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Contents

Resilience, tolerance, robustness and genotype x environment interaction in Merino sheep breeding

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Abstract

The concepts of environmental resilience, robustness and tolerance in domestic livestock species are discussed in general and illustrated using specific examples from the Australian Merino industry. It is discussed how these concepts relate to the more commonly known notion of genotype x environment (GxE) interaction. The Merino sheep breed consists of genetic strains that have been selected for suitability to specific environments and has reached a high level of specification for quality wool production. At the same time Merino sheep produce across a wide range of climatic environments and next to wool contribute substantially to Australia's prime lamb production. By gathering scientific and anecdotal evidence, it is explored if the Merino sheep breed is resilient, robust or tolerant to environmental fluctuations, including the environmental differences that are generated by the stud and commercial sector. It is outlined how GxE interaction is currently considered in MERINOSELECT, the national genetic evaluation system for Merino sheep, and future opportunities to consider environmental resilience, robustness or tolerance in livestock breeding programs.

Introduction

Livestock production systems were historically simple and small in size, only large enough to provide food for one family. Modern livestock industries have evolved into highly specialized and sophisticated production units that supply nutritional components for a growing world population. These highly developed systems are at times exposed to a wide range of challenges in regard to their economic efficiency and viability by environmental influences such as climate, but also by public, political and economical dynamics. Production systems differ significantly between livestock industry sectors with pigs, dairy cattle and chickens being produced under conditions with a managed plane of nutrition, whereas sheep, cattle and goat production rely on pasture based systems with large variability in the availability of feed. The high level of specialisation in domestic livestock species has come at a price with reduced ability to sustain production, health and reproduction under challenging conditions, which has led to breeding objectives that include functional traits next to production traits (Knap, 2009). A key question is whether specialisation and inability to cope is displayed in extensive livestock species that have to produce under quite variable conditions compared to intensively kept livestock species? In this study we discuss the example of the Australian Merino industry, specifically, whether the industry has reached a high level of specialisation such that the ability to respond to challenges in production conditions is compromised, and whether the ability to do so needs to be considered in future Merino sheep breeding programs.

Genotype x environment interaction and tolerance

Genotype x environment (GxE) interaction can generally be described as the variation in the extent of phenotypic modification that can be observed in a specific genotype as a result from varying environmental influences (Via, 1987). GxE interaction can be exploited by matching environments with genotypes that thrive under these particular conditions. However, in extensive livestock consistency of production across highly variable environments is more favourable and GxE interaction is undesirable. In livestock breeding GxE interaction is considered to be a constraint on genetic progress (Dickerson, 1962), because animals that are selected in one environment may not exhibit a similarly high level of productivity, phenotypically and genetically, in a different environment. This may introduce uncertainty for livestock producers, and pose an economic problem should production be reduced.

Genotype x environment interaction has been defined as a genetic correlation between two traits in different environments significantly lower than one (Falconer, 1952). The approach has the advantage that the environment does not have to be specified in detail, but it limits the number of environments that can be compared at the same time. An elegant concept to bypass this problem is to use a reaction norm approach. The concept of the reaction norm was developed by Woltereck (1909) and describes the mean response in a phenotype to changes in the environment. Later, reaction norm models were extended into the more complex analytical frame work of random regression (Henderson, 1982; Kirkpatrick and Heckman, 1989). Both approaches illustrate environmental sensitivity as the slope of the regression lines across environments (e.g. Fig. 1, from Corrêa *et al.*, 2010) with the advantage that the number of environments under evaluation is unlimited. The variation in environmental sensitivity and the re-ranking across environments that can be observed in at least two genotypes defines the level of existing GxE interaction (Heldane, 1946; Mather and Jones, 1958).

