The Use Of Breeding To Improve Animal Welfare

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Introduction

Since the domestication of livestock some 10,000 or so years ago, man has been selectively breeding animals to align with our human needs for wool, hide, meat, milk and draft. It has only been in the last 60 years or so, that the rate of genetic change in some livestock species has accelerated considerably due to the application of quantitative genetics and selective breeding, taking advantage of evolving computer technology and software developments (e.g. BLUP). The improvements in production performance as a result of implementing such technology is impressive, with broiler chickens reaching target 2 kg slaughter weights in half the time (36 vs 65 d) in 1999 compared to 1976 (McKay et al., 2000), and the average dairy cow now producing more than 6 times the amount of milk of that needed to rear a calf. With the world's population predicted to increase by 2-3 billion in the next 40 years (Defra, 2010) and along with it an increase in the consumption of animal products, the use of animal breeding technologies will undoubtedly be required to meet the challenge of feeding the world in the future.

However, there have been recognised problems that have arisen largely as a consequence of a narrow focus only on production traits in the past, which have given cause for concern for animal welfare (Rauw et al., 1998). The focus of these problems has mainly been for species with high reproductive rates and short generation intervals such as pigs and poultry that have undergone relatively more generations of selection compared to other species, although latterly problems of health and functional fitness have also been highlighted in ruminants. The main animal welfare issues have arisen because of failure to include health and welfare traits in breeding programmes and to recognise and deal with antagonistic genetic correlations among some production, health and fitness traits. Another major issue is the mismatches that occur between the new genotypes and their existing environments.

Freedom from hunger, thirst, discomfort, pain, injury, disease, fear, distress and freedom to express normal behaviour are the core animal welfare principles for those that use animals (FAWC: www.fawc.org.uk). Recently, more positive definitions of 'a life worth living' and 'a good life', evaluated on a graded scale have been suggested to assess the status of animal welfare (FAWC, 2009). Both of these sets of welfare principles are intended to meet human expectations of how animals should be kept, and are backed by specific legislations. National and EU legislations (e.g. the European directive 98/58/EC) provide legal frameworks for the use of animal breeding to protect animal welfare, and state that 'no animal shall be kept for farming purposes unless it can reasonably be expected, on the basis of their genotype or phenotype, that they can be kept without detrimental effect on their health and welfare' (Welfare of Farmed Animals Regulations 2000, England, UK). The Standing committees (e.g. T-AP, 2005b) of the European convention for the protection of animals kept for farming purposes, which covers all major farmed species includes in its recommendations an article

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on 'changes of genotype' which emphasises that breeding goals should include health and welfare traits. Despite this, the use of legislation to improve animal welfare is a blunt tool and in some cases new animal welfare legislation can lead to unforeseen deterioration in animal welfare, at least in the short term. For example the ban on stalls for pigs in the UK led to problems of aggression, bullying and tail-biting in some loose-housed systems, and the imminent ban on beak trimming in laying hens potentially could lead to similar problems. In the longer term, these issues can be resolved, but these problems highlight the need to consider the immediate consequences of well-intentioned actions. Industry codes of practice are welcome initiatives, such as those drawn up by CODE-EFABAR promoted by the recent EU Sustainable Animal Breeding technology platform (SABRE) and its predecessor projects, as they have made some inroads to address public concern and interest in the impact that animal breeding can have on animal welfare. This paper will briefly review how animal breeding has negatively affected animal welfare in the past, and illustrate with examples how it is being used to improve animal welfare for the future.

