Who benefits from Genetic Improvement?

R. G. Banks
AGBU, c/- UNE, Armidale, Australia
AGBU is a joint unit of University of New England and NSW Department of Primary industries

ABSTRACT: Genetic improvement delivers benefits in the form of trait changes, informed markets for seedstock, and expertise and capacity among breeders. The primary beneficiaries of the trait changes have generally been believed to be consumers. This is not automatically the case. This belief has been used to support arguments for community support for genetic improvement. Re-framing the question "who benefits" as "what changes are valuable, and how best to fund the improvement" is suggested as a more useful approach. From this perspective, more traits and a longer time horizon are preferred. The challenge of supporting the phenotypic recording required in the face of market failure remains, and a mechanism is proposed for addressing this, applicable where there are collective funds available for industry development.

Keywords: Investment costs and returns; Phenotypic recording

Introduction

The title for this paper is deceptively simple, and almost rhetorical. Theory and practice for genetic improvement have been well-developed and implemented over more than six decades now, and a general belief that consumers are the greatest beneficiaries from that seems widely accepted. Behind this conclusion lurk some uncertainties and complexities, and this paper will examine some of them, in an attempt to extract insights particularly relevant to implementation of genetic improvement. The paper draws mainly on experience in the extensive livestock industries in Australia.

To focus this exploration, the title can be extended with three additional questions:

- What is genetic improvement?
- How does anyone benefit from it, and therefore can we value it?
- Why does it matter who benefits?

The topic is inevitably economic, or at least involves consideration of genetic improvement from an economic perspective. On raising aspects of this paper with economist colleagues, concern was expressed regarding the dangers of "tyros" exploring questions around the nature and distribution of benefits from innovation and productivity improvement (Julian Alston, *pers. comm.*). Those dangers are about to become apparent.

Basic Principles

Genetic improvement simply means using genetic evaluation and selection to change the genetic make-up of a population, and through that, changing the phenotypic mean of the population for some trait(s). It is well established that this is possible (e.g. Hill, 2008), and methods exist to both predict and estimate genetic change in any trait(s) undergoing selection.

Given that we can predict and estimate genetic changes, and can in principle identify the marginal benefits of such changes at any point in a production chain, we can therefore in principle value the changes at any point in such chains and across the entire chain. Individual enterprises, industries and/or consumers can benefit if some product or attribute which they value is improved, either in cost (reduction through improvement of production efficiency), quality, or some combination of the two.

These two aspects – valuing change, and predicting it, are combined in selection index theory (Hazel, 1943) to allow selection that is optimal given the genetic space for selection and the values placed on changes. These analytical tools together make investment in genetic improvement extremely low risk, provided that genetic parameters are reasonably accurate, that the values used to guide or weight selection are wise, and selection is on estimated genetic merit.

Extending this, investments in genetic improvement can be evaluated *a priori*, knowing that improvement in a trait ultimately depends on having performance data for it or correlated traits, meaning that the "genetic improvement investment algorithm" is very simple:

- Decide what to improve
- Invest in the appropriate records
- Evaluate candidates, then select and mate
- Multiply up and harvest returns

And of course it is possible to conduct the same analysis *ex poste*, with more precise capacity to diagnose results than applies to many other forms of investment.

However, compared with many other sorts of investments, genetic improvement of livestock typically involves two features that introduce some interesting complexity:

- The pyramidal structure of many industries means that improvements made in a small sector (the nucleus) are multiplied up many times to deliver the end product(s) to consumers. On its own this is not different from many other industries – in car-making for instance, designs are developed in (relatively) small labs, and multiplied up many times through production plants. However in livestock improvement, the "designs" are changing continuously and are not uniform, which has consequences discussed further below.
- There are usually multiple owners through the production chain from breeder (nucleus) to consumer, and frequently many owners within any one sector of that chain. For example, the US and Australian beef industry chains include a seedstock sector (with approximately 10,000 enterprises in the US, and 2,000 in Australia), commercial cow-calf sector (734,000 and 50,000 enter-

prises), backgrounding (estimated 50-100,000 and 2-5,000 enterprises), feedlots (2,000 or 300 enterprises), processors (3 and 5 main companies), and then retailers (estimated thousands) (Van Eenennaam, 2014).