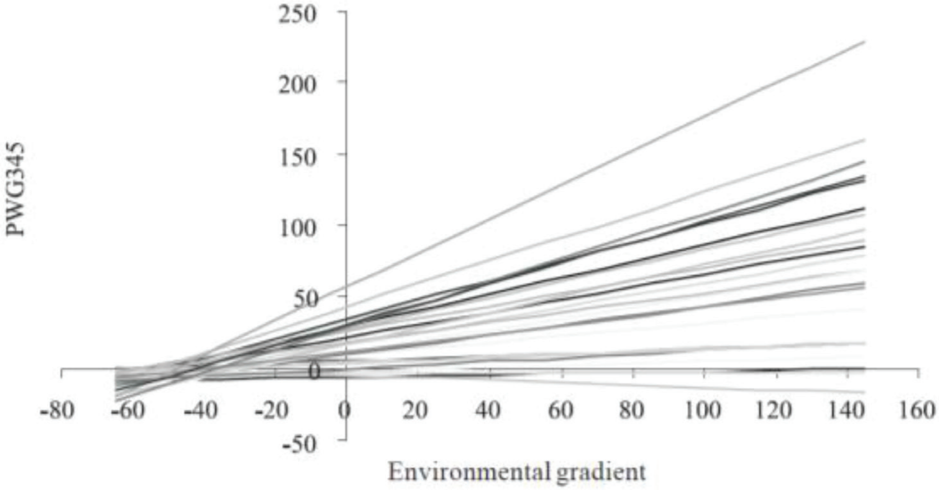

Figure 1 Example of a reaction norm for post-weaning weight gain adjusted to 345 days of age (PWG345) for 25 sires of the Devon cattle breed (Corrêa et al., 2010). The steeper the slope the higher the level of environmental sensitivity.

Another term that is often used in association with GxE interaction is the biological notion of "tolerance". How do these two concepts relate? In the context of parasite infection, the term "tolerance" has been graphically described by Bishop (2012) (Fig. 2) as the slope of the regression of performance on increasing level of parasite infection. The definition of tolerance to parasite infection can readily be translated to tolerance to environmental challenges by replacing the x-axis in Figure 2 with e.g. increasing environmental stress. This demonstrates that by definition, the slope of the regression as evaluated in a reaction norm approach (Fig. 1) and tolerance (Fig. 2) are the same under the assumption that the environment can be defined as a continuum on the scale of interest. Therefore, the term "GxE interaction" would define the variation in tolerance and re-ranking in performance that can be observed when at least two genotypes are exposed to an environmental gradient.

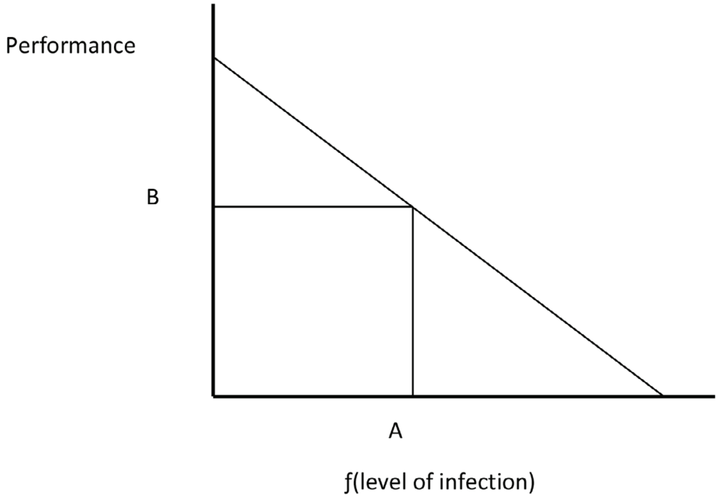

Figure 2 Schematic representation of performance and level of infection. Regression slope represents Tolerance, point A indicates Resistance and point B represents Resilience (Bishop, 2012).

Robustness and environmental resilience

Robustness and resilience both describe the outcome of processes that buffer a system from challenging circumstances, but they are not the same: Bankes (2010) defines "robustness" by describing it as a property of a castle wall, which withstands challenges until it breaks down and safety is compromised, whereas, the defence mechanism could be "resilient" if there is for example another wall or another strategy in place to maintain safety. In the livestock context, robustness describes the ability to maintain consistent production through the application of some stabilizing mechanisms despite variation in the production environment (Veerkamp *et al.*, 2009). Eventually, if the environmental pressures are too high, the stabilizing mechanisms fail, production breaks down and the characteristic of robustness is that the individual does not recover. Dairy cattle are a good example of a livestock species that is robust under specialised management, but have limited scope to respond to environmental variation (Veerkamp *et al.*, 2009). A resilient process on the other hand would mean that under challenging conditions, production would decrease and resources are allocated to processes such as immune defence and movement to browse for food. As a consequence, production is maintained at a lower level and resumes when production challenges ease. *Bos indicus* cattle display resilience for a number of traits whereby their production attributes are traded downwards when resources are limiting, but they are able to adapt to become more productive when resources are non-limiting. Depicting the concept of environmental resilience in an equivalent manner to Figure 2 for resilience to parasite infection (Bishop, 2012), the variable "performance" on the y-axis could be defined as combinations of characteristics, such as health, production and reproduction.

