \mathbf{v} is a vector of economic values. More detailed information about how we calculated the relative contributions is in section 5.C of the additional files. We also calculated the correlations between breeding objectives for each region (r_{H_i, H_j}) using the equation

$$r_{H_i, H_j} = \frac{\mathbf{v}_i^T \times \mathbf{G} \times \mathbf{v}_j}{\sqrt{\sigma_{H_i}^2 \times \sigma_{H_j}^2}}$$

Where \mathbf{v}_i are the vectors with the economic values for breeding objectives i and j , \mathbf{G} is the genetic variance-covariance matrix and σ_H^2 is the variance of breeding objectives i and j . The correlations between breeding objectives show how much the breeding objectives are genetically different.

Response to selection

Response to selection is the expected genetic change in each trait when selecting on the index defined by the economic values. When multiple traits are included in a breeding objective then the response to selection is the response in the aggregate genotype, which is the product of the economic values for all traits and the

responses per trait. The ease of changing traits depends on the additive genetic variance of each trait, but also the heritability and the genetic correlations with other traits in the aggregate genotype. Traits with higher genetic variation have a higher potential to be improved. Because the aggregate genotype also includes the genetic correlations between traits, putting more emphasis on one trait will also change traits that are correlated.

The expected response to selection with the economic values from each climatic region was calculated using SelAction (Rutten *et al.*, 2002). For each region, we assumed that the same breeding program and genetic parameters, from the MERINOSELECT database (Brown *et al.*, 2006), were used (see Table 5.2 and Table 5.3) so that differences between regions were due to differences in economic values and not due to differences in breeding programs. We assumed first mating at 19 months of age with a ewe to ram ratio of 20 to 1. Each ewe gave birth to 0.8 lambs once per year with 10% death and culling for ewes and 50% for rams. We used 7 age classes representing one year each, with weaning weight, yearling weight, fibre diameter and clean fleece weight measured at age 1 and hogget weight measured at age 2, and adult fibre diameter, clean fleece weight and live weight and number of lambs weaned recorded for classes 3-7. Rams and ewes were selected based on own performance and based on 15 half sibs from 19 dams for all traits apart from number of lambs weaned. For number of lambs weaned ewes were selected based on own performance and 7 half sib sisters from 9 ewes. For number of lambs weaned, rams were selected based on the performance of 8 half sib sisters from 10 dams. For all traits at all ages, ewes and sires were selected based on BLUP-EBV. Selection responses were predicted with a pseudo-BLUP selection index (Rutten *et al.*, 2002).

Table 5.3 genetic (above diagonal) and phenotypic (below diagonal) correlations between breeding objective traits from MERINOSELECT database (Brown *et al.*, 2006).

	wwt	ywt	hwt	awt	hcfw	acfw	hfd	afd	nlw
wwt		0.70	0.66	0.36	0.24	0.17	0.05	0.02	0.04
ywt	0.47		0.90	0.61	0.30	0.23	0.18	0.14	0.13
hwt	0.41	0.70		0.65	0.26	0.26	0.18	0.16	0.12
awt	0.60	0.80	0.89		0.15	0.15	0.20	0.20	0.35
hcfw	0.20	0.24	0.24	0.26		0.80	0.30	0.30	-0.10
acfw	0.05	0.15	0.19	0.22	0.58		0.26	0.34	-0.10
hfd	0.10	0.20	0.19	0.19	0.27	0.23		0.90	0.00
afd	0.10	0.15	0.16	0.17	0.23	0.29	0.78		0.00
nlw	0.15	0.30	0.34	0.15	-0.01	0.02	0.00	-0.01	

wwt = weaning live weight; ywt = yearling weaning weight; hwt = hogget live weight; hcfw = hogget clean fleece weight; acfw = adult clean fleece weight; hfd = hogget fibre diameter; afd = adult fibre diameter; nlw = number of lambs weaned.

Statistical analysis of breeding objectives and response to selection

For each trait we tested if the relationship between the CV of annual pasture growth was significant with economic values, relative contribution to breeding objective, and response to selection. We tested the significance using analysis of variance in the R software (R Core Team 2012). Our first null hypothesis was that CV does not significantly explain differences in economic values, relative contribution to breeding objective, and response to selection. If we rejected this null hypothesis, we then tested a second null hypothesis that a linear function fits the data better than a quadratic function. We rejected the null hypothesis if the probability of a better fit was less than 0.05. These tests were important to interpret how economic values, relative contribution to breeding objective, and response to selection are affected by pasture growth and variation in each region.

5.3 Results

Effect of varying pasture growth on profit

Profit decreased when the CV of pasture growth between years increased (Figure 5.2). This decrease in profit was mostly because less sheep could be managed per ha when CV of pasture growth increased (Figure A5.6). Additionally, income and costs decreased as the CV of pasture growth increased (Figure 5.2), but the contribution of income and costs to profit changed for each pasture growth region with grain costs having more influence on profit as the coefficient of variation of pasture growth increased (Figure A5.7). This increase in grain requirements was because the frequency and length of drought periods increased as the CV of pasture growth increased. Therefore, as pasture reliability decreased, stocking rate decreased and grain costs increased which decreased profit.

Economic values and breeding objectives

The economic value of weaning weight, hogget live weight and adult live weight were close to zero and mostly negative (Table 5.4). These economic values were mostly negative because of higher energy requirements when live weight increased. The relationship between economic values and CV of pasture growth were quadratic ($p < 0.01$) and regions with high and low CV of pasture growth had higher economic values for these traits than regions with medium CV of pasture growth.

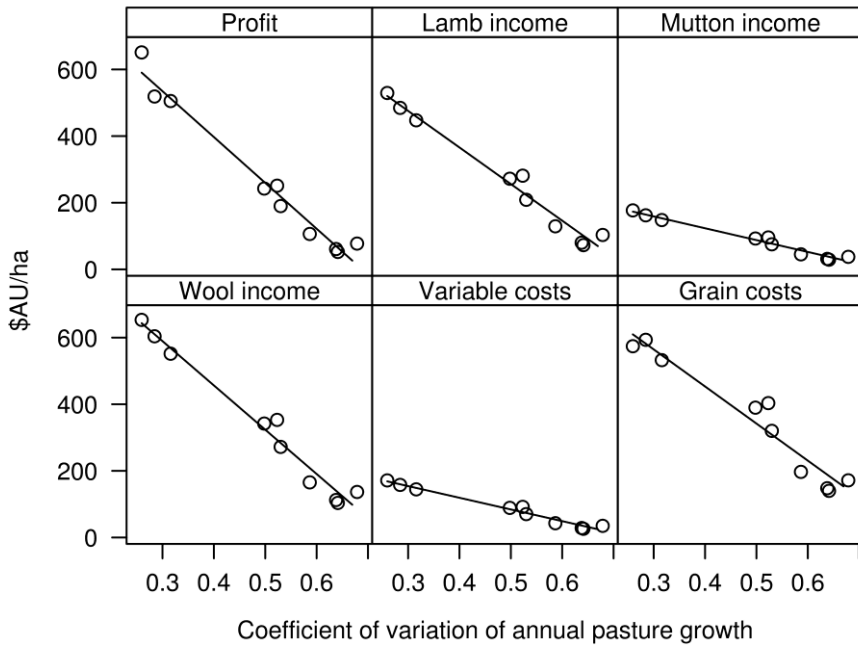


Figure 5.2 Profit, incomes and costs for each region are represented as a function of coefficient of variation of annual pasture growth.

Table 5.4 Economic values/ha per genetic standard deviation across regions represented by coefficient of variation of annual pasture growth (CV).

CV	wwt ²	ywt ¹	hwt ²	awt ²	hcfw ¹	acfw ¹	hfd ¹	afd ¹	nlw ²
0.68	0.8	6.1	-0.8	1.7	7.7	9.6	-3.6	-3.6	9.7
0.64	0.7	4.3	-0.6	0.5	5.7	7.6	-2.7	-2.7	7.0
0.64	0.8	4.5	-0.4	0.8	6.2	8.1	-3.1	-3.1	7.6
0.59	0.8	5.0	-3.2	-1.3	8.7	11.7	-5.0	-5.0	9.5
0.53	-0.6	6.7	-5.2	-3.5	12.3	17.4	-8.7	-9.8	14.5
0.52	-0.2	12.7	-4.8	-4.8	17.0	22.6	-11.6	-11.7	17.4
0.50	-1.2	9.0	-4.6	-5.2	15.4	20.7	-12.3	-12.5	16.3
0.32	3.0	15.4	-1.4	-4.0	30.3	38.6	-15.1	-14.5	35.5
0.29	3.1	19.9	-0.5	-2.9	33.9	42.5	-16.7	-16.0	40.8
0.26	3.5	17.2	0.1	-4.4	36.2	45.8	-17.7	-16.7	45.0

wwt = weaning live weight; ywt = yearling weaning weight; hwt = hogget live weight; hcfw = hogget clean fleece weight; acfw = adult clean fleece weight; hfd = hogget fibre diameter; afd = adult fibre diameter; nlw = number of lambs weaned

¹ linear relationship between economic value and coefficient of variation of pasture growth ($P < 0.05$).

² significant quadratic relationship between economic value and coefficient of variation of pasture growth ($P < 0.01$).

Yearling weight, hogget fleece weight, adult fleece weight and number of lambs weaned had the largest effect on income, and their economic values decreased as the CV of pasture growth increased. As the CV of pasture growth increased, these traits had less value per ha because less sheep could be managed, and the benefits of improving traits in each sheep was lower. The economic value for fibre diameter traits increased as the reliability of pasture growth decreased. The economic values for yearling live weight and wool traits increased linearly with increasing CV of pasture growth ($p < 0.01$) but the economic value for number of lambs weaned had a quadratic relationship with CV ($p < 0.01$). The slope of the economic value for lambs weaned decreased as CV of pasture growth increased and economic values were similar between regions when CV was higher than 0.5. This can be seen in more detail in Figure A5.8, with economic values for all traits changing profit by a higher proportion when the CV of pasture growth was highest.

The relative contribution of traits to the breeding objective was highest for adult fleece weight, hogget fleece weight and number of lambs weaned (Table 5.5). The next main contributors were yearling live weight and fibre diameter traits, depending on the relationships between economic values and reliability of pasture growth. The relationship between CV of pasture growth and relative importance of all traits was quadratic across regions ($P < 0.01$), apart from hogget fleece weight which was linear ($P < 0.01$) and adult fleece weight which had no relationship with CV of pasture growth. The relative importance of weaning live weight, yearling live weight, adult live weight, and number of lambs weaned had a minimum around CV of annual pasture growth of 0.5, increasing as CV increased and decreased. The relative importance of hogget and adult fibre diameter had a maximum around CV of pasture growth of 0.5 and decreased as CV increased and decreased. The relative importance of hogget live weight and hogget fleece weight decreased linearly as CV of pasture growth increased. The relative importance of adult fleece weight was the same for all regions. These results show that relationships between relative contributions and CV of pasture growth for each trait are a consequence of the relationships between economic values and CV of pasture growth.

The non-linearity of relative contribution of traits was caused by non-linearity in economic values, particularly for live weight traits and number of lambs weaned. Therefore, in regions with high or low CV of pasture growth, the number of lambs weaned and live weight traits contributed more to the breeding objective compared to fibre diameter traits. Alternatively, in regions with medium CV of pasture growth, the opposite was found with fibre diameter traits contributing more to the breeding objective than lambs weaned and live weight traits.

Table 5.5 Relative contribution of each trait (%) to the breeding objective across regions represented by coefficient of variation of pasture growth (CV).

CV	wwt ²	ywt ²	hwt ¹	awt ²	hcfw ¹	acfw ⁰	hfd ¹	afd ²	nlw ²
0.68	1.7	18.6	-1.8	4.9	22.7	28.5	0.1	0.2	25.0
0.64	1.8	16.8	-1.7	1.9	24.5	33.1	0.3	0.3	23.2
0.64	2.2	16.4	-0.9	2.7	23.8	31.3	0.5	0.5	23.6
0.59	1.0	9.5	-2.8	-2.0	27.7	38.6	3.9	3.6	20.5
0.53	-0.2	5.2	-0.7	-2.0	23.4	35.1	8.9	9.9	20.4
0.52	-0.1	11.9	-2.1	-3.5	26.6	35.8	7.1	6.9	17.4
0.50	-0.4	5.9	-0.9	-2.3	23.9	33.0	12.1	11.9	16.7
0.32	1.3	10.3	-0.6	-2.4	28.3	36.4	1.6	1.4	23.8
0.29	1.3	12.7	-0.2	-1.7	27.1	34.0	1.1	1.0	24.7
0.26	1.3	9.7	0.0	-2.3	27.5	35.2	1.3	1.1	26.3

wwt = weaning live weight; ywt = yearling weaning weight; hwt = hogget live weight; hcfw = hogget clean fleece weight; acfw = adult clean fleece weight; hfd = hogget fibre diameter; afd = adult fibre diameter; nlw = number of lambs weaned.

¹ no relationship between economic value and coefficient of variation of pasture growth.

¹ linear relationship between economic value and coefficient of variation of pasture growth ($p < 0.05$).

² quadratic relationship between economic value and coefficient of variation of pasture growth ($p < 0.01$).

Table 5.6 Correlations between regions represented by coefficient of variation of annual pasture growth (CV) for relative contribution (above diagonal) and response to selection (below diagonal).

CV	0.68	0.64	0.64	0.59	0.53	0.52	0.50	0.32	0.29	0.26
0.68		1	1	0.94	0.87	0.93	0.86	0.98	0.99	0.98
0.64	1		1	0.96	0.89	0.95	0.88	0.99	1	0.99
0.64	1	1		0.96	0.89	0.94	0.88	0.99	0.99	0.99
0.59	0.89	0.92	0.91		0.98	0.99	0.97	0.99	0.98	0.98
0.53	0.71	0.75	0.74	0.94		0.99	1	0.94	0.93	0.94
0.52	0.88	0.91	0.9	1	0.96		0.99	0.98	0.97	0.97
0.50	0.73	0.77	0.75	0.95	1	0.96		0.93	0.92	0.92
0.32	0.97	0.98	0.98	0.98	0.86	0.97	0.87		1	1
0.29	0.99	1	0.99	0.95	0.81	0.94	0.82	1		1
0.26	0.98	0.99	0.98	0.97	0.84	0.96	0.85	1	1	

5 Breeding objectives for different regions

These differences in relative contributions across regions affected the correlations between breeding objectives (Table 5.6). There appears to be three distinct groups of regions;

1. High pasture reliability; Mt Barker, Kojonup and Cranbrook with CV of pasture growth from 0.29-0.32,
2. Medium pasture reliability; Broomehill, Tambellup, Katanning and Dumbleyung with CV of pasture growth from 0.50-0.59, and
3. Low pasture reliability; Narembreen, Kondinin and Kulin with CV of pasture growth from 0.64-0.68.

The breeding objective of the high and low pasture reliability groups was highly correlated (0.98-1.00) whilst the medium reliability group had lower correlations with both the low and medium group (0.86-0.98). Therefore, there appears to be two breeding objectives, one breeding objective for low and high reliability pasture regions and one breeding objective for medium reliability pasture growth regions.