The consequences of these features that are relevant to livestock genetic improvement are that:

- The breeding sector is small in capital terms relative to the rest of the chain, and is usually comprised of many very small businesses, none of which have the capacity to fund either research or extensive performance recording
- Commercially relevant trait expression occurs outside the breeding sector (the stud or nucleus). This is economically efficient – high multiplication from nucleus to consumer spreads the selection-multiplication overheads over many copies of the products (Bichard, 1971), but
- There is typically poor or non-existent flow of price signals from the consumer back through the production chain, and
- There may be conflicting incentives at different points of the chain. For example, the processing sector may seek high yield, whereas consumers may seek eating quality, typically meaning some amount of intra-muscular fat in meat animals, while yield and intra-muscular fat are unfavorably genetically correlated (Banks, 2013).

Together, these consequences can mean that breeders do not receive sufficient return to support optimal investment in recording, and that the direction of selection at the top of the chain may not be optimal for the production chain as a whole.

What benefits are delivered?

Benefits of genetic improvement are generated most clearly in the form of changes in trait means over time. Examples of reported genetic trends are increasingly available in the public domain via websites for breeds and genetic evaluation organisations. Such reports typically include both individual traits and index trends.

These changes include cost-reducing (e.g. fertility, growth rate) and quality enhancing (e.g. meat eating quality, fibre diameter of wool) changes, which can contribute to improved margins at one or more points in the production chain.

A secondary benefit of genetic improvement, or more precisely of the genetic evaluation that is essential to it, is the information available on animals offered for sale, where this information is public. Where some form of estimate of breeding value is available to the buyers, they can make informed decisions on which animals will best suit their enterprise needs and budget. The value of this benefit can be estimated as = r σ_P n, where r is the regression of price on estimated merit, σ_P is the standard deviation of price, and n is the number of animals offered for sale. Van Eenennaam (2012) observed r=0.4 and σ_P=$2,816 in analysis of bull prices across a number of Angus sales in Australia. From this data, the value of information on animals' genetic merit is therefore $1,127 per bull sold. The bull-breeding herds (known as studs) providing data for that analysis are among the leaders in both performance recording and client education in Australian beef breeding, suggesting that the value of r obtained here, and likely the standard deviation of price itself, is higher than for the total population. However, this simple analysis, together with results from sheep (not shown), suggests that the market value of information on animals offered for sale can be considerable, and exceeds the cost of recording and evaluation per animal sold.

A third, intangible benefit delivered alongside genetic improvement itself, at least in countries and industries where individual breeders are involved in making decisions about recording and selection, is increased technical expertise distributed amongst the seedstock sector. Breeders with expertise and knowledge of genetic improvement are a respected source of information and leadership for others in industry, and they make a substantial contribution to increasing the adoption of objective methods of genetic evaluation and improvement.

Whether this dispersed expertise constitutes a benefit, depends on whether a potential loss of selection differential due to more decision-makers is outweighed by any risk reduction. Such risk reduction could be postulated simply from having a diversity of views and perspectives on the value of improvement in various traits, and where there is diversity of production systems, having, some amount of recording distributed across the systems.

It is also possible that having a diversity of decision-makers may result in maintenance of greater genetic diversity.

This diversity can be measured in the form of evidence of improvement i/L (i =selection differential, L= generation interval) and accuracy of estimated breeding values or index over time, and in variation in direction of selection (Lee et al, 2014). Valuing learning could be extrapolated from increasing rates of genetic progress over time, if observed, but it is not so clear how the diversity of selection direction can be valued.

This diversity and number of decision makers is frequently cited as a cause for lower rates of genetic improvement in industries with these characteristics (Lindsay, 1988, Van Eenennaam, 2014), but it is hard to see how one could disentangle the effects of these parameters from those arising from the overall structure of such industries. Further, it is not clear whether the rate of genetic improvement itself is what is driving market share for pork and poultry, distinct from the inherent lower cost of production for these commodities.