The problems

Selection for high, lean growth and feed efficiency

Breeding faster-growing young animals to meet target slaughter weights in shorter time periods has in many cases inadvertently led to larger, mature breeding animals with higher mature weight and consequentially, higher maintenance requirements (Morris et al., 1992; Archer et al., 1998). This has occurred because there are usually strong, positive genetic correlations between live weights at different ages. Even though growing fast and having a larger size is not in itself considered to be a welfare problem, there are two main welfarerelated concerns. Firstly, larger mature animals that are kept for breeding are often managed in out-dated housing conditions that were originally built for smaller genotypes, leading to difficulties in lying and standing, for example small sow farrowing crates and cow cubicles that are not long enough. Another example is shoulder sores on sows which are considered to occur more frequently specifically because larger, leaner genotypes no longer 'fit' into their environment. The satiety mechanisms of some broiler chicken strains are reported to have been compromised by narrow selection objectives for high growth, with hypothalamic failure to diminish the hunger drive leading to over-consumption. Selected chickens consistently consume feed above their metabolic requirements until they reach a limit set by gastrointestinal capacity (Burkhart et al., 1983; Barbato et al., 1984; Siegel and Dunnington,

Second, there are other structural and functional problems associated with rapid growth. The main cardiovascular condition associated with high growth in broilers is ascites (Thorp and Luiting, 2000; Navarro et al., 2001). Ascites is a metabolic disorder in broilers that is associated with insufficient oxygen supply relative to oxygen demand of tissues (Julian, 1993). It used to only be a problem of poultry reared at high altitude but it is now seen in birds at sea level. A condition caused similarly by a shortage of oxygen to tissues is oregon disease which occurs as a result of lack of blood supply to affected tissues (Henckel, 2002). Sudden death syndrome (SDS) with heart failure of otherwise apparently healthy birds is seen as being a lung condition, as well as being an indication of a cardiovascular disorder (Rauw et al., 1998; Chambers, 1986). Other problems include hypothyroidism (Scheele et

al., 1992 and Buys et al., 1999, cited by Henckel, 2000) and metabolic 'exhaustion' leading to high pH and a high number of glycolytic muscle fibres in poultry (Henckel, 2002). Larger muscle fibres brought about by selection for growth have also been associated with enhanced susceptibility to stress (Henckel et al., 2002). However in mice, it has been shown that selection for antagonistically-correlated growth and stress simultaneously, results in improvements in both traits (Bünger et al., 1994).

Extreme muscular hypertrophy of genetic origin in cattle, commonly referred to as double muscling, is an inherited condition, and is found in many breeds of cattle. The highest frequency of occurrence is found in the Piedmontese and Belgian Blue breeds, where deliberate effort was made in the last few decades to increase the frequency of double muscling. This syndrome is associated with some production problems such as reduced fertility, increase in dystocia and reduced calf survival.. The double muscling example of Piedmontese and Belgian Blue cattle has been often used to demonstrate the negative side effects of heavy muscling on fertility and welfare as a high proportion of these and other similar breeds require caesarean sections to give birth, which from a welfare point of view is unacceptable. If double-muscled breeds have a role to play in beef and dairy-beef production systems in a country it is recommended that the breeding female herd is kept free from double muscling. A terminal sire breeding system is suggested, whereby normal females are mated to double muscled sires and all progeny slaughtered. It is also worthwhile to consider to use breeds where the phenotypic expression of the myostatin mutation is less drastic, due to epistatic interactions (Wiener et al., 2002; Wiener et al., 2009)

Selection for high milk yield and litter size

In recent years, declining fertility in high-yielding dairy cows has been the subject of many reports (Calus et al., 2005; Royal et al., 2000, amongst others). Again, this can be explained in part, by the use of production-only breeding goals for selection programmes in the past. Antagonistic correlations among growth rates, linear type traits and body condition score with milk indicate that bigger animals tend to have poorer fertility; higher producing cows are more likely to have lower growth rates in first lactation and lose body energy during the peak of first lactation, and thinner cows are likely to have longer calving intervals (Pryce et al., 1998; Wall et al, 2007). The understanding of some unfavourable genetic correlations among production traits and fertility, growth rate of heifers and body condition score has led to the incorporation of fertility traits into dairy indexes in some countries. In pigs, the focus of selection for higher litter size without the corresponding ability of sows to rear the piglets, has led to high and unacceptable levels of piglet mortality (Knol et al., 2002; Roehe et al., 2009; Edwards et al., 2002), and unfavourable genetic relationships of total genetic merit with survival have been reported (Cecchinato et al., 2008). In sheep, the introgression of fertility genes into breeds (e.g. Booroola) where the management conditions for rearing large numbers of low-birthweight lambs is not in place, has led to poor growth and high lamb mortality rates (Fogarty, 2009).