Response to selection

The response to selection in genetic standard deviations per year was highest for live weight traits and fleece weight traits (Figure 5.3). The response in fleece weight traits was the same for all regions, whilst all other traits had a quadratic relationship ($P < 0.01$) between CV of pasture growth and response to selection. Live weight traits and number of lambs weaned had a minimum response around CV= 0.5, increasing as CV increased and decreased. Fibre diameter traits had a maximum negative response around 0.5 CV of annual pasture growth, increasing as CV increased and decreased. The response in number of lambs weaned was low, despite having a high relative contribution to the breeding objective whilst the response to selection for live weight traits was high despite low relative contributions to the breeding objective for weaning, hogget and adult live weight. The correlations between responses across the regions had the same pattern as the correlations between breeding objectives (Table 5.6). The responses to selection of the high and low pasture reliability groups was highly correlated (0.97-1.00) whilst the medium reliability group had lower correlations with both the low and medium group (0.71-0.98). The correlations between responses reflect the correlations between regions for breeding objectives.

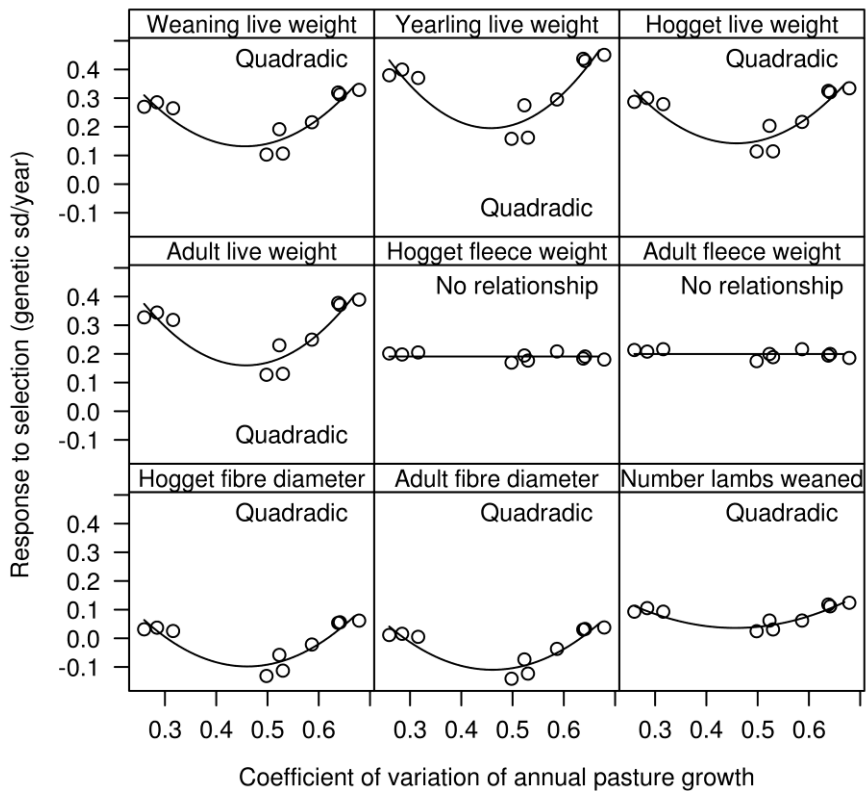


Figure 5.3 Response to selection in genetic standard deviations across regions represented by coefficient of variation of annual pasture growth for relative contribution for each trait.

5.4 Discussion

Variation in pasture growth across years influenced the optimum breeding objectives for Merino based sheep production systems in different regions of Western Australia. As the reliability of pasture growth across years decreased the profit per ha decreased because less sheep could be managed per ha. Additionally, as the reliability of pasture growth decreased, the economic value of most traits decreased, although this decrease was not always linear. This non-linear decrease for some traits caused differences in the relative contribution of traits to the breeding objective, which also affected the response to selection. Therefore, we accepted the hypothesis that economic values and response to selection of sheep breeding objective traits change depending on the distribution and variation of pasture growth across years.

Furthermore, based on correlations between breeding objectives and responses to selection we found that a single breeding objective was suitable for regions with high or low reliability of pasture growth between years. This single breeding objective existed despite big differences in the amount and variation of pasture growth between regions with low and high pasture growth reliability. Additionally, regions with medium pasture growth reliability had a different breeding objective to regions with low and high pasture growth reliability. The first breeding objective had more emphasis on live weight and number of lambs weaned and the second had more emphasis on fibre diameter traits.

Interactions between how traits change energy requirements and potential intake with the amount and distribution of pasture growth across years caused the differences in economic values, relative contributions of traits, and the response to selection of the traits. These interactions suggest that breeding programs should be customised based on the amount and distribution of pasture growth across years.

Regions with low or high reliability of pasture growth had similar breeding objectives because differences in the distribution of pasture growth in each month caused quadratic responses in economic values to changes in CV of pasture growth for live weight traits and the number of lambs weaned. Live weight traits at weaning, hogget and adult ages had more value in regions with high or low reliability of pasture growth than regions with medium reliability of pasture growth because increasing live weight increases potential intake or intake capacity of sheep (Freer *et al.*, 2007). This increase of potential intake is important because dry pasture has low digestibility and takes longer to digest limiting the amount of pasture that can be eaten. If sheep can eat more dry pasture, a higher proportion of their energy requirements can be met from dry pasture, and the costs of supplementary feeding are reduced, especially in regions with low reliability of pasture growth which have long periods of drought. Regions with high reliability of pasture growth have big peaks in pasture growth during spring. Despite this high peak in pasture growth, stocking rate is limited by periods of drought. This limitation occurs because a lot of pasture grows in a short period in spring which is not utilised unless sheep are managed at a high stocking rate. The optimal stocking rate, however, is still limited by the short period of drought in each year. Therefore, increasing the potential intake reduces the influence of drought periods which means more sheep can be managed and more of the pasture grown in spring is utilised. The benefits of increasing intake capacity were not as high in the regions with medium pasture growth reliability because periods of drought were shorter than the low reliability regions, and the peak of pasture in spring were lower than the high reliability regions. This extra value of live weight is similar to what Groen

and Korver (1989) found in dairy cattle, where more forage can be given when potential intake increases, reducing the amount of concentrate required. We found that the benefit of increased intake capacity is not only relevant for regions with low pasture growth, but can be advantageous in regions with high pasture growth, which is an important conclusion.

The quadratic relationship between economic value for lambs weaned and CV of pasture growth was due to differences in distribution of pasture growth between years. Every region had pasture growth during July and August in most years, the months with peak energy requirements for pregnancy and lactation. Therefore, when the number of lambs and weaned increased, there was mostly green pasture available to match the increase in energy requirements. As regions became less reliable, the length of the growing season decreased due mostly to a later start to the season during autumn and early winter. The growing seasons shortened considerably between the 3 regions with high pasture growth reliability and regions with medium pasture growth reliability. Because autumn and early winter coincided with the start of pregnancy, the value of weaning more lambs was less for regions with medium pasture growth reliability than for regions with high pasture growth reliability. The decrease in length of growing season was not so extreme between regions with medium and low pasture growth reliability. Therefore, the decrease in economic values in relation to coefficient of variation of pasture growth between regions with medium and low pasture growth was also lower, causing a quadratic relationship between economic values for number of lambs weaned and CV of pasture growth, contributing to different breeding objectives between regions with low and high pasture growth reliability and regions with medium pasture growth reliability.

The magnitude of the relative contribution of traits to the breeding objective and the response to selection did not always match. For example, number of lambs weaned had a low response to selection despite a high contribution to the breeding objective. This low response was because number of lambs weaned was only measured in adult ewes which decreased the accuracy of selection compared to all other traits which were recorded at more ages. Additionally the heritability of number of lambs weaned is low decreasing the accuracy of selection. Live weight, fleece weight and fibre diameter traits were recorded at several ages, with high correlations between each age group. Therefore, high response to selection at one age caused a high response at all other ages. Live weight had a high value at yearling age which increased response at all other ages, even though their economic values were close to zero. These differences also caused the correlations between regions for responses to selection to be lower than for breeding

objectives. This difference in correlations has been demonstrated in cattle (Hirooka and Groen, 1999) and pigs (Dube *et al.*, 2013). Therefore, responses to selection need to be calculated before comparing breeding programs because the differences in economic weights do not directly translate into equal differences in selection responses.

We found that regions with different pasture growth have different breeding objectives but there could also be differences in the performance of animals within each region. This variation in pasture availability across regions can cause genotype by environment interactions changing the ranking of the best animals to select between environments (Falconer and Mackay, 1996). Additionally, within each region changes in pasture growth between years can also cause genotype by environment interactions. For example, several studies for beef cattle (Sousa Júnior *et al.*, 2012) and dairy cattle (Kearney *et al.*, 2004; McCarthy and Veerkamp, 2012) found genotype by environment interactions for production traits when resources were different either because of the time of year, amount of rainfall or amount of grain supplement provided. Therefore, genotype by environment interactions between regions could make it difficult to use one breeding scheme for all environments (e.g. Mulder *et al.*, 2006). Additionally, genotype by environment interactions between seasons make it difficult to select animals that have high performance in all seasons. For example, several studies have shown that selection for the best animals in good years can increase the sensitivity of animals to varying environments (Falconer, 1990; van der Waaij, 2004). This environmental sensitivity can reduce performance in poor years which can have economic and welfare consequences. Therefore, optimal breeding programs for regions could be further affected by the genotype by environment interactions between regions and between seasons.

Rose *et al.* (2014) reported that including varying pasture growth and prices increased the estimated economic values for different traits compared to using average pasture growth and prices. The study by Rose *et al.* (2014) used dynamic programming to simulate farmers altering their management decisions in response to changes in pasture growth and prices each year, whereas in this study we optimised sheep numbers across all years. We can compare the economic values from Katanning in this study to those of Rose *et al.* (2014). The economic values for number of lambs weaned decreased from \$AU26/ha to 15, for adult fibre diameter increased from -21 to -10 and for adult fleece weight decreased from 22 to 17. The magnitude of economic values decreased between the studies, however in this study the relative importance of fleece weight was higher than the study by Rose *et al.* (2014). This difference in economic values was because fleece weight made the

farm more vulnerable to changes in pasture growth and prices when management was optimised each year. Optimising management across all years meant that fleece weight made the farm less vulnerable because an optimal stocking rate across all years could be estimated. Although it is difficult to compare the two studies because they used different study years, it appears that there were big differences in the relative importance of traits when sheep numbers are optimised in each year or across years. In conclusion, this study provides a set of economic values for farmers that manage variation in pasture growth by managing the same number of sheep at a lower stocking rate, which is a different type of farmer simulated in the study by Rose *et al.* (2014).

We used the coefficient of variation as the indicator of pasture reliability but average pasture growth decreased as the coefficient of variation increased. Therefore, it was difficult to disentangle the effects of total pasture growth and variation across years. Within the groups of regions with low, medium and high pasture growth it is possible to investigate the effects of pasture growth because the coefficient of variation of pasture growth was similar within the groups. Additionally, we could have simulated pasture growth to have the same mean pasture growth and different variation across years. However, using real pasture growth data makes our research more relevant for farmers who have uncertain pasture growth across years than using simulated data.

Finally, we limited the amount of pasture in December to be at least 800 kg/ha and lowered the limit by 10kg DM/ha until the model became feasible. This lowering of the lower limit has implications for the optimisation of economic values. For example, in years with no pasture growth at all, or a drought for the whole year, there is no pasture left in December. Therefore, in the following years, there is no pasture available until pasture starts growing. Having no pasture in December has many consequences for soil health (Moore *et al.*, 2009) which could affect pasture growth in the following year. We had trouble finding relevant information about how pasture growth is affected in a year with high soil erosion. However, in our study the consequence of no pasture growth on the following year is still represented through not having any pasture available in summer and autumn in the following year.

Acknowledgements

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Additional files Chapter 5

Additional files 5.A – Pasture growth, prices and profit

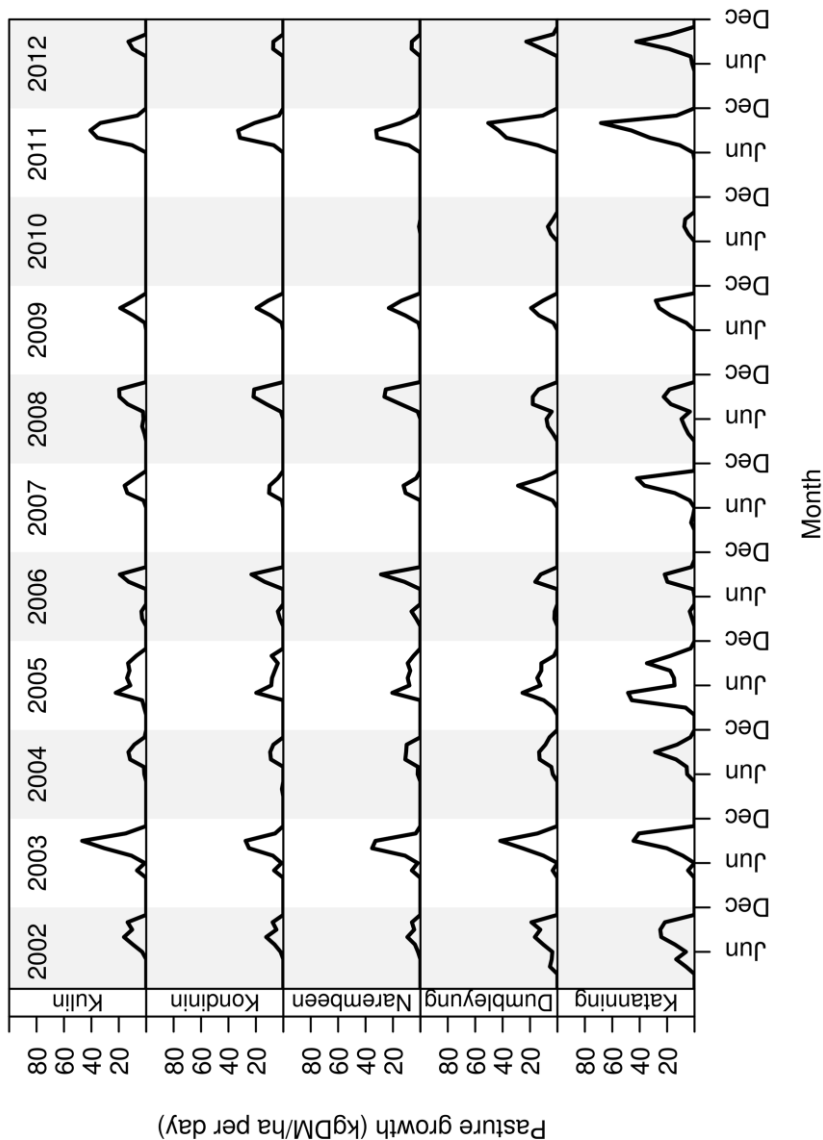


Figure A5.1a Pasture growth rate of the 5 least reliable climatic regions studied for the 11 years from 2002-2012.