So, there is widespread evidence for genetic change both in individual traits and combinations thereof, and evidence for markets valuing genetic information.

Evidence for benefits, and for their distribution

Analyses of investment returns from genetic improvement are not widespread in the literature; however Amer *et al.* (2007) and Amer *et al.* (2012) provide examples. Their estimate of the internal rate of return for genetic improvement in the UK beef and lamb industries combined was 32%, with a benefit:cost ratio greater than 8:1 at a 7% discount rate. The UK study (Amer *et al.*, 2007) did not attempt to estimate the distribution of benefits.

A series of papers in the 1970s and 1980s examined reconciliation of different perspectives in establishing economic values to guide selection (Miller and Pearson, 1979; Brascamp et al, 1985; Smith et al, 1986), and in doing so, touched on the distribution of benefits. Amer and Fox (1992) highlighted the importance of economic parameters of the production chain, in particular the elasticity of demand, for realized distribution of benefits.

Complexities – the economics

Agricultural research and development (R&D) is an area of study for applied economists, and an area where Australian workers have made a significant contribution (J. Alston etc). This contribution may reflect the contribution that agriculture has made to the national economy, coupled with uncertainty about how best to improve agricultural productivity and profitability in a harsh and highly variable climate. In addition, while Australia is a wealthy country, funds for support for agriculture are limited and declining, and accordingly, how best to invest in agricultural development has been and continues to be an important aspect of policy.

This has led to approaches to R&D investment relevant to the Australian situation, and which take into account the complexities noted above. The main innovation has been the Research and Development Corporation (RDC), whereby a levy is imposed on production, usually but not always at slaughter, and that levy is matched by Federal government funding. This generates funds approximately 2% of gross value of production, which are managed by not-for-profit corporations answerable to government and industry. This approach provides a basis for funding strategic and applied R&D and extension, which along with other (mainly public) funding sources, has been used to develop genetic evaluation knowledge, tools and systems for use in the main livestock industries in Australia (BREEDPLAN, ADHIS, Sheep Genetics and PIGBLUP).

This RDC model provides a means whereby funding from different sectors can contribute to costs of genetic improvement, but does not automatically solve two important problems. The first is that price discovery, which is essential for understanding the marginal returns to trait change at each point in the production chain, may still be difficult, either because firms do not collect data in a form that allows estimation of the marginal returns, or because they are not willing to share it. Overcoming this problem may require considerable careful analysis, drawing on intuition as much as data.

The second problem is that even if price signals relevant to each point in the chain can be estimated or derived, if they are not transmitted, there is no direct incentive to respond to them.

These two problems, both of which exist in beef and lamb production chains in Australia, have generated two industry-level responses. The first is targeted investment of R&D funds towards specific market opportunities – aimed at helping breeders and producers take up those opportunities. Examples of these include the Meat Research Corporation's Prime Lamb Key Program (1991-1996), aimed at producing lamb for the then very small North American export market, and the suite of R&D aimed at production for beef markets that placed premiums on marbled product, funded through the 1990s and early 2000s. From an economic perspective, these R&D investments were both quite risky, in that they could have failed technically, and more importantly, that incentives may not develop, so inhibiting adoption. Neither program failed technically, but incentives have taken some time to become clear, and even today can be quite variable.

Another potential response to poor price signals is risk-taking by breeders: a (usually small) number of breeders may invest in data recording for some new trait, or a trait that is not rewarded via price signals back to the breeder, in order to be better placed if/when such signals become clearer. Such breeders in the beef and sheep industries in Australia and no doubt elsewhere, see themselves as acting in the industry interest, although of course if markets change to reward the new traits, the innovators should benefit.