Environmental resilience can then be defined as the combination of performance in health, reproduction and production under a given environmental stress.

Genotype x environment interaction in the Australian Merino sheep industry

The Merino sheep breed represents the majority of the Australian sheep flock (Hassall and Associates Pty Ltd, 2006). It produces high quality wool and also contributes significantly to prime lamb production, both through Merino dams being mated to Terminal sire breeds and through dual purpose Merino flocks. Merino sheep are distributed all over southern regions of Australia. Strong and medium wool Merinos are predominant in South Australia, fine wool Merinos in high rainfall zones of New South Wales, Victoria and Tasmania, whereas medium wool Merino strains are common wool sheep in the wheat-sheep and pastoral zones of New South Wales, Western Australia and Queensland (Cottle, 1991). Therefore, specialised genetic strains might exist within the Merino sheep breed, because traditionally, strains of sheep are pre-selected for their suitability for certain production environments (Atkins *et al.*, 1999). However, despite the pre-selection Merino sheep produce both wool and prime lamb across a wide range of environments.

In this study we broadly group environmental influences into two classes, which have been summarised by Woolaston (1987). The first class includes external influences, such as geographical region, climate, feeding regime, etc. This class also includes environmental variation that is generated through different management systems in the stud and commercial sector. The second class relates to the economic, political or societal circumstances that influence product and production requirements. Environmental influences of the first class lead to phenotypic modification of a specific genotype and have the potential to cause changes in the relative phenotypic and genetic ranking.

Climatic and nutritional factors

Studies of GxE interaction in Merino sheep were extensive in the 80s, which have been comprehensively reviewed by Woolaston (1987), with fewer studies in Merino sheep following that period. Evidence for the existence of GxE interaction is variable across studies. Interactions of genotypes and the environmental factors of "year' and "location" have been reported for wool production and quality traits (Atkins 1980a,b,c, Eady *et al.*, 1990). In a study in South Australia, seasonal variation has not been reported to have significant effects despite extreme variation in the environment (Woolaston and Roberts, 1980). Pollott *et al.* (2004) reported GxE interactions in the form of varying genetic variance and heritabilities for traits related to parasite resistance and body weight across ages in Merino sheep in New South Wales and Western Australia. In a study conducted by Carrick and van der Werf (2007), the environment was characterised as quintiles of contemporary group means for body weight, clean fleece weight or weight of wool impurities. Genetic correlations ($r_G < 0.80$) between the top and bottom quintiles for wool impurities indicated significant GxE interactions for body weight, eye muscle and fat depth in yearling data and also for wool weight and wool impurities in yearling and hogget data. These examples demonstrate the difficulty to specify GxE interactions due to environmental differences. This problem causes concern in the sheep industries because the differences in management systems between the stud and commercial sector could quite possibly cause GxE interactions in production traits. Dominik *et al*. (1999) showed that differences in nutritional plane between the commercial and stud environment can cause GxE interaction for traits such as fibre diameter and clean fleece weight. A study conducted by Hatcher *et al.* (1999) investigated the effect of moving fine wool sheep to a region where traditionally medium to strong wool is produced. Significant GxE interactions were found for wool production and body weight traits with an increase in clean fleece weight and body weight, whilst wool quality was unaffected. Despite the existence of GxE interaction and the specialized use of Merino sheep genotypes in particular geographical regions, the Merino sheep appears to display a high level of capacity to cope with the variation in nutritional quantity and quality, which would indicate a high level of resilience. Evidence for the existence of GxE interaction in Merino sheep is conflicting, which is not surprising considering the large amount of possible combinations of genotypes and environments. In addition, studies that explore GxE interaction require large amounts of data with a representation of many sires across environments with sufficient number of progeny (Falconer and MacKay, 1996). Therefore, existing literature does not provide conclusive evidence on the level of environmental tolerance in the Merino sheep breed to climatic factors that affect nutrition.