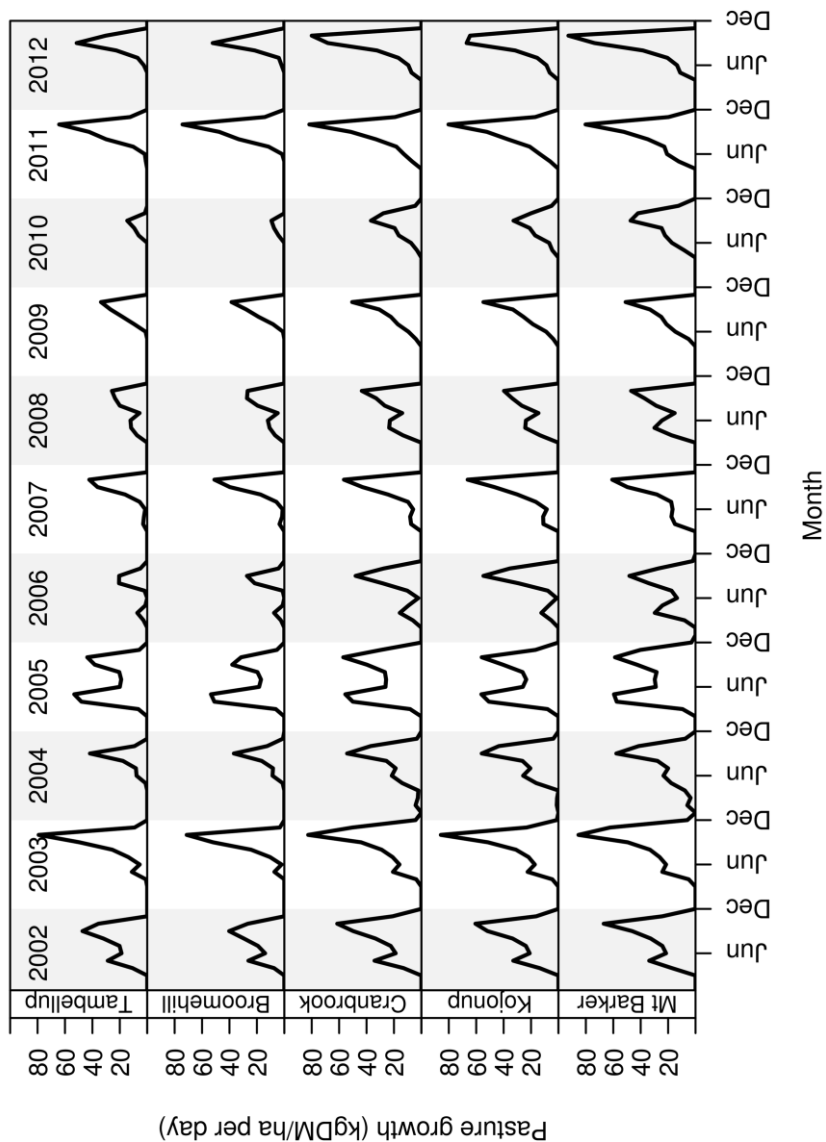


Figure A5.1b Pasture growth rate of the 5 most reliable climatic regions studied for the 11 years from 2002-2012.

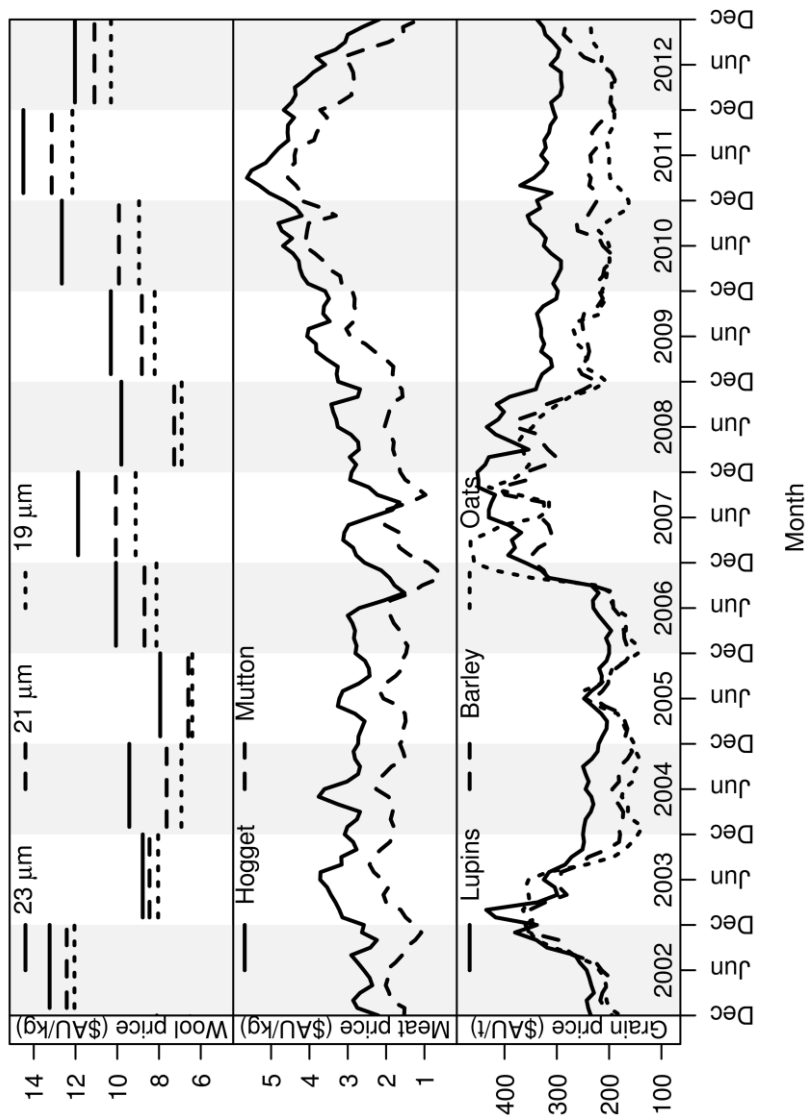


Figure A5.2 Wool, meat and grain prices from 2002 to 2012.

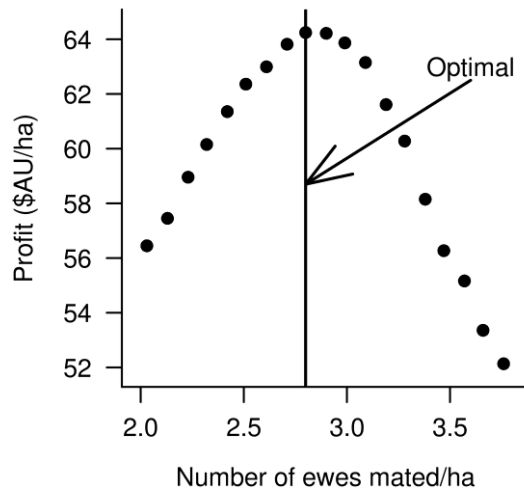


Figure A5.3 Example of how optimal stocking rate is found to optimise profit by increasing number of ewes mated by a small increment.

Additional files 5.B – trait characteristics

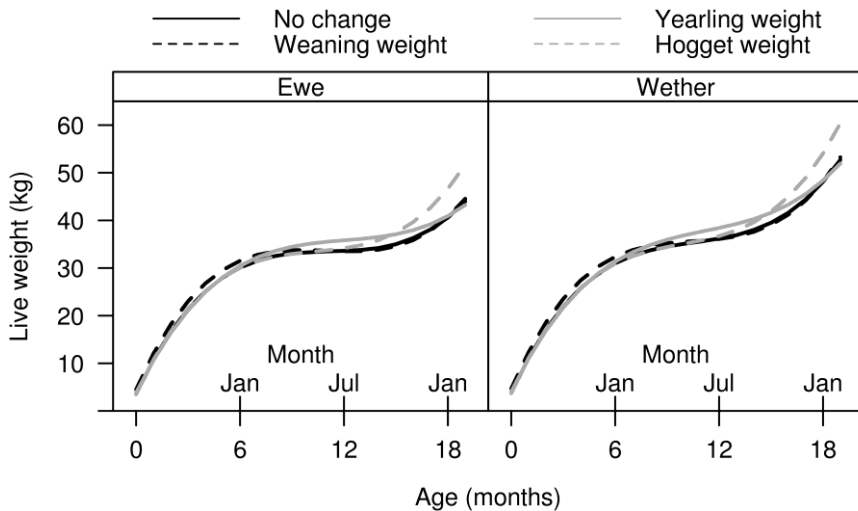


Figure A5.4 alterations of live weight for growing sheep used to calculate economic values of weaning, yearling and hogget live weight. Only lambs that were born and reared as one lamb are shown.

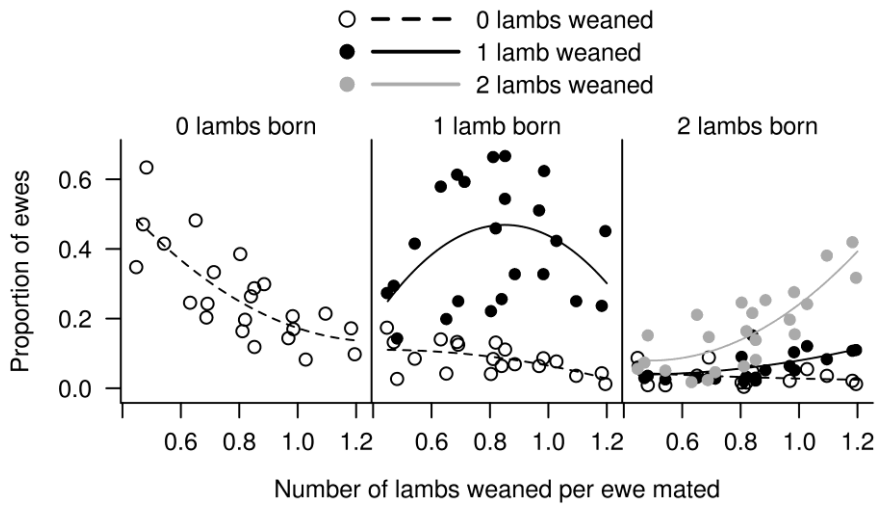


Figure A5.5 The number of ewes in each of the 6 birth and wean categories based on number of weaned per ewe mated estimated from 8 information nucleus flocks (Sheep CRC) from Australia over 3 years. We fitted curves to these points and estimated the number of sheep in the 6 litter size at birth and litter size at weaning category.

Additional files 5.C - Relative contribution calculations

We calculated the relative contribution of each trait to the breeding goal using the equation

$$c_x^2 = \frac{V \times G \times v}{v'Gv}$$

Where V is a matrix with economic values on the diagonal, G is the genetic variance-covariance matrix and v is a vector of economic values.

An example of the calculation using two traits with

$$v = \begin{bmatrix} v_1 & 0 \\ 0 & v_2 \end{bmatrix},$$

$$G = \begin{bmatrix} x & a \\ a & y \end{bmatrix} \text{ and}$$

$$v = \begin{bmatrix} v_1 \\ v_2 \end{bmatrix}$$

Where the variance of the breeding goal is

$$v'Gv = v_1^2x + v_1v_2a + v_1v_2a + v_2^2y$$

$$\text{And the relative emphasis for trait 1} = \frac{v_1^2x + v_1v_2a}{v'Gv}$$

Additional files 5.D – supplementary results

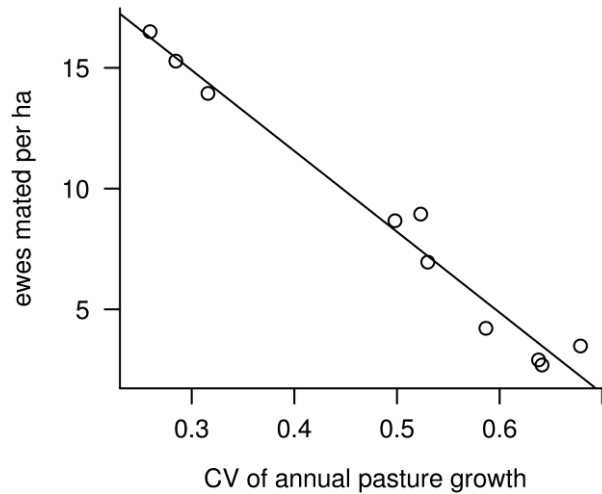


Figure A5.6 Number of ewes mated per ha plotted against coefficient of variation of annual pasture growth.

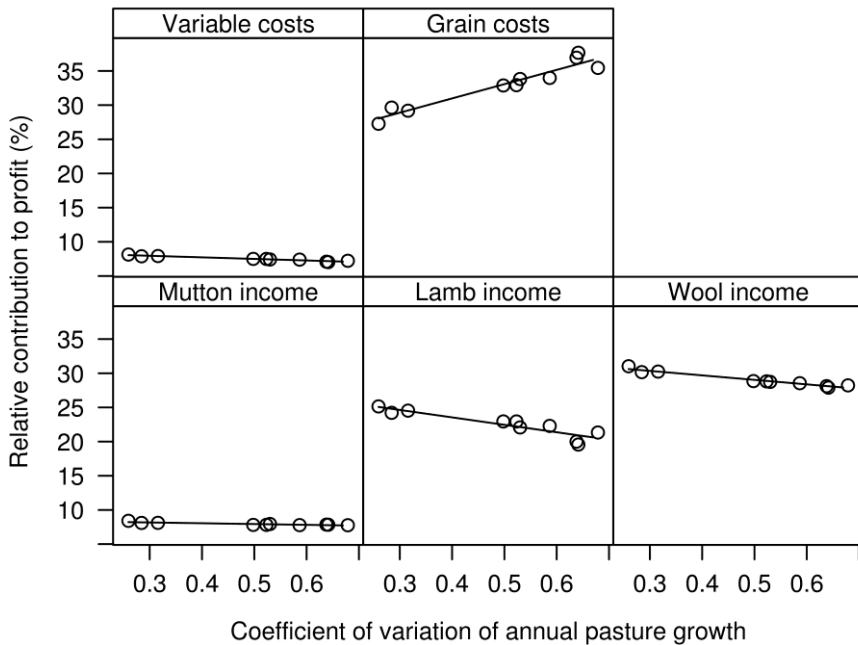


Figure A5.7 Relative contribution of each costs and income to profit plotted against coefficient of variation of annual pasture growth.