How animal breeding affects animal health and behaviour

Beilharz's 'resource allocation theory' suggests that given environmental resource restriction, the allocation of an animals' own resources to cope with high performance leads to a lower allocation to health and fitness functions (Beilharz et al., 1993). There is

considerable evidence that high performance in some species has been associated with reduced immune performance (see review by Rauw et al., 1998; Maatman et al., 1993; Yunis et al., 2000; Savory, 2002; Biscarini et al., 2009). Infectious diseases such as necrotic enteritis in poultry have been associated with high production performance (van der Sluis, 2000 cited by Savory, 2002).

Bone quality and health have been major foci of attention by some pig and poultry breeding companies to alleviate bone (and joint) problems including tibial dyschondroplasia (Whitehead, 1992; Bakken et al., 1998; Mercer and Hill, 1984; Chambers, Bishop et al., 1986). The physical difficulties associated with walking and mating are highly visible symptoms associated with bone problems that are of major concern for animal welfare. Poor bone quality in highly productive laying hens causing osteoporosis and bone fractures at the end of lay, has led to the development of breeding strategies and new diagnostic tools designed to alleviate these problems.

Genetic correlation estimates between somatic cell counts (an indicator trait for mastitis used in the dairy industry) and milk yield are reported by Conington et al. (2008) for dairy sheep and by Pryce et al. (2004) for dairy cattle. Even though the estimates do not agree on the magnitude, the general consensus for cattle is that cows with higher milk yields are genetically susceptible to having higher cell counts and clinical mastitis. Low to moderate unfavourable correlations among different aspects of cattle lameness and protein yield in Austrian cattle have been reported (Buch et al., 2009) although the converse was true for sheep lameness and some other production traits, where Blackface ewes that reared more lambs had lower footrot hoof lesions (McLaren et al., 2008).

There are numerous examples where a lack of balance in breeding programmes has led to both behavioural and physiological problems in animals. Pigs selected for high lean gain have more excitable temperaments and are more fearful than other genetic lines (Grandin 1993, 1994; Shea-Moore, 1998). Pigs with higher lean growth rates show an increased stress response to transportation leading to lower meat quality (Grandin, 1997). In cattle, stereotypic licking may be linked to selection for high milk yield (Grandin and Dessing, 1998). There may also be adverse effects on maternal care and during birth. Double-muscled beef cattle generally have more difficulty in calving unassisted and selection for docility in cattle may indirectly alter maternal defensive aggression (Turner and Lawrence, 2007). In terminal sire sheep breeds, where the lambs are often born indoors and given high levels of human care, the quality of maternal care given by ewes requiring assistance at birth is reduced compared to breeds that lamb without assistance (Dwyer and Lawrence, 2005). In laying hens, increased aggression and propensity to suffer from osteoporosis is related to selection for early sexual maturity and high egg production (Craig et al., 1975).

The solutions

The key to halting undesirable correlated responses to selection for high performance lies in the detail of the breeding programmes. Most of the genetic correlations among production and non-production traits are far from unity, so the incorporation of non-production traits into selection indices with appropriate weightings should at least halt their decline and at best lead to the selection of fitter, healthier breeding animals for the future. Even though their incorporation may lead to some compromise in the rates of genetic progress that are made in the key performance breeding goals, it is generally concluded that most of the traits for which a direct economic benefit is apparent (such as improvements in disease status), leads to overall economic and animal welfare benefits. There are now some examples of how breeding programmes have been broadened to include a wider spectrum of fitness-related traits into the breeding goal, although it may take several more generations before the benefits are realised in the commercial populations.