Methodology for estimating distributions of benefits

Equilibrium displacement modelling (EDM) (Zhao et al, 2000; Mounter et al, 2006) has been developed to allow examination of returns from investments in research and promotion in a number of Australian agricultural industries. With this approach, the industry is represented by a system of demand and supply relationships. Impacts of exogenous changes, such as new technologies or promotion campaigns, are modelled as shifts in demand or supply from an initial equilibrium. Changes in prices and quantities in all markets that arise when the system equilibrium is displaced due to these exogenous shifts are estimated as are the consequent changes in producer and consumer surplus, reflecting welfare changes to various industry groups. EDM modelling involves estimating large numbers of parameters, and so results should only be seen as a guide.

Table 1 shows results from EDM evaluations of the Australian beef and lamb industries. The overall message is that approximately 25-35% of returns from improvements in production efficiency are estimated to flow to producers, and the bulk of the remainder to consumers. Where domestic and export prices are in effect, set by world prices (which is largely the case for beef in Australia), the basis for the estimates for consumer benefits are not obvious.

Table 1: Distribution of Returns (%) by sector R&D investment into improved production or improved demand (Zhao et al, 2000; Mounter et al, 2006)

Sector	Beef		Sheep	
	Production Research	Promotion Research	Production Research	Promotion Research
Producers	24-34	20-30	24	20-26
Feedlots	0.1-0.2	0.3	-	-
Processors	1	1	8	9-12
Retailers	4	4-7	5.5	3-10
Domestic Consumers	50-55	50-65	31	20-48
Overseas Consumers	8-9	5-12	31	15-38

It is also possible to examine trends in price for seedstock animals. Amer (2012) analysed data on Angus bull prices together with data on genetic trends and prices for commercial steers. The analysis showed very clearly that prices for bulls tracked steer prices, with essentially no relationship between bull price adjusted for inflation and Index value/genetic merit over time. There do appear to be premiums for bulls and rams that have information on genetic merit compared to those without, with the premiums being approximately equal to recording costs per bull or ram sold.

Benefit from genetic improvement to seedstock breeders may come from increased market share – the breeders who invest in recording, genetic evaluation and make genetic progress may attract more buyers than breeders that are non-adopters, or less effective adopters. There is evidence that this occurs in the beef bull- and ram-breeding sectors in Australia, including at the between-breed level. Atkins (1993) modelled flows of benefits from genetic improvement in Merino sheep, and highlighted the significance of ram-buyer mobility – willingness to change ram sources – for the distribution of those benefits.

Taking a broader perspective, Carroll (2010, available from this author) explored the way in which farmers as a whole benefit from productivity improvements, concluding that rising land value may be the most obvious ultimate outcome.

Together, these results reinforce the view that consumers are significant beneficiaries of genetic improvement, along with producers, and some of the share of benefits to producers may be passed on to breeders. This share accruing to breeders may be in the form of market share rather than rising real prices.

Who funds genetic improvement?

Sustained genetic improvement requires investment into breeding programs themselves, and also into R&D and extension of some form. Table 2 summarizes the sources of investment into the total genetic improvement effort in beef cattle and sheep grown for meat in Australia over the period 2002-2012. Investments were analysed as being strategic research, applied research, extension, or implementation. Implementation refers to the costs of recording and genetic evaluation, usually borne by the breeding sector.

Table 2: Estimated distribution of investment by sector into genetic improvement RD&E in Australia, 2002-2012

Sector	Beef	Sheep
Breeders	24%	20%
Producers	6%	18%
Taxpayers	70%	62%

Total annual investment was approximately $24m in both species, with a high proportion coming from government (taxpayers), this component being mainly focussed on strategic research. This reflects the Cooperative Research Centres (CRC) programs (Rowe *et al.*, 2013).

The share of investment by breeders is based on estimated costs for recording (Archer *et al.*, 2004) and costs of evaluation. However, as noted above, breeders who have adopted genetic evaluation usually obtain some premium, and this premium appears to be similar to the cost of recording and evaluation, so in effect, commercial producers – the purchasers of bulls - are approximately off-setting the cost of recording and selection. If however, this premium declines as adoption of genetic evaluation within the breeding sector rises, which results in more of this cost ending up being borne by the breeders – it will have become a cost of doing business.

Table 2 shows that commercial producers' share of the total cost of genetic improvement is broadly in line with their share of the returns, as estimated by EDM modelling (Table 1).