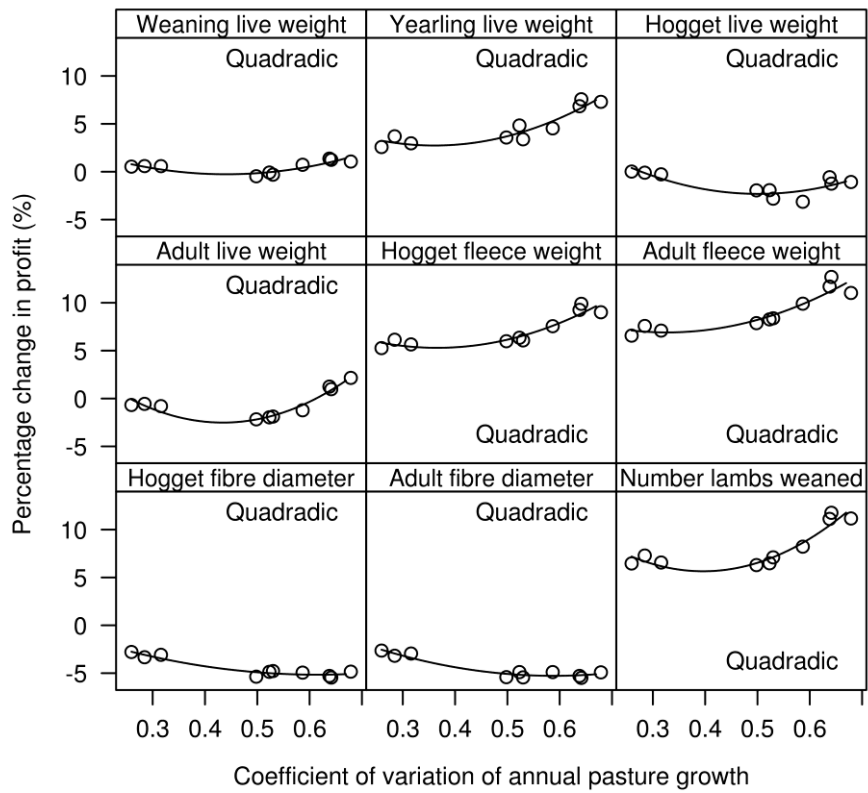


Figure A5.8 Change in profit after changing trait by 1 genetic standard deviation relative to profit before changing traits plotted again coefficient of variation of annual pasture growth.

6

General discussion

In this thesis, I studied breeding strategies for sheep in environments which have high uncertainty of pasture growth and wool, meat and grain prices between years. The main objective of breeding programs is to select the animals that will make the most money per hectare in a production system. Additionally, breeding programs should ensure the welfare level of animals is maintained and that production systems are sustainable. The objectives of breeding programs for production systems with varying pasture growth between years are difficult to clearly define because every year is different which requires different management systems and perhaps a different type of sheep. Breeding objectives, however, need to be longer term and therefore cannot be aimed at conditions in one particular year. Therefore, breeding objectives need to be estimated for a particular region of group of farms and aimed at selecting the sheep that will be most suitable for this region or group of farms in the future. Therefore, I aimed to provide farmers with breeding strategies to select sheep most suitable for farming systems in environments with uncertainty in pasture growth between years.

To provide clear breeding strategies for sheep farmers and breeders, this thesis had two aims; 1. Quantify how to make sheep more resilient to variation in pasture growth and 2. Quantify how to make farming systems more resilient to variation in pasture growth and commodity prices. In the general discussion, I compare these aims, and link these to the general topic of breeding better animals for the future. The discussion is split into four sections that explore how sheep can be bred to be resilient to uncertainty. I address two questions;

1. Can sheep be bred to be more resilient using live weight change as a trait?
2. Optimal breeding to reduce variation across years - are some traits more sensitive to variation in pasture growth and prices across years?

These questions will be addressed in the first two sections. In the third section I review definitions of resilience for production systems and breeding strategies. In the fourth section I relate the results of my thesis to the review of resilience and breeding, making conclusions about the best strategies to make farming systems resilient to uncertain pasture growth and commodity prices.

6.1 Breeding resilient sheep

In Chapter 2 I showed that live weight change can be selected for and in Chapter 3 that live weight change had important genetic correlations with reproduction. It is important to understand how live weight change is related to resilience to drought periods and hence determine if it could serve as an indicator trait for resilience to drought periods. Additionally, if live weight change is to be used as an indicator

trait for resilience to drought periods, an economic value for live weight and resilience is required before it can be used in a breeding objective. This will give an indication of the relative importance of resilience compared to other traits. Furthermore, since live weight change contains two live weight measurements, live weight change is expected to be correlated with the live weights. These correlations might make it difficult to simultaneously select for live weight change and live weight at the start and end of the live weight change period in different directions. Since farmers may have different desired directions to select for live weight change and live weights it is important to understand the consequence of selecting for live weight change on the selection response of live weight. Therefore, in this section I will discuss three subjects; first how live weight change might serve as an indicator trait for resilience to drought periods, second how an economic value can be estimated for live weight change as an indicator for resilience, and third, whether live weight change and live weight traits can be selected for simultaneously.

Live weight change as an indicator trait for resilience

If live weight change is an indicator trait for resilience, then resilient sheep may lose less weight during droughts. These resilient sheep may lose less live weight because they have lower energy requirements for maintenance or have increased intake or digestion capabilities when grazing poor quality feed (Silanikove, 2000; Fogarty *et al.*, 2009). Losing less live weight improves the efficiency of sheep and this improved efficiency would change the energy balance of sheep which could make the sheep easier to manage and improve the welfare status of sheep as they are able to withstand severe stress from drought periods. Being resilient to drought means sheep would have a better chance to survive and reproduce. Therefore, live weight change would qualify as a resilience trait based on the definition by Prayaga and Henshall (2005) and Barker (2009).

Live weight change gives an indication of the energy balance of sheep. Increasing live weight implies that animals have a positive energy balance, and therefore energy left over to gain live weight. There is a distinction between breeding for heavier sheep at a single time point and live weight change. If sheep are selected to be heavier it does not infer anything about how live weight changes between two time points. Additionally, live weight change could be important at difference times of the year. For example, sheep that lose less live weight change during drought periods indicates that sheep have to mobilise less energy stored as tissue into energy for other functions. Additionally, gaining live weight during periods of high pasture growth could be advantageous as an energy store which can be mobilised

during other periods when energy requirements are higher such as during pregnancy and lactation. In Chapter 2 I showed that live weight loss and gain can potentially be selected for independently, which gives farmers flexibility in choosing how they want to change the live weight profile of sheep during the year. Therefore, the live weight profile of sheep can be manipulated to increase the resilience of sheep to drought periods.

Selection can change the fat stores and energy balance of animals. Ermias *et al.* (2002) found breed differences in the ability of animals in storing body fat. They suggested that fat storage can be used as a way to manage sheep in years with good pasture growth because accumulated fat stores can then be used for pregnancy and lactation during years with poor pasture growth. Additionally, sheep that lose less live weight during drought periods will have more energy stores during pregnancy, lambing and lactation. This is a similar concept to dairy cattle where it is recommended to include body condition score in indexes to ensure that cows store enough energy resources that can be mobilised when energy requirements for milk production peak (Veerkamp and Brotherstone, 1997). Collard *et al.* (2000) also found that periods of negative energy balance are associated with increased incidence of health problems in dairy cattle. Therefore, a positive energy balance is important for storing tissue that can be utilised during periods of stress and to maintain the welfare status of animals. In conclusion live weight change could be included into sheep breeding programs to ensure enough energy is stored to be used during periods of drought.

In Chapter 3, I showed that live weight change has some important positive genetic correlations with reproduction, particularly in older ewes that bear and wean more lambs than younger ewes. Furthermore, I found a favourable genetic correlation between live weight gain during pregnancy and number of lambs born and live weight at lambing was important for total birth weight and number of lambs weaned. Genetic correlations between live weight change during lactation and reproduction were negative reflecting the high energy demands of pregnancy and lactation. This suggests that having enough resources at lambing by gaining live weight during pregnancy ensured better reproduction performance. Beilharz *et al.* (1993) defined fitness as the ability to pass genes from generation to generation. Reproduction and survival are two important components of fitness. Our results show that the ability of animals to store and mobilise body reserves can improve the reproductive performance of sheep, therefore improving fitness. Berube *et al.* (1999) found that body mass at the end of summer in 6-year-old ewes was positively correlated with longevity. Therefore, live weight change could be an important component of breeding programs for animals to indicate animals that

have a positive energy balance, and to improve the reproduction in survival, making sheep more resilient to periods of drought.

An economic value for live weight change

The relative value of live weight change as an indicator of resilience compared to other traits needs to be determined if live weight change is to be included in breeding programs. Farmers could put a high value on live weight change because they value resilience, or an economic value can be estimated based if resilience increases profit on a farming system. Animals could lose less live weight during drought periods due to reduced energy requirements for maintenance and or increased intake when grazing poor quality feed (Silanikove, 2000; Fogarty et al., 2009). Therefore, I can estimate the value of sheep that have lower maintenance requirements or eat more dry pasture, which could reduce supplementary feeding requirements and increase profit.

The economic value of live weight change as an indicator for resilience can be calculated by comparing the economic performance of a sheep that loses one kg of live weight less than another sheep. For example, consider two sheep that eat the same amount of energy. If one sheep loses live weight whilst the other gains live weight one assumption is that this sheep is more efficient and has lower maintenance energy requirements. If the farmer wanted to manage both sheep to have the same change in live weight, then the sheep that loses live weight would require more grain than the sheep that gains live weight or the sheep that gains weight could be run at higher stocking rates. Therefore, I could calculate an economic value for live weight change as an indicator for a sheep that requires less metabolisable energy when managed at the same live weight change as a sheep that loses more live weight. This would give an indication of the extra value of increasing the resilience of sheep to periods of drought.

Therefore, if I assume that sheep that lose less live weight have lower maintenance energy requirements, I can estimate an economic value of these lower energy requirements. To calculate the economic value of lower maintenance energy requirements I subtracted the energy stored in one genetic standard deviation of live weight change from the metabolisable energy requirements of sheep. I calculated the lower maintenance energy requirement using the equation;

$$ME_{\text{maintenance}} = \frac{\sigma_{\Delta WT} \times ME_{WT}}{\text{days}}$$

Where $ME_{\text{maintenance}}$ is the lower metabolisable energy requirements for maintenance per day for sheep that lose less live weight,

$\sigma_{\Delta WT}$ is the genetic standard deviation of live weight change for three-year-old ewes during pregnancy = 1.47 kg,

ME_{WT} is the metabolisable energy stored in 1 kg of live weight = 24 MJ metabolisable energy and

days is time between live weight post mating and pre lambing = 69 days.

Therefore, the metabolisable energy requirements for maintenance per day less sheep require if they lose less live weight is;

$$ME_{\text{maintenance}} = \frac{1.47 \times 24}{69} = 0.51 \text{ MJ metabolisable energy per day}$$

Therefore I subtracted 0.51 MJ ME/day from the metabolisable energy requirements of adult ewes during March and April. I then optimised management over 11 years for Katanning using the model in Chapter 5. I also calculated an economic value to having a sheep that loses 1.47 kg less live weight without decreasing metabolisable energy requirements. This provides a comparison of economic values with and without improvements in efficiency.

Increasing live weight change without reducing energy requirements had a negative economic value because losing less live weight reduced energy mobilised for other functions (Table 6.1). Keeping live weight change the same but assuming that ewes that genetically lose less live weight require less metabolisable energy had a positive economic value, because more sheep could be managed due to lower pasture intake per sheep and lower grain costs. These results highlight the importance of understanding why sheep have different live weight change during periods of drought.

Table 6.1 Ewes mated per ha, profit per ha and economic value per genetic standard deviation for live weight gain per ha.

Trait	Ewes mated /ha	Profit/ha	Economic value
No change	6.95	189.9	
Weight gain without less energy	6.91	186.4	-3.5
Weight gain with less energy	7.2	195.3	8.0

Furthermore, I estimated the economic value of live weight change for the 10 regions used in Chapter 5. The economic value for live weight change per ha decreased as coefficient of variation (CV) of pasture growth increased with a quadratic function ($p < 0.01$; Figure 6.1). The economic value per mated ewe was highest at high CV of pasture growth and followed a quadratic function ($p < 0.01$), decreasing to CV of 0.5 and increasing again as CV decreased. Therefore, sheep that require less energy during summer and autumn have a higher value in regions with low or high reliability of pasture growth, indicated by CV of pasture growth between years. This is a similar result to what I found in Chapter 5.

Regions with low or high reliability of pasture growth have a higher value when ewes require less energy during autumn because of the distribution of pasture across years and within years. Regions with low pasture growth reliability have long periods of drought so decreasing energy requirements decreases supplementary feed costs. Regions with high reliability of pasture growth have big peaks in pasture growth during spring. Despite this high peak in pasture growth, stocking rate is limited by periods of drought. This limitation occurs because a lot of pasture grows in a short period in spring which is not utilised unless sheep are managed at a high stocking rate. Therefore, increasing the potential intake reduces the influence of drought periods increasing stocking rate and pasture utilisation. Therefore, the value of resilience is different for regions, which could effect the relative importance of live weight change compared to other traits in the breeding goal.

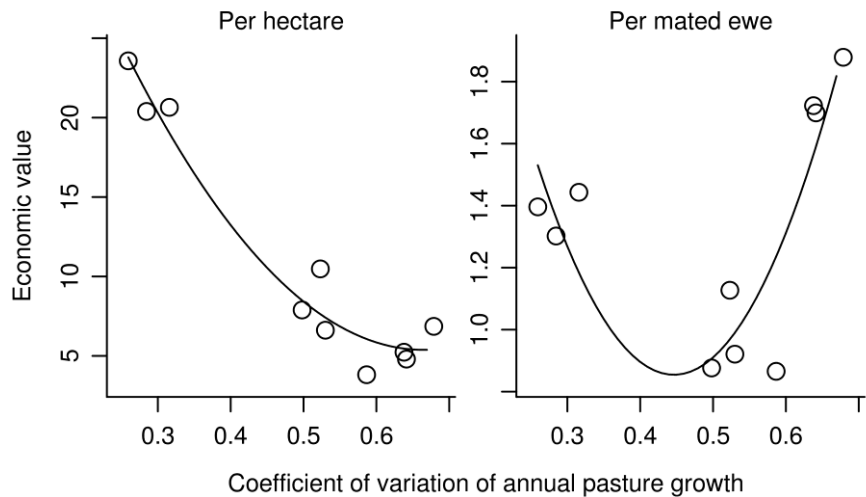


Figure 6.1 Economic value for live weight change assuming that it indicates a reduction in maintenance energy requirements. Coefficient of variation of annual pasture growth are from the 10 regions in Chapter 5 estimated across years 2002-2012.

Response to selection for live weight change and live weight

The economic values calculated in the previous section can be used to include live weight change in a breeding goal as an indicator of resilience to drought periods. I can use this economic value to estimate the response to selection of live weight change, and the expected response in other traits. The expected responses in live weight change and other traits in the breeding objective depend on the information used to estimate breeding values of selection candidates and the covariances between traits in the index and breeding goal. Given live weight change and live weight are likely to have high covariances, it might be difficult to change live weight change without changing live weight. The aim of this section is to identify if it is possible to select for live weight change and live weight in different directions.

It is important to understand if live weight change and live weight can be selected in different directions because farmers may have different preferences for the direction they want to change live weight. Conington *et al.* (2004), Wolvova *et al.* (2009) and Byrne *et al.* (2010) all found that adult live weight has a negative economic value whilst I found in Chapter 4 and 5 that the economic value for adult live weight ranges from negative to slightly positive depending on the region. Live weight had a positive economic value in my study because I included variation in pasture growth between and within years and the intake capacity of sheep. Including intake capacity increased the value of live weight compared to other studies because sheep were able to eat more poor quality pasture with higher live weight. Therefore, it is important to understand if live weight can be selected in different desired directions when also selecting for live weight change.