Crossbreeding is routinely used to obtain the benefits of high performance and to overcome the problems of susceptibility to disease or loss of functional fitness, in particular in tropical or limiting environments. Maintaining crossbred animals increases heterogeneity and hence maximises the expression of non-additive heterosis for health and fitness. The use of crossbred animals as the commercial populations of pigs, poultry, sheep and beef cattle is well-established and there is increasing interest in, and awareness of, the benefits of crossbreeding in dairy cattle.

Breeding for resistance to disease and behaviour

Breeding for disease resistance was observed by Morris (2000) to be a relatively new concept, which, before the 1990s, the wisdom of which was seriously questioned. Yet now it is generally accepted as being feasible and there are some useful demonstrations of how it can be implemented in practice. However, there are many more reports of the deleterious effects that animal breeding has had on health and welfare, than there are success stories of the impact that their inclusion into breeding programmes has had on reducing disease prevalence levels. One of the major problems that has to be overcome is to have good, reliable, cheap and repeatable phenotypic measurements of disease status that can be used on large numbers of animals for selection programmes. There is a recognised lack of consistent recording of disease issues on-farm that limits the use of breeding as a solution to disease. However, a proxy measure that correlates well with disease status can be used, for example Somatic Cell Count (SCC) is used in the dairy industry as a proxy measure for susceptibility to mastitis and the classification of hoof lesion scores according to severity can aid the selection of sheep for resistance to footrot (Conington et al., 2008; Nieuwhof et al., 2008).

The dairy breeding indices used in Norway have placed greater emphasis on non-production traits in their breeding programmes since 1970s, and in the UK, the introduction of new weightings to dairy cow indices in 2007 places more emphasis on health, welfare and fertility than in the past, compared with production performance traits (milk, fat and protein), i.e. in a ratio of non-production to production traits of 42:58 respectively (See Figure 1).

In poultry, strategies adopted by breeding companies to incorporate common diseases such as Marek's, Lymphoid leucosis, salmonellae and coccidiosis into breeding programmes have been summarised by Thorp and Luiting (2000), amongst others.

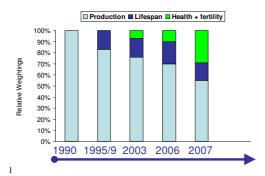


Figure 1: Evolution of UK dairy indices (E.Wall, pers.comm.)

In sheep, the use of faecal egg count (FEC) as a proxy trait for level of gastrointestinal nematode parasitism is a useful indicator to establish the extent of worm burdens in grazing livestock. FEC can be used both as a management tool for farmers on which to base decisions for grazing management, as well as timing for the administration of anthelmintics. Together with pedigree information, FEC can also be used to indicate genetic resistance to parasites and hence be included in genetic improvement programmes. In New Zealand and Australia, established breeding programmes that include faecal egg count as a breeding objective are currently being implemented. In the UK, farmers can obtain EBVs for FEC although it has not been integrated into selection indices. Aspects of breeding for resistance to footrot has also been reported (Skerman and Moorhouse, 1987; Raadsma et al., 2000), and the genetic information generated from the recent UK footrot research (Conington et al., 2008; 2008a; Nieuwhof et al., 2007; 2009) has been used in the development of new breeding indices for the Irish Republic (P. Amer, pers. comm.).