Social environment

The second class of environmental effects concerns situations where change occurs whilst the organisms stays constant without any phenotypic response. Examples include changes in public opinions, market strength and price signals or changes in legislations which cause production aims to change. The suitability of economic values in breeding objectives may be affected and as a consequence, shifts in relative phenotypic and genetic ranking of genotypes are caused by a change in the suitability of a product rather than differences in phenotypic expression. Changes such as these can be a risk to the whole industry, challenging its robustness, unless strategies and resources are available to respond. An example is the threat to the wool product from animal welfare groups due to controversy over the practice of mulesing (Smith *et al.,* 2009). Breeding and management strategies needed to be developed in order to respond to the societal concerns and phase out the practice of mulesing at a future point in time. The basic requirement for an industry to respond to changing market situations through breeding strategies is the existence of genetic variation for new traits of relevance. At the molecular genetic level, the Australian sheep breed is characterised through a high level of genetic diversity compared to meat sheep breeds (Kijas *et al.*, 2014) and in particular compared to an intensive livestock species such as dairy (Zenger *et al.,* 2006) and would indicate to have a high level of resilience to respond to future product and production requirements.

Breeding for environmental tolerance, resilience and robustness in Merino sheep

The concept of GxE interaction is a well recognised in the Merino sheep industry, but it is an open question as to how effectively it is currently captured within breeding programs. The question is, does the level of product specialisation and focus on production characteristics introduce GxE interaction, reduce tolerance to challenging environmental conditions and compromise the resilience of the Merino sheep breed and its industry? It is also important to consider the commercial aspects, i.e. cost and profit, for breeders and producers of addressing resilience and tolerance in breeding programs.

Traditionally, the Merino industry has attempted to tailor selection programs within an environment for specifically suited genotypes, as is demonstrated in the specific distribution of wool types across specific climatic regions of Australia (Cottle, 1991). Anecdotal evidence exists that commercial producers prefer to buy rams from stud environments bred in the same region as theirs or from environments that resemble theirs in terms of rainfall and temperature in order to avoid potential GxE interactions, with the expectation that genetic and phenotypic performance will be similar. However, environmental variation is complex and production environments can differ between paddocks of the same farm, seasons, parasite load, etc. (Woolaston, 1987) and management systems (Dominik *et al*., 1999). The complexity and the diversity of environmental factors make it difficult to clearly define robustness of a particular Merino sheep genotype and thus to match it with a specific environment. Therefore for extensive livestock species, such as Merino sheep, genotypes that are tolerant to environmental variation and do not react with unpredictable performance shifts on exposure to different environments would be favourable. They would have low levels of GxE interaction across production environments and therefore stable phenotypic expression and genetic value. From an industry perspective this would be of value to both seed stock producers and commercial wool producers. Commercial wool producers could reliably select stock for production in their production environment from any other location and predict the resulting performance. On the other hand, ram breeders gain a marketing advantage because they can provide seed stock that reduces risk to the business of their clients.

MERINOSELECT, the Australian provider of genetic services for Merino industries provides across-flock Australian Sheep Breeding values (ASBVs) as a tool for breeders to select rams on objective information (Brown *et al*., 2007). ASBVs account for bias due to GxE interaction by including the term of sire x year/flock in the model for breeding value estimation (Brown *et al*., 2007). The practical outcome of this approach is that the ASBVs provided to breeders represent an average breeding value across environments free of the effects of sire x year/flock interaction. This will be a reasonable compromise when the interaction effects are small, but a loss in the efficiency of selection across environments will occur as the size of the effects increases, which will be trait and environment dependent. Consequently, the true impact of GxE interaction in the MERINOSELECT system remains largely unknown. On the one hand, rates of genetic gain are significantly lower in the Merino sector compared to terminal and maternal sire breeds (Swan *et al.,* 2009) and GxE may be a contributing factor, but on the other a number of leading sires have been shown to perform consistently across environments with thousands of progeny in many locations. This leads to the conclusion that ASBVs that have been estimated across flocks and environments provide the best tool for selection of sheep with a high level of tolerance to varying environmental conditions.