To understand if live weight change and live weight can be selected in different desired directions, the response to selection of these traits under different selection directions can be estimated. I estimated responses to selection for live weight and live weight change using SelAction (Rutten *et al.*, 2002). Responses to selection were estimated using two methods; first using the economic values for live weight estimated for Katanning in Chapter 5 and the economic value for live weight change estimated in the previous section assuming a decrease in maintenance energy requirements and second using desired gains approaches. The desired gains approach involves putting different weightings on traits to change traits in different desired directions. These methods give an indication of how easy it is to change live weight and live weight change in different directions.

6 General Discussion

Table 6.2 Phenotypic variance and heritability of live weight post mating (WT2), live weight pre lambing (WT3) and live weight change during pregnancy (Δ WTPREG) for three-year-old ewes.

Trait	Phenotypic variance	Heritability
WT2	36.5	0.62
WT3	37.6	0.61
Δ WTPREG	9.1	0.16

Table 6.3 Genetic correlations between live weight change and live weight at each age group with standard errors in brackets. Δ WTMATE = weight change during mating, Δ WTPREG = weight change during pregnancy and Δ WTLACT = weight change during lactation. WT1 = live weight at pre mating, WT2 = live weight at post mating, WT3 = live weight at lambing, WT4 = live weight at weaning.

Weight change	Weight	Age 2	Age 3	Age 4
Δ WTMATE	WT1	-0.37 (0.11)	-0.19 (0.14)	-0.22 (0.19)
Δ WTMATE	WT2	-0.15 (0.13)	0.10 (0.14)	0.00 (0.20)
Δ WTMATE	WT3	-0.27 (0.12)	0.03 (0.14)	-0.06 (0.21)
Δ WTMATE	WT4	-0.39 (0.13)	-0.16 (0.16)	-0.15 (0.21)
Δ WTPREG	WT1	0.27 (0.12)	0.00 (0.15)	-0.36 (0.17)
Δ WTPREG	WT2	0.18 (0.13)	-0.07 (0.14)	-0.41 (0.15)
Δ WTPREG	WT3	0.42 (0.10)	0.19 (0.13)	-0.13 (0.19)
Δ WTPREG	WT4	0.36 (0.13)	0.09 (0.16)	-0.20 (0.19)
Δ WTLACT	WT1	-0.21 (0.13)	-0.10 (0.19)	0.24 (0.14)
Δ WTLACT	WT2	-0.29 (0.14)	-0.22 (0.20)	0.20 (0.14)
Δ WTLACT	WT3	-0.28 (0.14)	-0.27 (0.21)	0.16 (0.15)
Δ WTLACT	WT4	0.54 (0.06)	0.43 (0.09)	0.52 (0.07)

Table 6.4 Phenotypic and genetic correlations between live weight post mating (wt2), live weight pre lambing (wt3) and live weight change during pregnancy (Δ WTPREG) for three-year-old ewes.

Traits	Phenotypic correlation		Genetic correlation	
	WT3	Δ WTPREG	WT3	Δ WTPREG
WT2	0.73	-0.22	0.96	-0.07
WT3		0.27		0.17

To estimate the response to selection for live weight and live weight change I assumed the same selection intensity, selection groups and generation interval used in Chapter 5. Additionally, I used the phenotypic variance and heritabilities for live weights (WT2 and WT3) and live weight change (Δ WTPREG) estimated in Chapter 3 for 3-year-old ewes during pregnancy (Table 6.2). To calculate response to selection between live weight and live weight change, the genetic and phenotypic correlations between live weight and live weight change are required. I calculated these correlations from the analysis in Chapter 3 (Table 6.3). Most of the genetic correlations between live weight change and live weight were low to moderate (-0.41 to 0.54) and in different directions. Table 6.4 shows the phenotypic and genetic correlations between live weights and live weight change estimated from the analysis in Chapter 3. Therefore, all the required information is available to estimate response to selection of live weight and live weight change. Using the economic values for live weight calculated with the bio-economic model in Chapter 5 for Katanning and the economic value for live weight change resulted in a positive response in live weight change and a negative response in both live weights. I also found using desired gains techniques that live weight change during pregnancy can have the same response to selection whilst changing live weights in any desired direction (Table 6.5). The response in the second live weight is always a more positive response than the first live weight. This is to be expected since increasing live weight change implies either a decrease in the first live weight or an increase in second live weight. The results in Table 6.5 suggest that live weight change and live weight can be changed in the desired direction simultaneously.

Table 6.5 Economic values and response to selection in kg for live weight and live weight change estimated using the bio-economic model in Chapter 5 and with desired gains techniques. Traits are live weight post mating (WT2), live weight pre lambing (WT3) and live weight change during pregnancy (Δ WTPREG) for three-year-old ewes. Response to selection in genetic standard deviations in brackets

Economic values (\$AU/kg)			Response to selection (kg)		
WT2	WT3	Δ WTPREG	WT2	WT3	Δ WTPREG
Bio-economic model					
-0.15	-0.15	5.4	-1.08 (-0.23)	-0.82 (-0.17)	0.20 (0.17)
Desired gains					
0.85	-0.90	10	0.00 (0.00)	0.29 (0.06)	0.23 (0.19)
1	1.15	10	-2.89 (-0.61)	0.00 (0.00)	0.23 (0.19)
-0.2	-0.2	10	-0.78 (-0.16)	-0.51 (-0.11)	0.23 (0.19)
0.2	0.2	10	0.95 (0.20)	1.22 (0.25)	0.23 (0.19)
-0.80	0.67	10	-0.15 (-0.03)	0.15 (0.03)	0.23 (0.19)

These estimates of responses to selection for live weight and live weight change do not include all traits in the breeding objective which could change the responses in live weight and live weight change. In Chapter 5 I showed that adult live weight had a positive response to selection despite having a low economic value in relation to other traits. This high response was due to high a positive economic value of yearling live weight which increased the response in adult live weight due to the high genetic correlation between these traits. Therefore, it is also important to understand how live weight change would interact with other traits, considering I found significant genetic correlations between live weight change and reproduction in Chapter 3.

The genetic parameters estimated in Chapter 2 and 3 showed it is possible to select adult Merino ewes that lose less weight during summer and autumn, whilst having mostly favourable responses in reproduction. Live weight change has a positive economic value only if sheep that lose less live weight are more energy efficient. Additionally, I have shown that although the heritability of live weight change is largely determined by the correlation between weights at start and end of the interval, it is possible to select for live weights and live weight change in different directions. In conclusion, the results in this thesis demonstrate that live weight change could be a potential trait to select sheep that are more resilient to years with poor pasture growth.

6.2 Breeding sheep to make sheep farms more resilient to uncertainty

In Chapters 4 and 5 I showed that variation in pasture growth and commodity prices affects the optimum breeding objectives of sheep farmers. Chapters 4 and 5 investigated two different management types, optimising management in each year and across years. These different management styles may change optimum breeding objective of sheep farming systems. Chapter 4 showed that including variation in pasture growth across years changed the relative importance of traits in the breeding objective. Chapter 5 showed that different regions have different breeding objectives based on how much pasture growth varies across years. These results can be used to customise breeding programs that select the most appropriate sheep for the environments that differ in the degree of uncertainty on or variation in pasture growth. These chapters explored how breeding animals affect the profitability of farming systems that experience uncertainty. This theme can be explored more by investigating how profit across years is sensitive to changes in pasture growth and commodity prices. Therefore, in this section I will

discuss three subjects; first the sensitivity of the economic value of traits to variation in pasture growth; second how different management types affect optimum breeding goals, and third, how different management types affect the sensitivity of economic values to variation in pasture growth and commodity prices.

Sensitivity of traits to variable pasture growth

A successful breeding program contributes to an increase in profit of a production system by improving traits that affect profit. In environments with uncertain pasture supply and prices, the farming system and/or sheep need to be resilient to uncertainty otherwise in years with low pasture growth the farming system is not profitable. Therefore, a resilient farming system needs to be defined. One definition of a resilient farming system is how stable is the system and how capable it is able to resist uncertainty (Holling, 1973; Ludwig *et al.*, 1996; Palumbi *et al.*, 2008). Therefore, a resilient farming system should be profitable in all years regardless of the availability and costs of resources. Assessing the profitability of traits across years gives an indication of how traits contribute to the resilience of the farming system over the long term.

To understand if some traits make farming systems more resilient to uncertain pasture growth, I plotted the economic values estimated for Katanning in Chapter 5 for yearling fleece weight and adult fibre diameter estimated in each year against the average pasture growth for years 2002-2012 (Figure 6.2). I also included the economic values for live weight change assuming a reduction in energy requirements estimated in Section 6.1. I chose these traits because they have a similar magnitude of economic value, hogget clean fleece weight = 12.3, adult fibre diameter = -9.8 and live weight change = 8.0. The economic value for hogget fleece weight varied a lot more (range -42 to 53) than adult fibre diameter (-12.6 to -2.6), and live weight change (3.7 to 11.7) (Figure 6.2). Additionally, increasing hogget fleece weight decreases profit in years with low pasture growth. The economic values for adult fibre diameter and live weight change decrease as average pasture growth increases whilst hogget fleece weight increases. This means that decreasing fibre diameter and increasing live weight change has more value in drought years than increasing fleece weight. The higher economic value of fibre diameter is more related to price than resilience to pasture growth because changing fibre diameter does not change energy requirements and there was a higher premium for fine wool in years with low pasture growth. Therefore I can conclude from the higher variation in economic values that fleece weight is more sensitive to variation in pasture growth than fibre diameter and live weight change.

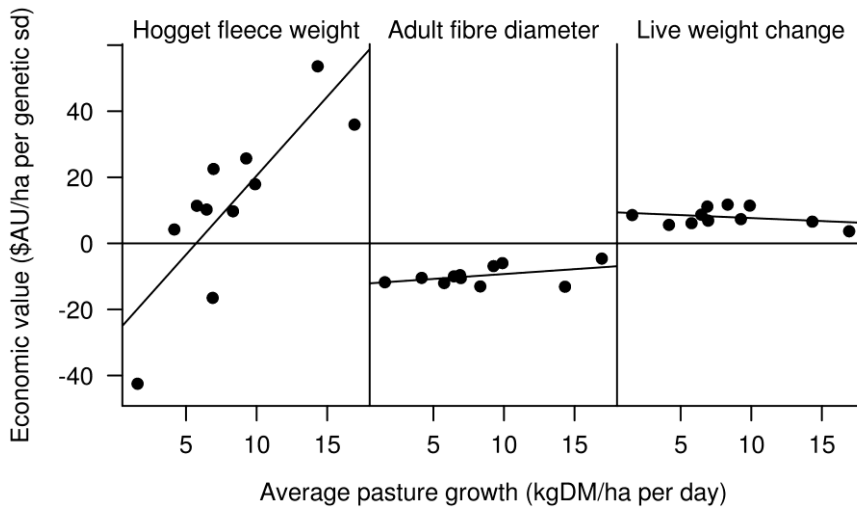


Figure 6.2 Economic values of hogget fleece weight, adult fibre diameter, and live weight change plotted against average daily pasture growth from 2002-2012. The economic values for hogget fleece weight and adult fibre diameter are from the analysis in Chapter 5 for Katanning whilst the economic values for live weight change are from the analysis in Section 6.1 assuming a reduction in energy requirements

This sensitivity to pasture growth of traits may affect farmers' preference for the type of sheep they would prefer based on Figure 6.2. Some farmers may prefer to make more money in the good seasons as a buffer for poor seasons and would give a preference to sheep with a relatively high clean fleece weight. Other farmers may prefer to have a more constant income across years and put more emphasis on sheep with low fibre diameter or less live weight loss, even though the average profit over years might be lower. Therefore, the emphasis that farmers put on each trait may not only depend on the value of trait across all years, but also how each trait affects profit in each year.

Resilience management and optimal breeding goals

In Chapter 4 and 5 I showed that the sensitivity of traits to pasture growth may also depend on the management of the production system. Additionally, hogget fleece weight was sensitive to variation in pasture growth (Figure 6.2) because profit across all years was maximised when the flock was managed at a high stocking rate. This optimal management meant fleece weight had high value in years with high pasture growth which offset the negative value in poor years. Sheep farmers in Australia often reduce sheep numbers to avoid having too many sheep in years with low pasture growth (Austen *et al.*, 2002; Robertson and Wimalasuriya 2004).

Therefore, I assessed how reducing stocking rates affects the economic value of traits.

When farms are managed at stocking rates below optimum, the profit decreases. However, the decrease in profit may also mean that profit across years is more constant, with lower sensitivity to changes in pasture growth. Therefore, I plotted profit in each year against pasture growth for Katanning from Chapter 5 (Figure 6.3). Profit was compared for different stocking rates below the optimum stocking rate, fixed at 5, 6 and 7 ewes mated per ha. As stocking rate decreased, profit in years with high pasture growth decreased but profit in years with low pasture growth increased. Therefore, decreasing stocking rate is a good strategy to reduce sensitivity of profit to changes in pasture growth.

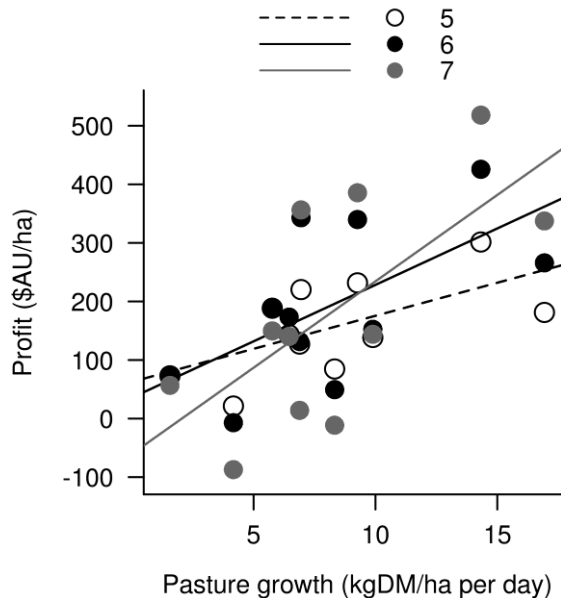


Figure 6.3 Profit plotted against pasture growth in years 2002-2012 for Katanning. Profit was estimated using the model in Chapter 5.

When the farm is managed at fixed stocking rates, the perspective of the breeding program changes and is no longer limited by the area of the farm, but by the number of sheep that are managed. This new perspective affects the value of traits depending on the density the stock are managed. Figure 6.4 shows profit calculated for Katanning using the model in Chapter 5 before genetic change (no change) and when number of lambs weaned and adult fleece weight are increased by one genetic standard deviation. Profit is plotted against the stocking rate of the farm (ewe mated per ha). Increasing number of lambs weaned has more value than

increasing adult fleece weight until a stocking rate of ~6.3 ewes mated per ha. When the farm is stocked higher than 6.3 ewes per ha then increasing adult fleece weight has more value than increasing number of lambs weaned. Therefore, if farmers reduce stocking rate in response to variation in pasture growth, number of lambs weaned would become more important than clean fleece weight.