The use of breeding techniques may also improve welfare of animals and the safety of their handlers, by selection for favourable temperament traits. For example, there are many studies that show that high levels of fearfulness in animals is related to lower production (beef cattle: Petherick et al., 2002; dairy cows: Drugociu et al., 1977; chickens: Barnett et al., 1992). Reducing levels of fear that animals show towards humans in routine handling procedures would be beneficial for welfare, and in the case of cattle, reduce the injuries caused to humans by cattle. There has been a number of studies investigating how best to quantify the fearfulness trait in cattle beef. In one case the test involves assessing the ease with which an animal can be moved to a corner of a pen and held there (e.g. Boivin et al., 1992) and in an other case it involves measuring the speed with which an animal flees a weighing or handling crate (Burrow et al., 1988). Both of these tests have been developed to the extent that they are now used to assess fearfulness or docility in cattle and EBVs are routinely calculated for Limousin and Brahman cattle respectively. This example shows that behavioural traits can be used in selection programmes, and offers the possibility that more can be done. Practical, economic and ethical considerations of incorporating behavioural traits into breeding programmes are discussed further by D'Eath et al. (2010).

Using molecular genetic information

The use of molecular genetic selection to avoid deleterious inherited diseases is well established where a major gene is responsible for a significant part of genetic variation. A summary of such conditions has been well-documented and is publicly available by the Online Mendelian Inheritance in Animals website (OMIA). In the EU, the industry implementation of selection against scrapie in sheep through the use of ram genotyping schemes (Leymarie et al., 2009; Elgin et al., 2005) was undertaken during the last decade. This was largely in response to the possible link between Scrapie and Bovine Spongiform Encephalopathy (BSE) although this was never established and hence there is no longer a legal obligation for such schemes to take place. In fish, selection to reduce Infectious Pancreatic Necrosis (IPN) in the farmed salmon industry is being implemented in industry (Houston et al., 2009) and in pigs and poultry, research into selection for increased generalised immunity using whole genome analyses may well pioneer the way that disease is controlled in the future (Biscarini et al., 2009). Genome-wide selection using information from several thousand single nucleotide polymorphisms (SNPs) is an opportunity to include disease resistance in breeding programmes (Fife et al., 2009) which is particularly beneficial because most disease traits have low heritabilities, are difficult or expensive to measure, and animals usually are subject to inconsistent exposure to disease that makes selection for disease resistance more complex. Several examples of using molecular information to breed more resistant animals to disease was the subject of a recent international conference 'Animal Genomics for Animal Health' (Paris, June 2010), where examples of using the latest SNP technology to identify susceptible genotypes was reported for coccidiosis in sheep, mastitis in cattle and PRRS virus in pigs, amongst others. (https://colloque.inra.fr/agah2010)

Breeding to better match genotype with environment

Breeding animals to adapt to their environment, rather than focus on changing environments to match new genotypes (such as altering housing and cubicle design) can minimise the mismatch between them. Legislation to ban battery cages and beak trimming may create temporary problems of feather pecking and bullying if the same strains that have been bred and adapted to suit cages are used for such new systems. Breeding sheep to shed their wool in the springtime to minimise the risk of fly strike, whilst reducing the need for shearing is an example of adapting to new, warmer environments and lower labour use. A discussion of how sheep can be bred to adapt to changing management and environmental systems is reported by Conington et al. (2010).

Conclusion

The use of broader breeding goals in animal breeding programmes can only be realised if robust phenotypes are available to distinguish variation between animals in their ability to resist disease, ability to express desirable behaviours or better adapt to changing management situations. A willingness to accept a compromise in the rates of genetic gain through the incorporation of such traits, will go some way to halt the decline that (in some circumstances) is predicted in fitness traits due to their largely unfavourable genetic relationships with production. Using desired gains, or additional (social or ethical) weightings on non-production traits (Olesen, 2006), will tip the balance in favour of fitter and healthier animals that will also be more productive and economic.

