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Measurement of phenotypic resilience to gastro-intestinal nematodes in Merino sheep and association with resistance and production variables

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ABSTRACT

A cross-over experiment was conducted to compare six different phenotypic measures of resilience to gastro-intestinal nematodes (predominantly *Haemonchus contortus*) in Merino sheep and their association with resistance and production levels. On each of six farms, 120 ewes born in 2006 and 120 older mixed age ewes were selected at shearing in 2007. Of these, 60 in each mob were serially treated with long-acting anthelmintics to suppress worm populations. The other 60 ewes were managed according to management practices employed on the farm (infected, INF). At shearing in 2008, the experimental sheep had their anthelmintic treatments switched. The experiment concluded at shearing in 2009. Measures of resilience were greasy fleece weight (GFW), live weight gain (LWG) and haematocrit (HCT) when infected and the difference in these variables between infected and suppressed. Resistance was determined from multiple faecal worm egg counts (WEC) when infected. Measures of resilience based on GFW, LWG and HCT were moderately correlated with each other ($r = 0.25$–0.50) suggesting that they represent different traits. Correlations between a measure in infected animals, and the difference in the same measurement between infected and uninfected animals were higher ($r = -0.37$ to -0.82), indicating that measurement during infection is an adequate measure of resilience. WEC was negatively correlated with LWG and HCT during infection but not GFW. Correlations with resilience measures based on difference between infected and uninfected were positive. Surviving infected sheep were found to have higher haematocrit (HCT), and lower WEC in summer and autumn than sheep that died following the measurement. These results show that measurement of performance traits while infected is a reasonable approximation of measurement of resilience based on the difference in performance between infected and non-infected. They also show that resilience to worm infection is not a single trait, but rather a suite of moderately correlated traits.

1. Introduction

Animals can counter the adverse effects of pathogens either by development of immune-mediated resistance to the pathogen (resistance), or by minimising the adverse consequences of infection (resilience). The measurement of resistance to infection with gastro-intestinal nematodes in sheep is uncontroversial, being based upon measures of faecal worm egg count (WEC) when infected. Selection for resistance to gastrointestinal nematodosis based on WEC is now widely used in sheep breeding programmes. On the other hand, there is far less agreement on measures of resilience to gastrointestinal nematodosis and their application. In general terms resilience can be defined as

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the 'ability to maintain a relatively undepressed production level when infected' (Albers et al., 1987). However this definition requires measures of performance under infected and non-infected conditions, something not easily achieved in practice, resulting in the proposal that growth rate in the face of uniform challenge be used instead (Bisset and Morris, 1996). Furthermore, resilience is generally referred to as a single trait, and yet there are many potential measures of performance that could be used to measure resilience. For example, in wool-producing sheep in an environment characterised by infection with the haematophagous *Haemonchus contortus*, resilience could be defined in terms of ability to maintain wool or body growth, or haematocrit in the face of infection. It is important therefore to define the extent to which selection for resilience based on these are correlated. A key aspect of this study was therefore to investigate a broad range of phenotypic measures of resilience in such an environment to determine to what extent phenotypic resilience is a single trait, like resistance, or a family of traits? Resilience measures used were based on both differential performance under infected and non-infected conditions and on performance under field challenge.

In addition to defining the interrelationships between measures of resilience, defining their association with resistance is important. Breeding sheep resistant to infection with gastro-intestinal nematodes (worms) is widely promoted as a management option for the control of worms. Resistant sheep have lower faecal worm egg counts (Eady et al., 1996) and worm burdens (Barger et al., 1985), leading to a decrease in larval pasture contamination (Bisset et al., 1997) and a reduced reliance on anthelmintic control (Besier and Love, 2003). Resistance implies an antagonistic host response acting against the development and continued presence of the parasite (Riffkin and Dobson, 1979) and is a manifestation of an immunological response. Mounting evidence suggests that the immune response against worm infection comes at a cost to production (Colditz, 2008). In Romney sheep, resistance has a negative genetic correlation with body weight and fleece weight (Wheeler et al., 2008). In Merino sheep, resistance is not correlated with these traits but neither does it confer the expected phenotypic production advantage (Eady et al., 1998). With other worm control practices available to reduce treatment frequency and mortality associated with worm infection (Kelly et al., 2010), selecting sheep for resistance to worms may not always offer the most advantageous strategy for reducing the production loss caused by worms.

In response to reports of undesirable relationships between worm resistance, production and dag score, Bisset and Morris (1996) proposed that breeding objectives that aim to improve resilience may better ameliorate the cost of disease associated with worms. However, as noted above there are many potential measures of resilience using traits such as body growth, fleece growth, and haematocrit. The FAMACHA system for managing haemonchosis by identifying animals resilient to the adverse effects of *H. contortus* on haematocrit (Van Wyk and Bath, 2002) is therefore a practical example of phenotypic selection for resilience. Other potential measures of resilience include measuring the efficiency of energy utilisation (Greer et al., 2009). Given the difficulties of measuring resilience, it is important to determine to what extent conventional measures of performance in a parasitised environment identify resilient animals.

Improving resilience may have implications for worm control. For example, Simpson et al. (2009) showed that animals selected for high fleece weight when infected had an attenuated immune response and higher worm egg counts. However, in sheep infected with *H. contortus*, resistance is also associated with reduced production loss due to worms (Albers and Gray, 1987) and so the phenotypic expression of resilience may not be independent of resistance. This suggests that selection for resilience, as measured by low production loss, may also improve resistance (and vice versa) in environments dominated by *H. contortus*.

In light of the above, the objectives of this study were (i) to assess the relationships of productivity traits to different measures of resilience; (ii) to assess the phenotypic relationship between measures of resilience and in doing so; (iii) provide comment on potential phenotypic markers for resilience in Merino sheep in a summer rainfall environment.

2. Materials and methods

2.1. Experimental site and design

The experiment was a $2 \times 2 \times 2 \times 2$ factorial crossover design. There were two levels of farm management (regional or best practice worm management) each with two levels of worm control (infected or suppressed), in two age groups of ewes (young or mature), conducted over two years (2007–08 and 2008–09). The worm control treatments were swapped between years 1 and 2 so that each animal had a year in each treatment. The effects of farm management and worm control treatment have been reported elsewhere as has a full description of the experimental design and location (Kelly et al., 2010). In brief, the experiment was conducted on six commercial farms located on the Northern Tablelands of New South Wales, Australia. The region has summer predominant rainfall and *H. contortus* is the dominant internal parasite of sheep.

On each farm, two spring-lambing Merino mobs ($n > 300$) based on age (young ewes or mature ewes) were selected at shearing in 2007 (June–October). Young ewes were those having their first shearing as yearlings in 2007 and lambing in 2008. Older ewes were drawn from a mixed age ewe mob (>4 years). Each mob was exposed to natural infection from pasture, and selected sheep were randomly allocated to receive either a worm-suppressed treatment to maintain suppressed sheep (SUP, $n = 60$) or farm management (i.e. infected and treated as farm manager required, INF, $n = 60$). Treatment groups grazed together for the duration of the experiment. Worm-suppressed treatment consisted of the repeated administration of an albendazole capsule (Extender® or Extender Junior® dependent on manufacturer's recommendations, Merial Australia Pty Ltd., Parramatta, NSW, Australia) and an oral dose of an albendazole and levamisole combination drench