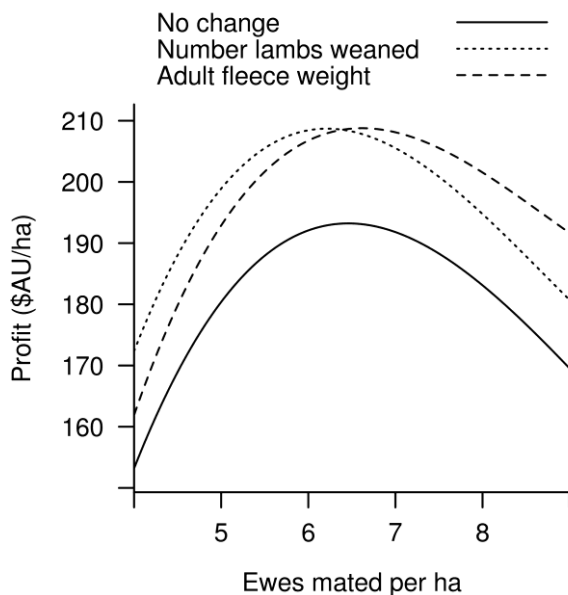


Figure 6.4 Profit plotted against stocking rate (ewes mated per ha) when there is no change to traits (no change) and when number of lambs weaned and adult fleece weight are increased by one genetic standard deviation. Profit was estimated using the model in Chapter 5 across years 2002-2012 for Katanning.

This change in the relative importance of number of lambs weaned and adult fleece weight is because there is a different optimum stocking rate when both traits are improved. This change in relative importance of traits is similar to optimal breeding objectives for dairy cattle. When a farming system has a quota or fixed amount of milk that can be produced the optimal breeding objective changes compared to when there is no limit on the amount of milk produced (Veerkamp *et al.*, 2002). Additionally, different perspectives between production systems can impact on the economic values (Brascamp *et al.* 1985). Therefore, it is important to consider how farming systems are managed in response to variation in pasture growth because this changes the optimal breeding program of the farming system.

Resilience management and breeding to increase resilience

I have shown in this section that some traits are more sensitive to variation in pasture growth. Additionally, reducing stocking rate to increase the resilience of the farm to variation decreases the sensitivity of farm profit to changes in pasture growth and changes the optimal breeding objectives of the farm. The next step is to investigate whether decreasing stocking rate to make the farm more resilient changes the sensitivity of economic values to changes in pasture growth and commodity prices. Therefore, I plotted economic values for hogget fleece weight, adult fibre diameter and live weight change assuming a decrease in maintenance energy requirements against pasture growth in each year when stocking rate was fixed. The estimated are from the model in Chapter 5 where stocking rate was optimised across all years.

Decreasing stocking rate decreases the sensitivity of all traits to variation in pasture growth (Figure 6.5). This decrease in sensitivity of traits to variation in pasture growth caused a re-ranking between stocking rates for hogget fleece weight with low stocking rates having higher economic values at low pasture growth and high stocking rate having higher economic values at high pasture growth. The economic value becomes more negative for adult fibre diameter and more positive for live weight change as pasture growth decreases. This change in economic values caused a scaling effect for fibre diameter and live weight change for stocking rate on pasture growth. Therefore, decreasing stocking rate had more effect on the economic values for hogget fleece weight across years than adult fibre diameter and live weight change.

The re-ranking for hogget fleece weight occurred because managing sheep at a higher stocking rate would require more grain when pasture growth is low and consequently profit from high wool sales would be lower in that those years compared to years when pasture growth is high. For adult fibre diameter the scaling effect is related to price because there was higher premium for fine wool in years with low pasture growth. For live weight change the scaling was because increasing the efficiency of sheep has a higher economic value when sheep are managed at high stocking rate. Decreasing maintenance energy requirements decreases the amount of dry pasture eaten by sheep. If low sheep numbers are managed then pasture growth does not limit production and there is no value of decreasing energy requirements of sheep. Therefore, live weight change and efficiency has more value when farmers are managing their flock close to the optimal stocking rate compared to farmers that manage at lower stocking rates.

In conclusion, decreasing stocking rate in response to variation in pasture growth also reduces the sensitivity of traits to variation in pasture growth. Additionally, the

relative importance of traits across all years when sheep are managed below optimal stocking rates changes. Therefore, managing production systems at lower stocking rates to reduce high losses in years with poor pasture growth also increases the value of production traits in years with poor pasture growth compared to production system managed at higher stocking rates.

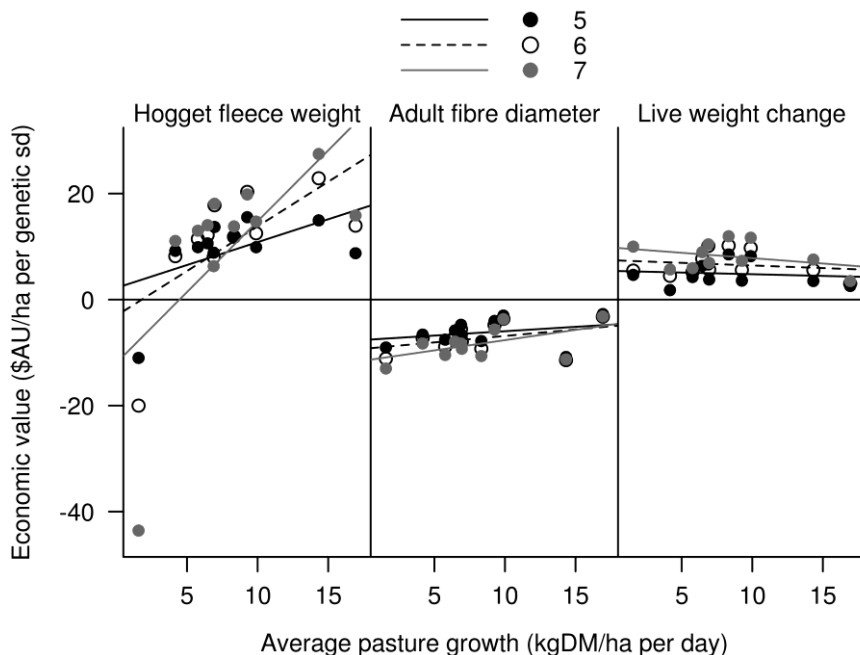


Figure 6.5 Economic values (\$/ha/genetic standard deviation) plotted against average pasture growth for 2002-2012 for hogget fleece weight, adult fibre diameter, and live weight change when ewes per ha are fixed at 5, 6 or 7. The economic values for hogget fleece weight and adult fibre diameter were taken from the analysis in Chapter 5 for Katanning whilst the economic values for live weight change are from the analysis in section 6.1 assuming a reduction in energy requirements.

6.3 Breeding to making farming systems resilient

The role of breeding in making farming systems resilient has been explored in many other livestock and plant species. Additionally, there are many theories about how to make farming systems and resilient. To understand the role of breeding in making farming systems resilient I will discuss three subjects in this section; first the characteristics of a resilient farming system, second how plants and animals have been selected to have increased resilience, and third, how breeding objectives have been used to increase resilience of farming systems.

Characteristics of a resilient farming system

Howden *et al.* (2007) suggest production systems need to be adapted to reduce sensitivity to climate variations, the biggest cause of variation in production in many regions. This adaptation means farms need to become more resilient to climate variation. Studies into resilience investigate how periods of gradual and rapid change interact with a system (Folke, 2006). There are two main definitions of resilience in the literature. The first is the time after a disturbance that a system needs to return to equilibrium (Ives, 1995; Mittelbach *et al.*, 1995; Neubert and Caswell, 1997; van Apeldoorn *et al.*, 2011). The second is how stable a system is (Holling, 1973; Ludwig *et al.*, 1996; Palumbi *et al.*, 2008) which implies that resilient systems are managed to avoid being out of equilibrium and to avoid bankruptcy. The overall aim of resilience is to maintain income whilst ensuring the farming system is healthy to avoid future losses in profit.

The most common recommendation to make farming systems resilient is by maintaining diversity (Altieri, 1999; Tscharnkte *et al.*, 2005; Hajjar *et al.*, 2008; Darnhofer *et al.*, 2014). Maintaining diversity increases the stability of farming systems by buffering against environmental and economic risks and increases the ability of farms to be productive during stresses and shocks (Altieri, 1999). Kenny (2011) suggests there is variation in resilience across farms, with some farmers managing uncertainty better than others. Ghimire *et al.* (2012) found that integrating crop and livestock increases profit. This increase was from optimising the use of available resources by minimising economic risks and negative environmental effects of more specialised systems. Gunderson (2000) suggested farmers can buffer against poor years by managing more animals than required in good years as a buffer that can be removed in poor years. These management techniques increase resilience, but there is little research about how breeding can make sheep farming systems more resilient to variation in pasture growth and prices. To understand the role of breeding to increase the resilience of farming systems, research from other animals and plants can provide insight.

Selecting animals with increased resilience

All animal and plant species are managed in a range of environments with differences in management, disease, feed availability, price and quality, and temperatures (Star *et al.*, 2008). To match these differences, animals and plants require appropriate breeding programs to optimise production across these differences. Prayaga and Henshall (2005) and Barker (2009) suggest resilient animals should be able to reproduce and survive in uncertain environments, with good performance across all years. Therefore, most research into breeding and

resilience suggest that functional or robustness traits need to be incorporated into breeding objectives due to the negative impact that high selection on production has on robustness (Rauw *et al.*, 1998). In this section I will discuss how animals and plants have been bred to be more resilient.

In poultry breeding, high selection for production and intensification of production systems have increased behavioural, physiological, and immunological disorders (Rauw *et al.*, 1998). Therefore, Star *et al.* (2008) suggested that traits related to cannibalism, growth problems and diseases should be incorporated into chicken breeding goals. Knap (2005) in his review of robustness in pig breeding suggested that robustness traits have an economic value similar to production traits. Additionally, pigs can be more robust by improving fitness traits such as leg quality, mortality rates, and longevity.

In pasture based industries, resistance to parasites is a common breeding goal in sheep (Bisset *et al.*, 1994; Baker *et al.*, 2003). In dairy cattle traits such as lameness, body condition score and hock lesions are included in breeding goals to increase longevity (Jørgensen *et al.*, 2010). There has also been an effort to use breeds more suited to certain production system environments, for example, production systems which rely on pasture or systems that rely on concentrates (Horn *et al.*, 2013). Also energy balance and feed capacity have been researched to make dairy cattle more resilient during lactation when requirements for energy are high (Veerkamp *et al.*, 2001).

Plant breeders use similar techniques to select for resilience as animal breeders by increasing genetic diversity by including more functional traits in breeding goals seen as the best way to combat uncertainty in farming systems (Reusch *et al.*, 2005; Hajjar *et al.*, 2008). For example drought, salt and water-logging-resistant species and varieties of crops and short-duration crops have been recommended to increase resilience (Verulkar *et al.*, 2010; Mijatović, 2013).

Another approach is to breed for a stable performance in production traits to decrease environmental sensitivity (Brown, 1988; Louw, 1990). This type of selection ensures plants and animals perform well in a range of environmental conditions (Knap, 2005). Identifying animals with low sensitivity to an environment involves estimating the breeding value in relation to the environment by fitting a reaction norm or slope to the breeding values. Animals with reaction norms with high slopes have a high sensitivity to the environment and a genotype by environment interaction is said to exist.

Therefore, there are similarities in techniques between plants and animals for the best way to breed for increased resilience by increasing the resilience of individual breeds and animals. There is limited information about how it is applicable in

systems. For example, there are many studies into how to make the system resilient and how to breed animals to be resilient. There is a gap in joining the two to find out how to breed to make the system resilient.

Breeding objectives to increase the resilience of farming systems

Selecting animals that have a lower sensitivity to variation in the environment can also be applied to breeding objectives, to make farm income more resilient to variation. This type of modification to breeding objectives has been used by applying risk to breeding objectives. Farmers that are risk adverse may prefer to select for traits that are more resilient to variation as a way to increase cash flow in years with unfavourable conditions. Although the overall profit may be lower, the distribution of profit across years is more consistent.

This concept of risk has been used by Eskridge and Johnson (1991), Kulak *et al.* (2003) and Okeno *et al.* (2012) who recommend breeding objectives for beef cattle and chicken, and recommend soybean cultivars based on farmer preferences for stability of income and yield. Kulak *et al.* (2003) and Okeno *et al.* (2012) calculated optimal economic values when discounts for variation in profit were included in the profit equation (farmers adverse to risk) and compared it to profit without considering variation in profit (risk neutral). These methods were useful for optimising management within a system when farmers prefer stable profit. These or similar methods could also be considered in comparing the differences in production systems.

Additionally, farmers' attitude to risk can also be reflected in their individual preference to traits in breeding programs. Many studies have used choice modelling to investigate how farmer and breeder preferences are affected by differences in production system and environments (Sae-Lim *et al.*, 2011, Byrne *et al.*, 2012). These techniques capture the perspectives of farmer attitudes towards management of animals and the perceived value of traits. This perceived value of traits could depend on how the farmer was taught to breed animals in the past, their experiences or perception of future climate or prices.

Byrne *et al.* (2012) found significant differences between economic values from bio-economic modelling and choice modelling for traits that do not have a straight forward value, such as adult live weight and fat. These differences between bio-economic modelling and choice modelling experiments may also be attributed to the complexity of farming systems where the value of traits is often not clear. Therefore, based on farmers' experiences with animals losing lots of live weight in drought years, they might prefer to select for resilience traits to breed sheep that are easier to manage in drought years. Additionally, farmers may put more

emphasis on traits that are less sensitive to the environment. Therefore, our study could provide farmers with more insight into the type of sheep they prefer to select for on their farm. Apart from these techniques, there is limited information about how breeding objectives are affected by variation in pasture growth prices.

6.4 Contribution of my research to breeding and resilience and conclusions

Most of the research into breeding for resilience has focused on improving the robustness of animals and plants. There is limited information about how to optimise breeding programs when the availability and price of resources is uncertain. In our study I showed that some production traits reduce the resilience of sheep production systems more than others because they have a higher sensitivity to changes in pasture growth and prices. Therefore, including variation gives a more accurate estimate of the economic values of production traits. Additionally, the variation of traits can be used by farmers who can make informed decisions about which traits ensure a more stable income across years.

In Section 6.1 I showed that live weight change as an indication of reduced maintenance energy requirements has a high economic value in relation to other production traits. Additionally, live weight change was less sensitive to variation in pasture growth than some production traits and increased profit in years with low pasture growth. In Chapter 4 longevity also had a high economic value which increased when variation in pasture growth and prices were considered. Therefore, selecting animals and plants for robustness and functional traits can increase the resilience of farming systems. There were other production traits, however, such as fibre diameter that also increased the resilience of farming systems. Therefore, although robustness traits are required to ensure that animals have an adequate level of welfare, production traits can also be used to increase the resilience of farming systems to variation. Furthermore, since breeding objectives have focused mainly on production traits in the past, and production traits are easier to select for than robustness traits, it is important that the right emphasis is put on production. The emphasis on production traits is important because an unbalanced breeding program can significantly reduce the resilience of farming system which may be difficult to reverse.