At the other end of the spectrum, demand-led solutions, using breeding as a way to improve animal welfare, could accelerate the inclusion of welfare traits into breeding programmes. This might be done by creating a mechanism whereby certain high-end supermarkets or consumer groups who demand a higher standard of welfare can pay a premium for the product. These buyer groups might use a customised index approach to create a list of sires with good EBVs for health and welfare traits which the subscribing farmers must use before they can sell their produce through such supermarkets. Alternatively, using their considerable influence on producers, supermarkets can decide if purchasing milk from farmers with lame cows is an acceptable price to pay for cheap milk. This could create a surge in demand for sires with good EBVs for locomotion scores. Whichever way that animal breeding develops in the future, it is paramount that breeding for resistance to disease, or for animals to adapt better to 'poor' environments (e.g. arid conditions), does not discourage the development of higher standards of stockmanship and good quality environment. More emphasis needs to be put on the implementation of selection for resistance to disease, monitoring the impact that it is having on reducing disease prevalence levels, and communicating the results to the public, in particular to welfare interest groups.

References

Archer, J.A., Herd, R.M., Arthur, P.F. and Parnell, P.F. (1998) Livest. Prod. Sci. 54:183-192

Arthur, P.F. (1995). Australian J. Agric. Research 46: 1493-1515.

Backken, M., Vangen, O. and Rauw, W.M. (1998). 6th World Congress on Genetics Applied to Livestock Production, Armidale, Australia. Vol 27: 381-388.

Barbato, G.F., Siegel, P.B., Cherry, J.A. and Nir, L. (1984). Poultry Science 63: 11-18

Barnett, J.L., Hemsworth, P.H. and Newman, E.A. (1992) British Poultry Sci 33:699-710

Beilharz, R.G., Luxford, B.G. and Wilkinson, J.L. (1993). J. Anim. Breed Genet. 110: 61-170

Boivin, X., Le Neindre, P. and Chupin, J.M. (1992). Appl. Anim. Behav. Sci. 32:325-335

Biscarini, F., Bovenhuis, H., Van Arendonk, J.A.M., Parmentier, H.K., Jungerius, A. and Van Der Poel, J. (2009) *EAAP* 45:5: P.504

Bishop, S.C., Fleming, R.H., McCormack, H.A., Flock, D.K and Whitehead, C.C.(2000). *British Poultry Science* 41:1 pp.33-44

Buch, L.H., Sørensen, A.C., Lassen, J., Berg, P., Jakobsen, J.H., Eriksson, J.Å and Sørensen, M.K. (2009) *EAAP* 11:11. P108.

Bünger, L., Renne, U. and Dietl, G. (1994). *Proc. 5th World Congress on Genetics Applied to Livestock Production*, Guelph 16-19.

Burkhart, C.A., Cherry, J.A.9, Van Krey, H.P., Siegel, P.B. (1983). *Behavioural Genetetics* 13: 295-300.

Burrow, H.M., Seifert, G.W. Corbet, N.J. (1988) Proceedings of the Australian Society for Animal Production, 17:154-156

Buys, N., Scheele, C.W., Kwakernaak, C. And Decuypere, E. (1999). Brit. Poult. Sci. 40, 140-144

Cecchinato, A. Bonfatti, V., Gallo L. and Carnier P.J. (2008) *Anim Sci.*, doi: .2527/jas.2007-0825 May 9, 2008.

Conington, J., Cao, G., Stott, A. Bünger, L. (2008) Veterinary Record 162: 369-376

Conington, J., Collins, J. And Dwyer (2010) Animal Welfare 19(S): 83-92...

Conington, J. Nieuwhof, G.J., McLaren, A., Hosie, B., Bishop, S.C. and Bünger, L. (2008) *EAAP* Paper No. 3133. Lithuania, August 24-27.

Conington, J, Hosie, B., Nieuwhof, G.J., Bishop, S.C., and Bünger, L. (2008a). *Vet. Res. Comm.* 14 May 2008 doi:10.1007/s11259-008-9062-x.

Craig, J.V., Jan, M.L., Polley, C.R., Bhagwat, A.L. (1975). Poultry Science. 54, 1647-1658.

D'Eath, R.B., Conington, J., Lawrence, A.B., Olsson, I.A.S. and Sandøe, P. (2010) *Animal Welfare* 19(S) 17-27.

