SURVIVAL OF ADULT SHEEP IS DRIVEN BY LONGEVITY GENES

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SUMMARY
Genetic parameters for survival of adult Merino wethers were estimated using annual ‘roll-calls’ based on continued presence at the annual research sampling of a mixed bloodline flock run in the cereal belt of central NSW. Mortality rates were consistently 4 % annually resulting in an average survival of 88 % to 5 years of age. Phenotypic variation within age periods (1-2, 2-3, 3-4 and 4-5 years of age) was very small as was variation between sires and flocks. Phenotypic variation in cumulative survival was higher and along with variation between sires tended to increase with increasing age as did the heritability (0.00, 0.07, 0.10 and 0.13 at 2, 3, 4 and 5 years of age respectively) which suggests that longevity genes are driving survival in adult Merino sheep.

INTRODUCTION
One of the implications of widespread adoption of precision sheep production systems in Australia (Rowe and Atkins 2006) will be a change from age based culling to variable age culling. At present, selected individuals, based on a select/cull decision after their first shearing, are kept in the flock until culling at a set age (Atkins et al. 2006) commonly 6 years. The set culling age is a compromise between age related changes in wool production and quality traits (Hatcher et al. 2005) and the opportunity for more intense selection among young animals when selecting replacements (Atkins et al. 2006). Such trade-off’s between wool traits, selection differential and generation length have been the main determinants of the optimum age structure of a flock (Turner and Young 1969). However recent work (Lee et al. 2009) identified potential gains to be made in lifetime reproductive rate by retaining high performing ewes longer in the breeding flock. Consequently a system of variable age culling, where an individual animal’s level of superiority over others governs the length of time it remains in the flock (Atkins et al. 2006), will be a necessary tool to optimise wool production and quality, reproductive performance and genetic progress in both the current and future generations. Under this scenario survival or longevity of individuals within a flock, particularly high performing individuals, becomes a critical issue. Functional traits, including fitness and longevity, of dairy cows have recently been extensively studied due to their impact on herd profitability (Coelho and Barbosa 2006; Essl 1998; Sewalem et al. 2006) and in response to evidence that exclusive selection of production traits caused a correlated reduction in longevity (Essl 1998; Wall et al. 2006). Given the long history of age based culling in Australian sheep production it is not surprising that there is no published work relating to aspects of survival or longevity in adult Merino sheep. This paper reports a preliminary analysis of the genetic basis of survival of adult Merino sheep.

MATERIALS AND METHODS
The data used in this study were ‘roll-calls’ of adult Merino wethers run at Condobolin Agricultural Research and Advisory Station (ARAS) between 1992 and 2001. Condobolin ARAS is located in the centre of the NSW cereal belt just above the floodplain of the Lachlan River at an elevation of 195m. The average annual rainfall recorded at the station is 424 mm and non-seasonally distributed, although high summer evaporation rates (8-10 mm per day) render much of the summer rain ineffective. Temperatures range from 2.7°C in July with an average 23 days below 0°C to 33.5 °C in January with an average of more than 5 days above 40°C. Grazing
animals rely on naturalised medics (*Medicago* spp), some native grasses which grow during autumn and spring and are offered grain and hay based rations where appropriate to maintain body condition. The majority of wethers (80% as 20% remained at Armidale) born between 1991 and 1996 in the CSIRO Fine Wool Project flock at Armidale (Swan et al. 2000) were transferred to Condobolin ARAS following their hogget shearing at 10 months of age where they remained for 4 consecutive shearings.

A tag list of all wethers trucked to Condobolin ARAS established the initial population of each drop (1991, 1993, 1994 1995 & 1996) of wethers at the station. The subsequent appearance or otherwise of each wether at the annual midside sampling, shearing and off-shears liveweight activities, undertaken over 2-3 weeks in August, was used to code each wether as either 0 = dead or 1 = alive at 2, 3, 4 and 5 years of age. The 1,800 wethers represented 11 bloodlines (6 superfine, 3 fine and 2 medium) and each had an identified sire. The data set contained 315 sires with an average of 29 progeny (range 4 - 132). Cumulative survival at each age and survival between ages of those wethers that survived to the previous age were analysed separately with a univariate binary analysis that included the fixed effects of flock (11 levels), year (5 levels) and the flock x year interaction using ASReml (Gilmour et al. 2006). Random effects were estimated for sire ($\sigma^2_s$) and flock ($\sigma^2_f$) in separate univariate analyses that included the appropriate fixed effects from the binary analyses. The heritability and standard errors were estimated using ASReml as 4 times the sire variance divided by the phenotypic variance. The phenotypic variance was the sum of the sire and within animal components.

RESULTS AND DISCUSSION

The average survival of the Merino wethers at Condobolin to 5 years of age was 87.6%. Mortality rates were reasonably consistent across ages being about 4 % per year (Table 1). The phenotypic variance was low within each age interval (range 0.002 to 0.052) highlighting the difficulty in partitioning variation at this low level of mortality. Similarly, due to very low estimates ($4.4 \times 10^{-10}$ to $8.1 \times 10^{-4}$ and $7.5 \times 10^{-13}$ to $5.1 \times 10^{-9}$ for sire and flock respectively) there was effectively no between sire or between flock variation in survival within ages. In contrast phenotypic variation in cumulative survival increased with increasing age from 0.00 at 2 years to 0.11 at 5 years. Variation between sires also increased with increasing age but to a lesser extent, from 0.000 at 2 years to 0.003 at 5 years. There was little evidence of between flock variation in cumulative survival; the largest estimate was $3.3 \times 10^{-5}$ at 5 years of age.