Additionally, to make farming systems more resilient, producers can adapt their management or their breeding program (Hoffman, 2010). Hoffman (2010) suggests that farmers first change management and only change genetics when it is unavoidable. I showed in Chapters 4 and 5 and Section 6.2 that changes in

management in response to variability also changes optimum breeding objectives. Therefore, I have shown that farming systems will become more resilient if management and breeding are adapted simultaneously. In conclusion, it is important to understand the value of traits at the level of the production system, because all of the interactions between environment and production can be included. Therefore, studies into resilience should be done at the farm level and not at the animal level.

Studying resilience at the farm level, incorporating all elements of variation is different to incorporating risk into profit equations such as the studies by Kulak *et al.*, (2003) and Okeno *et al.*, (2012). This difference is because economic values of traits need to be assessed within the constraints of the system and at the correct perspective, such as flexible stocking rates or fixed stocking rates. Therefore, our methods are useful and distinguished from other studies into risk as it considers profit across a range of years.

Furthermore, investigating the sensitivity of economic values to changes in the environment can be applied to all livestock systems that have variation in environments, prices and disease across years. For example, diseases may on average have low impact on profit, but a serious outbreak could make a farming system unviable. Severe outbreaks of disease can have serious implication for fish (Leung and Bates, 2013), shrimp (Chen, 1996) and pig (Elbers *et al.*, 1999) farms causing many deaths and replacement of stock. In these cases, resilience to disease outbreaks would not have a high value most of the time but extremely high value during outbreaks. Therefore, understanding sensitivity of economic values to changes in the environment gives a more robust analysis of the value of traits across all possible scenarios.

Bio-economic models, such as those in Chapter 4 and 5, can therefore be used to estimate the reaction norm of traits in relation to their economic value, estimating the economic by environment interactions. I showed in Chapter 4 and 5 that these economic by environment interaction can occur within a production system and between production systems in different regions. Because genotype by environment interactions can occur with and between environments, these bio-economic models can incorporate the genotype by environment interactions to understand how selecting sheep that are resilient to variation in pasture growth can further make the production systems resilient.

Additionally, bio-economic modelling of variation across years has advantages over using choice modelling (Sae-Lim *et al.*, 2011, Byrne *et al.*, 2012). Bio-economic models can include long term price and pasture information which indicates long term profit and economic values. Incorporating this long term information is one

advantage of bio-economic models, because choice modelling captures farmers' preferences at one point in time. This preference could be biased by the pasture growth and prices in the current years, which may be why Byrne *et al.* (2012) found differences between bio-economic models and choice modelling. Therefore, bio-economic models are a useful tool for calculating long term impacts of pasture growth and prices, which can assist farmers in choosing the optimal breeding program for their production system.

Conclusions

Breeding sheep to make farms resilient to uncertainty and profitable across all years, may involve selecting sheep for resilience traits, but could also involve adapting the emphasis of production traits to decrease sensitivity to a varying environment. Additionally, the value of resilient sheep depends on how farmers manage their sheep. I found that sheep can be selected to lose less live weight during periods of drought which, if related to with lower energy requirements, has a high value in relation to production traits. Breeding for resilience also decreases the environmental sensitivity of farms, although other production traits, such as wool quality, also have a low environmental sensitivity. In conclusion, resilience traits have value on farms with high variation in pasture growth, but should be balanced with production traits to maximise profit across all years.

Additionally, most studies into resilience aim to make the animal or plant more resilient. In this thesis I show that the effectiveness of breeding for resilience depends on how the system is managed. Therefore, studies into breeding and resilience should be done at the farm level and not on the individual level. Furthermore, variation in pasture growth and prices should be incorporated into breeding objectives to understand how to select the best animals that will make the farming system resilient in the long term.

This thesis has contributed strategies that could help increase the profitability and viability of sheep production systems in Western Australia. These strategies could help sheep farmers overcome the challenge of managing sheep on farms with high pasture growth and commodity price uncertainty. This improved management could help reverse the downward trend in sheep production and profitability of the Western Australian sheep industry. Additionally, the techniques used in this thesis can be applied to other animals and plants to devise strategies to make farming systems more resilient to uncertainty in resource availability and diseases.

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Summary

The sheep industry in Western Australian has had many challenges over the last 20 years which have caused sheep numbers to decline from 35 million to 15 million. The move away from sheep has been driven by farmers' preference for cropping because it has had higher rates of productivity gain and profitability compared to sheep. Sheep management remains labour intensive and farmers have trouble managing profitable sheep systems due to high variation in pasture growth and commodity prices between years. Nevertheless, it is important that farming systems remain diverse to be resilient to environmental and economic changes and sheep will remain an important component of Western Australian farm systems especially if systems can be developed to improve their profitability.

One way to improve resilience and profitability of mixed farming systems is through breeding of sheep. These improvements are cumulative and permanent and are easy to integrate into current management. Breeding for resilience can be investigated at the animal level, by selecting sheep that are resilient to variation in pasture growth, or at the farming system level, by selecting sheep that will maximise profitability at the farm level. Therefore, this thesis had two aims; 1. Quantify the potential to select and breed sheep that are more resilient to varying pasture growth and 2. Quantify how sheep breeding can make farming systems more resilient to varying pasture growth and meat, wool, and grain prices. The first aim involved investigating live weight change as an indicator of resilience to drought periods. The second aim involved investigating how variation in pasture growth and prices affect optimal breeding goals for sheep farms in different regions and using different management.

To determine if sheep can be bred to be resilient to varying pasture growth, in Chapter 2 I investigated if live weight change is a heritable trait. Selecting sheep that lose less live weight during drought periods could increase the resilience of these animals. I investigated live weight change measured on 2,336 pedigreed adult Merino ewes managed in a Mediterranean climate in Katanning in Western Australia. Live weight change traits were during mating when ewes on average lost weight and during lactation when ewes on average gained live weight. I used three methods to estimate variance components of live weight change: 1) as a trait calculated by subtracting the first live weight from the second, 2) multivariate analysis of live weight traits, and 3) random regression analysis of live weight traits. The multivariate model fitted the data better than random regression based on Akaike and Bayesian information criterion so I considered the results of the multivariate model to be more reliable. The heritability of live weight loss (h^2 range = 0.05 to 0.16) was smaller than that of live weight gain (h^2 range = 0.14 to 0.37). Based on these heritabilities I concluded that live weight change could be included

in breeding programs as a potential indicator trait for resilience to variation in pasture growth.

To include live weight change in a breeding goal, correlations with other traits in the breeding objective need to be known. In Chapter 3 the genetic correlations (r_g) between live weight change during mating, pregnancy and lactation, and reproduction traits were estimated using records from ~7350 fully pedigreed Merino ewes managed at Katanning in Western Australia. Reproduction traits were number of lambs and total weight of lambs born and weaned. Genetic correlations between live weight change and reproduction were estimated within age classes. In two-year old ewes, live weight change during the mating period had a positive genetic correlation with number of lambs weaned ($r_g = 0.58$); live weight change during pregnancy had a positive genetic correlation with total weight of lambs born ($r_g = 0.33$) and a negative genetic correlation with number of lambs weaned ($r_g = -0.49$). All other genetic correlations were not significantly greater magnitude than zero but estimates of genetic correlations for three-year-old ewes were generally consistent with these findings. The direction of the genetic correlations was consistent with variations in the energy requirements of the ewes during pregnancy and lactation, and the stage of maturity of the ewes. In conclusion, most of the genetic correlations between live weight change and reproduction traits across the three age groups were not significant. The significant correlations were mostly in favourable directions. Therefore, optimised selection strategies can select for live weight change and reproduction simultaneously.

In Chapter 4 I investigated how variation in pasture growth and meat, wool, and grain prices affect the economic values of sheep traits. I modelled a sheep farm with a self-replacing Merino flock bred for wool and meat in a Mediterranean environment. Management decisions were optimised across 5 years using dynamic recursive analysis to maximise profit when commodity prices and pasture growth varied annually. The economic value of seven traits in the breeding objective were compared for a scenario with average and a scenario with varying pasture growth and commodity prices over years. Variation in pasture growth and commodity prices decreased average profit and increased the economic value of all breeding goal traits compared to the average scenario. The economic values that increased the most when variation in pasture growth and commodity prices were included were for traits that had increases in profit with the smallest impact on energy requirements such as yearling live weight, longevity and fibre diameter. Therefore, our results showed that it is important to account for variation in feed availability and commodity prices when determining the expected profit and economic values for traits.

In Chapter 5 I investigated if breeding goals need to be adapted for different regions depending on the reliability of pasture growth across years. I did this because within Australia's Mediterranean climate zone, the distribution of annual pasture growth is different between regions. I modified the model in Chapter 4, optimising management across 11 years for 10 regions in Western Australia. These 10 regions represented different levels of reliability of pasture growth with mean annual pasture growth decreasing and the coefficient of variation of annual pasture growth increasing as the pasture growth became less reliable. I calculated economic values and selection responses for nine traits by optimising sheep management across 11 consecutive years. I identified two potential breeding goals, one for regions with low or high pasture growth reliability and one for regions with medium reliability of pasture growth. The breeding goal for regions with high or low reliability of pasture growth had more emphasis on live weight traits and number of lambs weaned. The second breeding goal for regions with medium reliability of pasture growth had more emphasis on decreasing fibre diameter. Regions with low or high reliability of pasture growth had similar breeding goals and response to selection because the relationship between economic values and the coefficient of variation for pasture growth were not linear for live weight traits and number of lambs weaned. Therefore, this study can be used by farmers to customise breeding goals depending on the reliability of pasture growth on their farm.

In the general discussion (chapter 6) I combined the results of chapters 2 to 5 to bring together breeding sheep for resilience and how breeding can be used to make sheep farms more resilient. An economic value for live weight change during pregnancy was estimated using the model from Chapter 5. This economic value was calculated assuming that sheep that lose less live weight have lower metabolisable energy requirements and showed that increasing the efficiency of animals during drought had high value compared to production traits. Additionally, I showed that live weight change and live weights can be selected independently depending on the desired direction of change for each trait. I also showed that the economic value of fleece weight is more sensitive to variation in pasture growth across years than fibre diameter and live weight change and this sensitivity decreases if sheep are managed at lower stocking rates in response to variation in pasture growth across years. From this study, I concluded that breeding sheep to be resilient to variation in pasture growth across years can contribute towards making farming systems more resilient to variation in pasture growth and prices, but some production traits were also effective at increasing the resilience of farming systems. In addition, the economic value of traits depends on the

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management of the farming system, which means resilience studies should be done at the farming system level and not on the animal level.

This thesis has contributed strategies that could help increase the profitability and viability of sheep production systems in Western Australia. These strategies could help sheep farmers overcome the challenge of managing sheep on farms with high pasture growth and commodity price uncertainty. This improved management could help reverse the downward trend in sheep production and profitability of the Western Australian sheep industry.

Samenvatting

De schapensector in West-Australië heeft de afgelopen 20 jaar een moeilijke tijd gehad waardoor het aantal schapen is gedaald van 35 naar 15 miljoen. Boeren zijn gestopt met het houden van schapen omdat er met akkerbouw meer te verdienen was. Het houden van schapen is arbeidsintensief en er is veel onzekerheid over de opbrengsten van de schapenhouderij vanwege grote schommelingen in grasgroei en prijzen van vlees en graan over de jaren. Het is belangrijk dat landbouwsystemen voldoende divers blijven om zo bestand te zijn tegen veranderende milieu en economische omstandigheden. De schapenhouderij is een belangrijk onderdeel van de West-Australische landbouw, maar om dit voor de toekomst veilig te stellen is het nodig om systemen te ontwikkelen waarin de winstgevendheid groter is.

Fokkerij van schapen is een manier om gemengde bedrijfssystemen winstgevender te maken en bij te dragen aan vermindering van gevoeligheid voor fluctuaties in grasgroei en prijzen. Verbeteringen door fokkerij zijn cumulatief en permanent en zijn eenvoudig in het huidige systeem in te passen. Fokkerij dient gericht te worden op vergroting van de robuustheid van schapen door het fokken van dieren die beter kunnen omgaan met variatie in grasgroei en die bijdragen aan verbetering van winstgevendheid van het bedrijf. Dit vraagt om nieuwe methoden en inzichten. De doelstellingen van het onderzoek beschreven in dit proefschrift zijn om 1. te kwantificeren hoe groot de mogelijkheden zijn om schapen te fokken die robuuster zijn als grasgroei varieert en 2. te kwantificeren hoe fokkerij de schapenhouderij als systeem meer robuust kan maken voor variatie in grasgroei en prijzen van vlees, wol en graan. Voor de eerste doelstelling is gekeken of verandering in gewicht gebruikt kan worden als indicator voor robuustheid voor periode van droogte waarin grasgroei afwezig is. Voor de tweede doelstelling is gekeken hoe variatie in grasgroei en prijzen kan worden opgenomen in het fokdoel en wat de effecten hiervan zijn voor schapenbedrijven onder verschillende omstandigheden.

In Hoofdstuk 2 is gekeken naar de erfelijkheid van verandering in gewicht als indicator voor robuustheid voor droogteperiodes. Het selecteren van schapen die minder gewicht verliezen tijdens droogte, kan de robuustheid vergroten. Daartoe is verandering in gewicht van 2336 volwassen Merino schapen met bekende afstamming geanalyseerd die gehouden zijn in het mediterrane klimaat van Katanning in West-Australië. Er is gekeken naar gewichtsverandering tijdens het dekseizoen, periode waarin oaien gemiddeld gewicht verliezen, en naar gewichtsverandering tijdens lactatie, periode waarin oaien gemiddeld in gewicht toenemen. Drie methodes zijn gebruikt om de genetische parameters te schatten voor gewichtsverandering, te weten: 1. door gewichtsverandering te berekenen als verschil tussen gewichten en dit als kenmerk te analyseren, 2. door multivariate

analyse van gewicht op verschillende tijdstippen, en 3. door random regressie analyse van gewicht op verschillende tijdstippen. Op basis van Akaike en Bayesiaans informatie criterium is geconcludeerd dat met het multivariate model de data beter beschreven worden dan met random regressie. De resultaten van het multivariate model waren het meest betrouwbaar. De erfelijkheidsgraad van gewichtsverlies was kleiner ($0.05 - 0.16$) dan van gewichtstoename ($0.14 - 0.37$). Gebaseerd op deze erfelijkheidsgraden kan geconcludeerd worden dat gewichtsverandering kan worden meegenomen in het fokprogramma als potentiële indicator voor robuustheid.