Defra, (2010) http://www.defra.gov.uk/foodfarm/food/pdf/food2030strategy-summary.pdf

Drugociu, G., Runceanu, L., Nicorici, R., Hritcu, V. and Pascal, S. (1977) *Anim. Breed. Abstr.* 45:1262

Dwyer, C.M. and Lawrence, A.B. (2005). Appl. Anim. Behav. Sci., 92, 235-260.

Eglin, R.D., Warner, R., Gubbins, S., Sivam, S.K. and Dawson, M. (2005) *The Veterinary Record* 156: 433-437

FAWC, Farm Animal Welfare Council (2009) http://www.fawc.org.uk/pdf/ppf-report091012.pdf

Fife, M., Watson, M., Howell, J. and Kaiser, P.(2009) *EAAP* 45: 3:. 503

Fogarty, N.M. (2009). Small Ruminant Research 85:2-3:75-84.

Grandin, T. (1993). Appl. Anim. Behav. Sci. 36: 1-9.

Grandin, T. (1994). Vet. Med. 89: 989-998.

Grandin, T. (1997). J. Anim. Sci. 75: 249-257.

Grandin, T., and Deesing, M.J. (1998). In: *Grandin, T. (Ed.), Genetics and the Behaviour of Domestic Animals*. Academic Press.

Henckel, P. (2002). 7th World Congress on Genetics Applied to Livestock Production August 19-23, Montpellier, France.

Houston, R.D., Haley, C.S., Hamilton, A., Guy, D.R., Gheyas, A., Mota-Velasco, J., Tinch, A.E., Taggart, J.B., Bron, J.E., Mcandrew, B.J., Verner-Jeffreys, D., Paley, R., Tew, I. and Bishop, S.C. (2009). *EAAP 45:2 P.503*.

Julian, R. J. (1993). Avian pathology 22: 419-454.

Knol, E.F., Leenhouwers, J.I. and van der Lende., T. (2002). Livest. Prod. Sci. 78:47-55

Leymarie, C., Astruc, J.M., Barillet, F., Bibe, B., Bonnot, A., Bouffartigue, B., Bouix, J., Dion, F., Francois, D., Jouhet, E., Jullien, E., Moreno, C., Boscher, M.Y., Palhiere, I., Raoul, J., Tiphine, L., Bouchel, D., Chibon, J., Raynal, A. and Tribon, P. (2009). *EAAP* 45:11 P.507.

Maatman, R., Gross, W.B., Dunnington, E.A., Larsen, A.S., and Siegel, P.B. (1993). *Archiv fur Geflugelkunde* 57: 249-256.

Mckay, J.C., Barton, N.F., Koerhuis, A.N.M., and McAdam, J. (2000) In: *The challenge of genetic change in animal production. BSAS Occasional publication no.* 27 eds: by W. G.

Hill, S. C. Bishop, B. Mcguirk, J. C. Mckay, G. Simm, A.J. Webb.

McLaren, A., Conington, J., Lambe, N.L., Nieuwhof, G.J., Bishop, S.C. and Bünger, L. (2008) *Abstract 107. Proc BSAS, Scarborough 31st Mar-2nd Apr, 2008.*

Mercer, J.T and Hill, W.G. (1984). Heredity 53: 1: 193-203.

Morris, C.A., Baker, R.L. and Hunter, J.C. (1992). Livest. Prod. Sci. 30: 33-52.

Morris, C.A. (2000) *In: Axford, R.F.E., Bishop, S.C., Nicholas, F.W. and Owen, J.B.* (eds) *Breeding for resistance to disease in farm animals. 2nd edn.* CAB International, Wallingford, UK.

Navarro, P.,Koerhuis, A.N.M., Chatziplis, D., Visscher, P.M. and Haley, C.S. (2002). 7th World Congress on Genetics Applied to Livestock Production, Montpellier, France.

Nieuwhof, G.J., Conington, J., Bünger, L., and Bishop, S.C. (2008) *Animal* 2: 9: 1289-1296.