How is the "who benefits" question impacted by genomics?

Much of current exploration of genomic technologies relates to how to use particular tools, and how to make those tools more useful – which is basically all about improving their price: accuracy relationship. At the same time, various authors have noted the potential for tackling new traits, or traits that have been difficult to deal with in the past (e.g. Hayes et al., 2013), but in this context, the sting is in the tail. It has become increasingly clear that the utility of genomic tools depends entirely on the quantity and quality of the phenotypic records that support them, which neatly leads to the real question – what phenotypes to record, and how to fund them? It follows that "genomics" can free us to think of what to breed for in a very broad sense, or what to record, rather than simply making the best of whatever data is available.

This has the potential to shift thinking in the design of animal breeding programs to what is much more like a design perspective in consumer goods – to ask "what would the consumer like?", followed by "how do I deliver that?" This implies adopting a much more holistic view on what to breed for, driven by having adopted a wider view on "who benefits and how?" And this could extend to "how can I maximize benefits for as many people as possible?" To return to the economic perspective, this simply means aiming to maximize positive externalities, and minimize negative ones. Expressed very simplistically, design of animal breeding programs would become much more focused on the fact that phenotypes = opportunities.

A Different Perspective

The overview presented here simply highlights the fact that genetic improvement is effective, and that benefits arising from it end up being captured predominantly by individuals and sectors other than those who actually generate that improvement. The exact distribution of benefit depends on what traits are changed, and on economic parameters of the production chain concerned.

As noted, the low return to the breeding sector has frequently been used to justify some form of external or collective investment in and control over genetic improvement. This may be via:

- Collective funding of R&D, but with funding for genetic improvement itself the responsibility of the breeding sector. This approach is broadly speaking the one taken in beef and sheep in Australia. Within this approach, there are important nuances regarding how the direction of selection (the breeding objective) is established, and the degree to which any "industry breeding objectives" are actually followed in practice. This approach does not automatically result in optimal investment in recording or optimal selection, however that might be defined. At the same time, it allows for diversity in both, and through this, for some degree of risk spreading and potentially greater genetic diversity maintained.

- Collective funding of R&D and of genetic improvement activity, and some degree of control over selection decisions. This approach has been exemplified by beef and sheep breeding in France (J-M. Elsen, *pers. comm*.) This approach does not automatically optimize either recording or selection, and includes greater dependence on technical expertise for key decisions.

How do these approaches relate to the question posed in the title of this paper? If we return to the genetic improvement algorithm, we can see a different way of thinking about benefits, and through that, about essentially all aspects of genetic improvement programs. The approach to breeding program design outlined in the textbooks suggest that the starting point is to define the breeding objective, then identify criteria for selection, collect records for those criteria or correlated traits, and proceed to select (Harris and Newman, 1992). However, as the foregoing discussion attempts to highlight there can often be a mismatch between the objective developed from a "whole of chain" or industry perspective, and that developed from the perspective of the primary investors, the breeding sector.

In a very general sense, the best objective from a whole of industry or even community perspective will almost invariably include more traits than that developed from a more limited breeding sector or commercial producer perspective, and place more equal weighting on traits, or trait groups. For the breeder taking the long view, all traits are important, and while some may be more directly important than others, there is a risk in allowing such importance to lead to undesirable changes anywhere. This leads to all selection being based on some combination of formal economic values overlaid with desired gains (Knap, 2014).

By contrast, our new perspective challenges the selection index notion of optimizing selection emphasis, and simultaneously raises the possibility that there is real advantage in having diversity in decision-making. It implies that both price discovery – in the form of determining the weightings to place on traits, and selection direction are unavoidably uncertain, and that under-investment in phenotypes is inevitable. In addition, the price signal, and hence optimal investment in recording and direction of selection, can certainly vary between breeders, depending on the market and product environment of their clients, and on their own current genetic merit, and how well they can quantify their price signals.