Table 1. Predicted values, variance components (± s.e.) and heritability (± s.e.) of survival of adult wethers within ages and cumulative survival

<table>
<thead>
<tr>
<th>Survival within ages</th>
<th>1 - 2 years</th>
<th>2 - 3 years</th>
<th>3 - 4 years</th>
<th>4 - 5 years</th>
</tr>
</thead>
<tbody>
<tr>
<td>Average</td>
<td>99.61</td>
<td>99.64</td>
<td>99.81</td>
<td>99.64</td>
</tr>
<tr>
<td>Between sires ($\sigma^2_s$)</td>
<td>0.000 ± 0.000</td>
<td>0.000 ± 0.000</td>
<td>0.000 ± 0.000</td>
<td>0.000 ± 0.001</td>
</tr>
<tr>
<td>Phenotypic variance ($\sigma^2_p$)</td>
<td>0.006 ± 0.000</td>
<td>0.004 ± 0.000</td>
<td>0.002 ± 0.000</td>
<td>0.052 ± 0.002</td>
</tr>
<tr>
<td>Heritability (h²)</td>
<td>0.000 ± 0.000</td>
<td>0.000 ± 0.000</td>
<td>0.021 ± 0.054</td>
<td>0.063 ± 0.054</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Cumulative survival to</th>
<th>2 years</th>
<th>3 years</th>
<th>4 years</th>
<th>5 years</th>
</tr>
</thead>
<tbody>
<tr>
<td>Average</td>
<td>99.44</td>
<td>95.56</td>
<td>92.59</td>
<td>87.59</td>
</tr>
<tr>
<td>Between sires ($\sigma^2_s$)</td>
<td>0.000 ± 0.000</td>
<td>0.001 ± 0.000</td>
<td>0.002 ± 0.001</td>
<td>0.003 ± 0.001</td>
</tr>
<tr>
<td>Phenotypic variance ($\sigma^2_p$)</td>
<td>0.006 ± 0.000</td>
<td>0.043 ± 0.001</td>
<td>0.069 ± 0.002</td>
<td>0.108 ± 0.003</td>
</tr>
<tr>
<td>Heritability (h²)</td>
<td>0.000 ± 0.000</td>
<td>0.073 ± 0.049</td>
<td>0.096 ± 0.050</td>
<td>0.126 ± 0.054</td>
</tr>
</tbody>
</table>
For survival within ages, flock was significant at all time periods (P<0.01 for 2 - 3 years and P<0.001 for all other time periods). Year was significant (P<0.001) for all age periods except 4 - 5 years old. Flock and year were both significant sources of variation in cumulative survival to 2 years of age (P<0.001) but not at older ages. Despite being statistically significant, these effects represent differences between flocks and years of 2 or 3 wethers dying. As a result there were no clear trends in survival evident between flocks or years. The flock x year interaction was not significant for survival within any age period or for cumulative survival at any age.

The heritability of adult survival, both within ages and cumulative, was negligible at 2 years of age but tended to increase with increasing age (Table 1). Heritability estimates ranged from 0 between 1 and 2 years of age to 0.06 between 4 and 5 years with the cumulative survival estimates ranging from 0 at 2 years of age up to 0.13 at 5 years of age. The increasing heritability estimates for cumulative survival with increasing age suggest that longevity genes are driving survival in adult Merino sheep. Clearly more research is required in this area to increase our understanding of adult survival and longevity in Merino sheep. Genetic and phenotypic relationships between longevity and other traits including wool production, wool quality and reproduction are required. While there are no published reports concerning relationships between wool traits and longevity, ecological studies of undomesticated species of sheep suggest that individuals with high lifetime reproductive performance have greater longevity (Clutton-Brock et al. 1996; Hamel et al. 2009). However from a Darwinian point of view artificial selection for production traits should generally lead to a deterioration of longevity (Essl 1998). This has certainly been demonstrated in dairy cattle where selection for production traits including milk yield, live weight and growth rate resulted in negative correlated responses in fitness or longevity traits (Essl 1998; Wall et al. 2006). Similar effects may well occur in Merino sheep as Hatcher and Atkins (2007) found that phenotypic selection for high clean fleece weight leads to fewer progeny surviving to weaning. Lee et al. (2009) quantified heterogeneity of lifetime reproduction in Merino sheep. Similar analyses of lifetime performance in other traits of economic importance including wool production, wool quality and disease resistance are warranted together with their relationships with longevity. These relationships will allow the benefits of variable age culling to precision production systems for sheep to be accurately quantified. The challenge will be to identify existing datasets where individuals (ewes and wethers) were kept in the flock beyond 6 years of age that are adequate for survival analysis. It would also be interesting to compare genetic parameters for adult ewe survival with that of wethers to determine the effect of ewe selection for reproduction traits.

This analysis has demonstrated an annual death rate of 4% for adult Merino wethers grazing in a relatively benign environment. Indeed a mortality rate of 4% seems to be the ‘acceptable norm’ across the Australian sheep industry. However, in other production regions prevailing environmental conditions may well result in higher death rates, particularly for adult ewes that have to contend on an annual basis with the high physiological burden of pregnancy and lactation.

ACKNOWLEDGEMENTS

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REFERENCES