Nieuwhof, G.J., Conington, J., Bishop, S.C. (2009). *Genetics Selection Evolution* 41:19. d.o.i: 10.1186/1297-9686-41-19

Olesen, I., Navrud, S., Kolstad, K. (2006) *Proc. 8th World Cong. Genet. Appl. Livest. Prod.* Aug., 13-18, 2006, Belo Horizonte, Brazil. CD-ROM: 31:538-1710.

Online Mendelian Inheritance in Animals, OMIA. Reprogen, Faculty of Veterinary Science, University of Sydney and Australian National Genomic Information Service (ANGIS), University of Sydney, {25/02/2010}. World Wide Web URL: http://omia.angis.org.au/

Petherick, J.C., Holroyd, R.G., Doogan, V.J., Venus, B.K. (2002). *Aust. J. Exp. Agric.* 42: 389-398.

Pryce, J. E., R. J. Esslemont, R. Thompson, R. F. Veerkamp, M. A.Kossaibati, and G. Simm. (1998). *Anim. Sci.* 66:577–584.

Raadsma, H.W. (2000) *In* Breeding for disease resistance in farm animals 2nd edition. Eds. Axford, R.F.E., Bishop, S.C., Nicholas, F.W. and Owen, J.B. CABI publishing.

Rauw, W.M., Kanis, E., Noorhuizen-Stassen, E.N., and Gommers, F.J. (1998). *Livest. Prod. Sci.* 56:15-33.

Roehe R., Shrestha, N.P., Mekkawy, W., Baxter, E.M., Knap, P.W., Smurthwaite K.M., Jarvis, S., Lawrence, A.B., Edwards S.A. (2009) *Livest. Sci.* 121: 173-181

Royal, M.D., Darwash, A.O., Flint, A.P.F., Webb, R. Woolliams, J.A. and Lamming, G.E. (2000) *Animal Science* 70:3: 487-501

Savory, C.J. (2002). *Proc.* 11th European Poultry Conference, Bremen, 6-10th Sept. Scheele, C.W., Decuypere, E., Vereijken, P.F.G., and Schreurs, F.J.G. (1992). Poultry Science 71: 1971-1984.

Siegel, P.B. and Dunnington, E.A. (1985). In: *Poultry breeding and Genetics. Proceedings of 18th Poultry Science Symposium.* P.59-72. Eds. Hill, W.G., Manson, J.M. and Hewitt, D.

Skerman T.M.., and Moorhouse S.R. (1987). New Zealand Veterinary Journal 35: 101-106.

Shea-Moore, M. (1998) *J. Anim. Sci.* 74 (Suppl. 1), 100. (Abstract). T-AP (2005b) *Standing committee of the european convention for the protection of animals kept for farming purposes (T-AP)*

Thorp, B.H. and Luiting, (2000). *In* Breeding for disease resistance in farm animals. P357-377. 2nd edition. Eds. Axford, R.F.E., Bishop, S.C., Nicholas, F.W. and Owen, J.B. CABI publishing.

Turner, S.P. and Lawrence, A.B. (2007). Livest. Sci. 106: 182-188.

Wall, E., Coffey, M. P. and Brotherstone, S. (2007). J. Dairy Sci. 91: 1527-1537

Whitehead, C.C. and Wilson S. (1992). In: *Whitehead, C.C. (Ed) Bone biology and skeletal disorders in poultry*, pp. 265-280 (Abingdon, Carfax Publishing)

Wiener, P., Smith, J.A., Lewis, A.M., Woolliams, J.A. & Williams, J.L. (2002). *Genetics Selection Evolution* 34: 221-232.

Wood, J.D., Homer, D. and Williams, J.L. (2009). Meat Science 83: 127-134.

Yunis, R., Ben-David, A., Heller, E.D. and Cahaner, A. (2000). *Poultry Sci.* 79: 810-816.