Om verandering in gewicht in het fokprogramma op te nemen, moeten de correlaties met andere kenmerken in het fokdoel bekend zijn. In Hoofdstuk 3 zijn de genetische correlaties (r_g) geschat tussen gewichtsverandering tijdens dekken, dracht en lactatie enerzijds en reproductiekenmerken anderzijds. Voor deze analyses zijn gegevens van circa 7350 Merino ooien geanalyseerd. Deze ooien werden in Katanning in West-Australië gehouden. Voor reproductiekenmerken is in deze studie gekeken naar het aantal lammeren, het totale gewicht van de lammeren bij geboorte en bij spenen. Genetische correlaties tussen gewichtsverandering en reproductiekenmerken zijn geschat binnen leeftijdsgroepen. In tweejarige ooien was de genetische correlatie tussen gewichtsverandering tijdens het dekseizoen met het aantal gespeende lammeren positief ($r_g=0.58$); tussen gewichtsverandering tijdens dracht met het aantal geboren lammeren was eveneens positief ($r_g=0.33$). De genetische correlatie van gewichtsverandering tijdens dracht met het aantal gespeende lammeren was echter negatief ($r_g=-0.49$). Alle andere genetische correlaties waren niet significant verschillend van 0. In driejarige ooien waren genetische correlaties in dezelfde richting als bij tweejarige ooien. De richting van de genetische correlaties stemde overeen met de richting die verwacht kan worden op basis van energiebehoefte van ooien tijdens dracht en lactatie en groei. Er is geconcludeerd dat de meeste genetische correlaties tussen gewichtsverandering en reproductie niet significant waren en dat de meeste significante genetische correlaties gunstig zijn. Daardoor is het goed mogelijk om middels selectie niet alleen gewichtsverandering, maar ook reproductiekenmerken in de gewenste richting te verbeteren.

In hoofdstuk 4 is gekeken naar hoe variatie in grasgroei en prijzen van vlees, wol en graan invloed hebben op de economische waarden van kenmerken van schapen. Daarvoor is een simulatiemodel ontwikkeld van een schapenbedrijf met eigen aanfok van ooien en rammen in een mediterraan milieu, waarbij Merino schapen gehouden worden voor de productie van wol en vlees. Management beslissingen in dit model zijn geoptimaliseerd om winst te maximaliseren over een tijdspanne

van 5 jaar waarbij grasgroei en prijzen van vlees, wol en graan varieerden tussen de jaren. Voor de optimalisatie is gebruik gemaakt van een dynamisch recursief model. Economische waardes van zeven kenmerken in het fokdoel zijn berekend. Deze berekeningen zijn uitgevoerd voor een situatie zonder verschillen tussen jaren in grasgroei en prijzen en een situatie met verschillen tussen jaren in grasgroei en/of prijzen. Variatie in grasgroei en prijzen zorgde voor een lagere gemiddelde winst, maar voor een stijging van economische waardes vergeleken met situatie zonder variatie. De toename in economische waarde met variatie in grasgroei of prijzen was het grootst voor kenmerken die slechts een klein effect hebben op de energiebehoefte van de schapenkudde, zoals het gewicht van eenjarige schapen, levensduur en de diameter van wol vezel. Op basis van de resultaten is geconcludeerd dat het belangrijk is om bij de berekening van winst en economische waardes van kenmerken rekening te houden met variatie in grasgroei en prijzen.

In hoofdstuk 5 is gekeken hoe fokdoelen aangepast moeten worden voor verschillende regio's als de omvang van variatie in grasgroei verschilt tussen jaren. In de mediterrane klimaatzone van Australië is de variatie in jaarlijkse grasgroei namelijk heel verschillend tussen gebieden. Het model uit hoofdstuk 4 is toegepast voor 10 regio's in West-Australië. Deze 10 regio's verschillen in de mate van variatie in grasgroei, waarbij de gemiddelde grasgroei afneemt bij toename van de coëfficiënt van variatie. Economische waardes en de genetische vooruitgang per kenmerk zijn berekend voor 9 kenmerken. Op basis hiervan zijn twee fokdoelen geïdentificeerd: één voor regio's met een lage of hoge coëfficiënt van variatie voor grasgroei en één voor regio's met een gemiddelde coëfficiënt van variatie in grasgroei. Het fokdoel voor regio's met een lage of hoge coëfficiënt van variatie in grasgroei legt meer nadruk op gewichtskkenmerken en het aantal gespeende lammeren, terwijl het fokdoel voor regio's met een gemiddelde coëfficiënt van variatie meer nadruk legt op het verfijnen van de wol vezel. Regio's met een lage of hoge coëfficiënt van variatie hadden vergelijkbare fokdoelen omdat de relatie tussen economische waardes en de coëfficiënt van variatie niet-lineair was voor gewichtskkenmerken en het aantal gespeende lammeren. Deze resultaten kunnen gebruikt worden om een bedrijfsspecifiek fokdoel vast te stellen dat is toegesneden op de omvang van variatie in grasgroei op het betreffende bedrijf.

In de algemene discussie (hoofdstuk 6) zijn de resultaten van de voorgaande hoofdstukken samengebracht. Op de eerste plaats wordt beschreven hoe enerzijds schapen gefokt kunnen worden die robuuster zijn voor variatie in grasgroei en hoe anderzijds schapen gefokt kunnen worden die bedrijven robuuster maken. Daartoe is beschreven hoe het model van hoofdstuk 5 gebruikt kan worden om de economische waarde te berekenen voor gewichtsverandering tijdens dracht. De

economische waarde is berekend door aan te nemen dat schapen die minder gewicht verliezen een lagere energiebehoefte hebben. De economische waarde was groot ten opzichte van productiekenmerken, omdat in feite de voerefficiëntie wordt vergroot tijdens droogteperiodes. Verder is aangetoond hoe er zowel op gewicht als op gewichtsverandering geselecteerd kan worden. De economische waarde van wolgewicht was gevoeliger voor variatie in grasgroei dan de economische waarde van diameter van wolvezel en gewichtsverandering. De gevoeligheid van economische waarden neemt af wanneer het aantal schapen per hectare afneemt. Er wordt geconcludeerd robuustheid van schapen verbeterd kan worden door het selecteren van schapen die minder gewichtsverliezen. Verder kan selectie van robuustere schapen bijdragen aan het robuuster maken van het schapenbedrijf voor variatie in grasgroei en prijzen van vlees, wol en graan. Ook het aanpassen van het fokdoel met betrekking tot de productiekenmerken zoals wol en vlees kan bijdragen van verbetering van robuustheid van het systeem voor variatie in grasgroei en prijzen. Tot slot wordt geconcludeerd dat studies naar verbetering van robuustheid uitgevoerd moeten worden op bedrijfsniveau en niet op dierniveau.

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Thanks Grigorios for the joy. You were a pleasant distraction away from my Discussion writing! Ρέα, 'η πιο ωραία'. Εμφανίστηκες στη ζωή μου απρόσμενα, η μικρή Ελληνίδα με την όμορφη πίσω όψη. Μαζί σου έφερες χαρά, πραότητα και μια αισιόδοξη προοπτική για τη ζωή. Ήσουν υπομονετική, μου παρείχες πολύτιμο feedback για τη δουλειά μου και στάθηκες δίπλα μου σε όλα. Σε ευχαριστώ που είσαι το πιο σημαντικό κομμάτι της ζωής μου.

Curriculum Vitae

About the author

Gus Rose was born on 13 March 1981 in Subiaco and raised on a sheep and grain farm in Tarwonga, Australia. In 1998 he graduated from Narrogin Senior High School. In 1999 Gus studied Civil Engineering for a year before starting a Bachelor of Animal Science at the University of Western Australia. In 2004 he received his Bachelor with an honours thesis comparing the profitability of sheep with different growth rates. From 2004 to 2007 Gus worked at the Department of Agriculture Western Australia evaluating how effectively the research project 'Lifetime wool' changed how farmers managed their sheep and quantifying the benefits of the project to the sheep industry. Between 2007 and 2009 he did a Master in Agricultural and Resource Economics at the University of Western Australia. He investigated how labour shortages on Western Australian farms effect farm profit. He also investigated outsourcing sheep management to companies as an option to increase the efficiency of farm management and increase farm profit. In 2009 Gus started a PhD at the Animal Breeding and Genomics Centre, Wageningen University. During his PhD, Gus investigated breeding strategies to make sheep farms more resilient to uncertainty, published in this thesis.

Peer reviewed publications

- G Rose, HA Mulder, JHJ van der Werf, AN Thompson and JAM van Arendonk. Breeding objectives for sheep should be customised depending on variation in pasture growth across years. Submitted to Animal.
- G Rose, HA Mulder, AN Thompson, JHJ van der Werf and JAM van Arendonk 2014. Varying pasture growth and commodity prices change the value of traits in sheep breeding objectives. Accepted to Agricultural Systems.
- G Rose, HA Mulder, JHJ van der Werf, AN Thompson and JAM van Arendonk 2014. Genetic correlations between live weight change and reproduction traits in Merino ewes depend on age. Journal of Animal Science 92, 3249-3257.
- G Rose, A Kause, HA Mulder, JHJ van der Werf, AN Thompson, MB Ferguson and JAM van Arendonk 2013. Merino ewes can be bred for live weight change to be more tolerant to uncertain feed supply. Journal of Animal Science 91, 2555-2565.
- Curnow M, Oldham C, Whale J, Gordon D, Rose G, Thompson A and Behrendt R 2009. Successful adoption of new guidelines for the nutritional management of ewes is dependent on the development of appropriate tools and information. Animal Production Science 51, 851-856.
- Jones A, Behrendt R, Curnow M, Gordon D, Oldham C, Rose G, Thompson A and Van Burgel A 2009 Lifetimewool: Evaluation of the impact on wool producers. Animal Production Science 51, 857-865.
- Dart J, Behrendt R, Curnow M, Oldham C, Rose G and Thompson A 2009. The national Lifetimewool project: a journey in evaluation. Animal Production Science 51, 842-850.

Conference proceedings

- G Rose, HA Mulder, JHJ van der Werf, AN Thompson and JAM van Arendonk. Optimal breeding strategies for sheep should consider variation in feed availability. Proceedings of the 10th World Congress on Genetics Applied to Livestock Production, Vancouver, Canada, 17-22 August 2014.
- G Rose and HA Mulder. Breeding can make sheep farming systems more resilient to climate uncertainty. The 64th Annual Meeting of the European Association of Animal Production, Nantes, France, 26-30 August 2013.
- G Rose, HA Mulder, JHJ van der Werf, AN Thompson, MB Ferguson and JAM van Arendonk. Genetically, Merino ewes that lose less live weight during joining have a higher chance of having lambs but the total weight of the born lambs is not affected. The 2nd Joint conference of the New Zealand and Australian Society of Animal Production, Lincoln, New Zealand, 2-5 July 2012.
- G Rose, HA Mulder, JHJ van der Werf, AN Thompson, MB Ferguson and JAM van Arendonk. Genetics show that adaptation to drought periods means less lambs for young ewes and more for old. The 63rd Annual Meeting of the European Association of Animal Production, Bratislava, Slovakia, 27-31 August 2012.
- G Rose, A Kause, HA Mulder, JHJ van der Werf, AN Thompson, MB Ferguson and JAM van Arendonk. Adult Merino ewes can be bred for live weight change to be more tolerant to climate change. The 19th Bi-annual meeting for the Association for the Advancement of Animal Breeding and Genetics, Perth, Australia, 19-21 July 2011.
- G Rose, A Kause, HA Mulder, JHJ van der Werf, AN Thompson, MB Ferguson and JAM van Arendonk. Adult Merino ewes can be bred for live weight change to be more tolerant to climate change. The 62rd Annual Meeting of the European Association of Animal Production, Stavanger, Norway, 26 August-2 September 2011.
- G Rose and Kingwell R. Seasonal labour is the most profitable use of labour in broadacre crop dominant farms, Contributed paper to the 53rd Annual Conference for the Australian Agricultural & Resource Economics Society, Cairns, Australia, 11-13 February 2009.

Training and supervision plan**The Basic Package (3 ECTS)**

	Year
WIAS Introduction Course	2010
Ethics and Philosophy of Animal Science	2010

Scientific Exposure (21.6 ECTS)*International conferences (10.5 ECTS)*

9 th WCGALP, Leipzig, Germany	2009
62 rd annual meeting EAAP, Stavanger, Norway	2011
19 th bi-annual meeting AAABG, Perth, Australia	2011
63 rd annual meeting EAAP, Bratislava, Slovakia	2012
2 nd Joint conference NZASAP, Lincoln, New Zealand	2012
64 th annual meeting EAAP, Nantes, France	2013
10 th WCGALP, Vancouver, Canada	2014

Seminars and workshops (3.1 ECTS)

Sheep CRC postgraduate conference, Coffs Harbour, Australia	2010
Healthy as a sport horse, Wageningen, The Netherlands	2011
WIAS science day, Wageningen, The Netherlands	2011
Genomics and Animal Breeding, Wageningen, The Netherlands	2011
WIAS Science Day, Wageningen, The Netherlands	2012
Fokkerij en Genetica connective dagen, Vught, the Netherlands	2012
WIAS Science Day, Wageningen, The Netherlands	2013

Presentations (9 ECTS)

Adult Merino ewes can be bred for live weight change to be more tolerant to climate change. 62 rd EAAP, Stavanger, Norway (Award winning poster)	2011
Adult Merino ewes can be bred for live weight change to be more tolerant to climate change 19 th AAABG, Perth, Australia (oral)	2011
Genetics show that adaptation to drought periods means less lambs for young ewes and more for old. 63 rd EAAP, Bratislava, Slovakia (oral)	2012
Genetically, Merino ewes that lose less live weight during joining have a higher chance of having lambs but the total weight of the born lambs is not affected. 2 nd NZASAP, Lincoln, New Zealand (oral)	2012
Breeding sheep for uncertain environments, WIAS science day, Wageningen, The Netherlands (award winning oral)	2013

Schapen klaar voor klimaatverandering, FnG, Vught, the Netherlands (oral)	2012
Breeding can make sheep farming systems more resilient to climate uncertainty. 64 th EAAP, Nantes, France,	2013
Optimal breeding strategies for sheep should consider variation in feed availability. 10 th WCGALP, Vancouver, Canada (oral)	2014

In depth studies (9.7 ECTS)

Disciplinary and interdisciplinary courses (9.7 ECTS)

Getting started with AS-REML, Wageningen, The Netherlands	2010
Quantitative genetics with a focus on selection theory, Wageningen, The Netherlands	2010
Genetic improvement of livestock, Wageningen University, The Netherlands	2010
Modern statistics for life sciences, Wageningen University, The Netherlands.	2011

PhD students discussion groups (1.5 ECTS)

Quantitative genetics discussion group, Animal Breeding and Genomics Centre, Wageningen University, The Netherlands	2009-2014
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Professional skills support courses (3.3 ECTS)

Communication with the Media and the General Public, Wageningen, The Netherlands	2012
Course Techniques for Scientific Writing, Wageningen, The Netherlands	2013
Communication in Interdisciplinary Research, Wageningen, The Netherlands	2013

Research skills training (7.6 ECTS)

Wrote PhD research proposal	2010
Introduction to R for statistical Analysis	2010
Reviewer Research Master Cluster	2011
Reviewer Research Master Cluster	2013

Didactic skills training (4 ECTS)

Supervising practicals and excursions

Genetic Improvement of Livestock, ABG-31306, Wageningen University	2011
Genetic Improvement of Livestock, ABG-31306, Wageningen University	2012

Management skills training (1.5 ECTS)

Organising of seminars and courses

WIAS science day committee 2012

Membership of boards and committees

PhD representative for staff meetings at Animal Breeding and
Genomics Centre 2011-2012

Education and training total

51 ECTS

Colophon

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Artwork on cover by Amanda Rose

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