The idea that there may be value in diversity in decision-making is reminiscent of Land's (1981) suggestion of the value of insurance stocks, but is significantly different in application. In the original formulation of the idea, insurance stocks would be maintained with different goals, "in reserve" for some future time when needs change. How the different goals would be established is not clear. In a technically-managed world, the approach might be to design a suite of breeding lines "aimed" in such a way as to maximize phenotypic diversity in trait-dimensional space, and underpin that with use of genomic information to maximize genetic diversity within and between lines (Banks, 1999). The likelihood of such a world existing seems low.

The approach that exists in beef and sheep breeding in Australia (and likely in other countries and industries with minimal collective management of genetic improvement, or without significant rationalization of the breeding sector) is not as extreme as this. In these industries, the diversity is between recording and selection strategies of individual, usually small enterprises. The result is less diversity on any dimension than one could expect from the insurance stocks concept, and simultaneously, likely less investment in records than would be ideal.

If we accept the proposal that breeding should ideally aim to target as many traits as possible, the main question is how to fund the recording required. One way this could be achieved in practice is by having some collective or industry co-investment in recording phenotypes, with those records being available to breeders via genomic prediction, perhaps with some recognition of such recording investment as individual breeders make, and possibly with adjustment to take account of genetic progress delivered and diversity maintained.

The current situation in Australia is slowly evolving towards this – with industry and government co-investment in recording in place, and ideas being explored for rewarding recording done by breeders. The design challenges inherent in such an approach include:

- Should all sectors in an industry be levied, or is an end-point royalty sufficient, in the expectation that the cost of that levy will be spread through the production chain? Banks (2013) alluded to an approach to determining shares of such levies based on benefits actually delivered in the form of trait changes, using selection index theory and/or observed trends.
- Is there an optimum level of recording, in terms of number of animals? Miller and Pearson (1979) and others noted that what is optimal for genetic improvement and for economic return may not be the same. Extending this, in a genomic world, additional records generate declining returns in terms of accuracy of genomic prediction (Hayes and Goddard, 2009), and so any co-investment would need to account for this. Kinghorn (2014) has developed thinking around a market for phenotypic information, but this carries with it challenges around ensuring that at least some genetic information is available to the market, so that the benefit of an informed market is not lost.
- How to reward providers of phenotypes? Doing so financially could be complex. Doing so via services, such as genotyping, requires developing ways of valuing data and services that are both efficient and equitable.
- Under the RDC model, any intervention must not crowd out private activity. This means that the initially appealing approach of simply having industry or government

fund all phenotype recording is not possible. Innovative breeders must be free to extend phenotyping into new traits, which simply reinforces the need for transparent, equitable and efficient valuing of phenotypes and genotypes.
- As breeding enterprises become larger, which is happening slowly in the Australian beef and sheep industries, the processes around defining what phenotypes are valuable and will accordingly be rewarded in some way becomes no less important, and industry as a whole must continue to think "beyond the market". Simply having large profitable breeding enterprises does not guarantee that possible future needs are adequately addressed.

This discussion has moved a long way from the initial question "who benefits from genetic improvement", but highlights the circularity inherent in the question:
- Who benefits depends on what changes are made
- What changes are made depends on what changes are desirable
- What changes are desirable depends on the interaction of industry structural factors (such as information or power imbalances, and imperfect price signals) with production systems and individual enterprise position
- From which one can conclude that it is sensible to deliver as many changes that seem in the right direction as possible – essentially overlooking any market failures
- Which implies recording the required number of phenotypes for as many traits as possible
- Which is difficult for all except very large enterprises, who might anyway seek to minimize investment and rely on market power to maintain sales
- And where there are many small breeding enterprises, co-investment from the rest of the production chain reduces the financial risk, or at least spreads it, and can support diversity of selection direction, thus allowing an industry to meet more current and future needs and wants of its participants and its customers.

If something like this approach is followed, some improvement in all traits recorded can be anticipated.

The main challenge arising from this re-framing of the original question is "how to fund genetic improvement?" Such funding needs to be equitable and efficient, which leads to questions touched on briefly in the discussion of the RDC system used in Australia. Imposition of some form of levy is best done at the simplest point and transparently, and should clearly relate to the value of production. End-point royalties, used in Australia to fund cereals breeding programs, achieve this. They are typically around 2% of value of the product, collected at the point of sale from the farmer. Efficient market theory suggests that the burden of this levy ends up being shared through the chain.