Resilience is not directly considered as a trait in MERINOSELECT. Selection practices focus on production traits such as fleece characteristics, but also incorporate reproduction and live weight traits as part of the selection index and often parasite resistance (Brown *et al.*, 2007). Culling also occurs on visual assessment criteria, such as soundness and structure of legs, hooves and jaw. More recently, longevity and lifetime performance have gained more emphasis due to the availability of genomic information (Brown *et al.*, 2013; Swan and Brown, 2013). Overall, the selection process encompasses criteria such as health and reproduction next to production traits, which maintain and enable a high level of resilience in the Merino sheep to repartition resources and buffer challenging production conditions. Ferguson *et al.* (2007) highlighted in a study on Western Australian Merino sheep that selection for production traits may affect reproductive performance, in particular under challenging nutritional conditions. A good sign of resilience in the Merino sheep is the annual variation of fibre diameter that can be observed (Brown and Crook, 2005). Fibre diameter reduces over periods of poor nutrition, indicating that nutritional resources are allocated to other processes than fibre production. Fibre diameter increases again when the nutritional plane is adequate. Rose *et al.* (2014) provided an economical perspective based on the relationship between trait improvement and energy requirements, which is the change in feed cost associated with favourable change in a trait. They evaluated that traits such as fibre diameter that are economically independent of energy requirements, increase the value of a kilogram of wool when they change into a favourable direction. However, for example fleece weight and growth, traits that are highly dependent on level of nutrition, affect profit of product with changes in pasture availability and feed cost. The study highlighted that breeding programs in environments that are underlying large fluctuations in feed availability optimally emphasise traits that are economically independent of variation in feed on offer. In an earlier study, Rose *et al.* (2011) investigated genetic and phenotypic parameters for weight loss and gain as means to address potential effects of climate change on sheep production systems in Mediterranean environment of Australia. They showed that changes in weight are lowly to moderately heritable and that it is possible to select sheep for tolerance to variation in the plane of nutrition.

In summary, the lack of conclusive evidence for GxE interaction and the level of environmental tolerance are due to the inability to define and gather sufficient information on highly complex environmental variables and insufficient use of genotypes across environments exist to generate the necessary statistical power to estimate interactions. However, the current breeding systems, in particular in combination with ASBVs are suitable to maintain environmentally tolerant and resilient Merino sheep that displays sufficient genetic variation to respond to future market requirements brought about by societal opinions.

New opportunities from genomics and phenomics

In recent years, new opportunities have emerged to address resilience and tolerance in livestock breeding programs. Livestock genetic research is increasingly moving into the use of high density genomic information ("genomics"), as well as complex phenotypes ("phenomics": Houle *et al.*, 2010; Rosa, 2011). In addition, environments can be described more comprehensively with easier access to national weather and climate databases and novel technologies such as satellite remote sensing (Hill *et al.*, 2000, Henry *et al.*, 2002; Gherardi *et al.*, 2003). The ability to specify genotypes, phenotypes and environments more comprehensively also provides the opportunity to specify combination of genotypes and environments, explore their interactions, and their effect on the phenotype. Lillehammer *et al.* (2009) and Dominik (2014) used a random regression approach to estimate the tolerance of sire performance for traits across environments in dairy and Merino sheep. Subsequently, genomic data was used and the level of tolerance was associated with genetic markers. In dairy cattle, potential gene candidates were detected that could be used in breeding programs to address environmental tolerance (Lillehammer *et al.*, 2009). No conclusive evidence for significant associations between tolerance of reproduction across environments and genetic markers were found in Merino sheep (Dominik, 2014), but it highlighted the need for large data sets to investigate multiple combinations of phenotypes and environments.

Phenomics in combination with systems biology offers the opportunity to describe new multi-dimensional phenotypes of relevance to environmental resilience (Houle *et al.*, 2010). Research is underway to investigate more detailed and complex phenotypes, for example at the tissue, protein or cellular level, or phenotypic observations of animal behaviour, grazing behaviour and animal movement as a predictor of disease onset. Such examples offer the opportunity to explore underlying variation of physiological processes that influence environmental resilience. Highly repeated measures increase the precision of phenotyping and remove environmental noise and can track changes over time. They can be used to increase our understanding of the complexity of environmental components and facilitate in disentangling the remaining variation attributable to environmental factors. This will increase accuracy of genetic predictions and provide a more holistic description of the environmental variance. The ultimate goal is to better describe and understand interactions between genotypes and environments, which through its direct relationship with the variation in resilience and tolerance will provide more effective and strategic approaches to genetically improve these characteristics in livestock breeding programs.

Conclusions

In conclusion, the approach to environmental tolerance, resilience and robustness in livestock breeding programs and applicability in commercial livestock production differs between extensive and intensive livestock species. It was illustrated that resilience of a genotype or an industry to environmental fluctuations can become an inherent property of an extensive livestock system despite it not being specifically considered in the breeding program. Novel developments in the area of genomics and phenomics will provide new approaches to specify and strategically manage GxE interactions and therefore environmental tolerance and resilience.

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