This approach, if applied, would represent an evolution in the relationship between sectors of the beef and sheep industries, from relatively unconnected sellers and buyers in a market for genetic material, to partners in their joint continued prosperity, or even survival. It would also move industry from using assumed consumer benefit as a justification for governmental support, to being the primary focus for broader breeding goals, while potentially still receiving community co-investment.

This approach also holds the potential to transform genetic improvement from being focused on relatively few attributes deemed to have what are almost ex-market values (producing more cheap, abundant food has some moral quality that trumps consumers' desires, and justifies industry support), to becoming an enterprise where low-cost and high quality continue to be fundamental, but have added to them as goals wider attributes of both the animal and the production system. This aspect of the transformation has already begun, as is evident in the evolution of trait economic values in dairy genetic evaluations (Van Eenennaam et al, 2014).

Acknowledgements

This paper has evolved through considerable discussion with many colleagues, in particular Pieter Knap and Peter Amer, all of which is greatly appreciated.

Literature Cited

Amer, P.R. and Fox, G.C. (1992) *Anim. Prod*.**54**:341-349

Amer, P.R., Nieuwhof, G.J., Pollott, G.E., Roughsedge, T., Conington, J. and Simm, G. (2007) *Animal* **1**(10):141-1426

Amer, P.R., Banks, R.G., and Garrick, D.J. (2012) *ICAR* **38**

Atkins, K.D. (1993) *Wool Tech. Sheep Breed.*, **41**:257-268

Banks, R.G. (1999) *Proc. Assoc. Advmt, Anim. Breed. Genet.* **12**: 648-655

Banks, R.G., Amer, P. R., and van der Werf, J.H.J (2013) *Proc. Assoc. Advmt, Anim. Breed. Genet*. **20**:45-48

Bichard, M. (1971) *Anim. Prod.* **13**:410-411

Brascamp, E.W., Smith, C. and Guy, D.R. (1985) *Anim. Prod*. **40**:175-180

Goddard, M.E. and Hayes, B.J. (2099) *Nature Reviews Genetics* **10**:381-391

Harris, D.L. and Newman, S. (1992) *Amer. Soc. Anim. Sci.* **84**(3): 1-17

Hazel, L.N. (1943) *Genetics* **28**:476-490

Hill, W.G. (2008) *Lohmann Information* **43**(1):3-20

Kinghorn, B. P. (2014) *Proc. 6th WCGALP*

Knap, P. (2014) *Proc. 10th WCGALP*

Land, R.B. (1981) *Livestock Prod. Sci.* **8(**2): 95-99

Lee, S.J., Nuberg, I.K., and Pitchford, W.S. (2014) *Proc. 6th WCGALP*

Lindsay, D. (1988) *Proc. 6th WCGALP* **23**:3-9

Miller, R.H. and Pearson, R.E. (1979) *Animal Breeding Abstracts* **47**(6):281-290

Mounter, S.W., Griffith, G.R., Piggott, R.R., Fleming, E. and Zhao, X. (2008) *Austr. Agribusiness Rev.* **16**:1-25

Rowe, J.B., Gill, S.R., Banks, R.G. and van der Werf, J.H.J. (2013) *Proc. Assoc. Advmt, Anim. Breed. Genet*. **20**:14-17

Smith, C., James, J.W. and Brascamp, E.W. (1986) *Anim. Prod.* **41**:545-551

Van Eenennaam, A. L., Weigel, K. A., Young, A.E., Cleveland, M. A., and Dekkers, J. C.M. (2014) *Annu. Rev. Anim. Biosci.* **2:**105-139

Van Eenennaam, A. L. (2012) *ICAR* **38**

Zhao, X., Mullen, J.D., Griffith, G.R., Griffiths, W.E. and Piggott, R.R. (2000) Economic Research Report No. 4, NSW Agriculture, Orange.