doi:10.1017/S0043933910000553

Layer breeding strategies: an overview

A.K. THIRUVENKADAN[1]*, S. PANNEERSELVAM[2] and R. PRABAKARAN[3]

[1]Department of Animal Genetics and Breeding, Veterinary College and Research Institute, Namakkal-637 002,Tamil Nadu, India; [2]Department of Animal Genetics and Breeding, Veterinary College and Research Institute, Namakkal-637 002, Tamil Nadu, India; [3]Madras Veterinary College, Tamil Nadu Veterinary and Animal Sciences University, Chenai-600 051, Tamil Nadu, India
*Corresponding author: drthirusiva @yahoo.com

Layer breeding companies apply selection criteria to improve over 30 traits important for commercial egg production. Intensive selection for egg production over the decades has resulted in a significant reduction in genetic and phenotypic variations in egg production, however the decrease in genetic variation observed in commercial lines are not yet critical. Peak production now approaches the biological limit of one egg a day, but in early production (at sexual maturity) and late production (persistency) genetic variation is still high. Including these traits in the selection criteria will improve the egg production in commercial birds. Due to high heritability and the absence of any significant negative effects on production parameters, residual feed consumption is used as selection criteria to improve the feed efficiency. Considerable research has been carried out on egg weight, eggshell strength and internal quality of the eggs and improvements have been made as a result of selection. With the reintroduction of floor system and increased consumer interest in processed eggs, in future more emphases have to be given to the eggshell strength and internal quality of the eggs. Poultry production in the unfavourable environmental conditions of the tropics is hindered by direct and indirect heat stress leading to a general depression in performance. Results on the utilisation of naked-neck and frizzle gene in high-ambient temperatures is encouraging, and, in future, will play an important role in production of layer lines suitable for overcoming such genotype-environment interaction. Feather pecking is an undesirable behaviour, which causes major problems in non-cage systems. Several authors have identified a hereditary basis of feather pecking behaviour, which is suggested by strain differences. Hence, selection of birds with no or very low tendency to perform feather pecking should reduce the incidence. Recent molecular genetic studies resulted in identification of QTL affecting different economic traits and identification of candidate genes causing variation in performance among birds. In future these findings will play a major role in further genetic improvement of layers without any negative effect.

Keywords: layer; breeding strategies; feed efficiency; feather pecking; molecular genetics

© World's Poultry Science Association 2010
World's Poultry Science Journal, Vol. 66, September 2010
Received for publication August 20, 2009
Accepted for publication March 28, 2010

https://doi.org/10.1017/S0043933910000553 Published online by Cambridge University Press

Introduction

In the early part of the 20th century, almost every small flock of chickens would have self-reproduced and the farmers considered themselves breeders as well as producers. Although they lacked most of the characteristics of today's primary breeders, these individuals were involved in selling breeding stock rather than table eggs and regarded their operations as a hobby. However, in the late 1940s, a few breeders began to develop poultry breeding as a business. Later on, stock intended for commercial egg production were selected according to a very specialized set of criteria. Considerable research has been conducted into the general area of breeding for egg production by different layer breeding companies. They applied quantitative genetics to selection of birds for egg production.

Since 1950, breeding firms have become much fewer in number and much larger in size. The reduction in number of breeding firms has been due to international competition and to the high cost of maintaining breeding, marketing and distribution programmes in comparison with potential income. However, following mergers, competition is still intense, some of it among companies within the same groups and also very little useful genetic variation was lost during the mergers. In fact, the current major players have a broad spectrum of breed combinations on offer, and are less vulnerable to changing demand than smaller companies with a limited range of products (Flock and Preisinger, 2002; Arthur and Albers, 2003).

The three major layer breeding companies in the world are Erich Wesjohann (with Lohmann Tierzucht (LTZ), Hy-Line and H & N (Heisdorf and Nelson Farms Inc.)), Hubbard-ISA (with ISA, Shaver, Babcock and Hubbard) and Hendrix poultry (with Hisex, Bovans and Dekalb) (Flock and Preisinger, 2002). Three- or four-way crossing is commonly used to produce the commercial layer, with four way being the most common. Hence, all the parent breeder males and females will be hybrids. Crossing is carried out to exploit hybrid vigour. Generally, the fitness traits for production and liveability are most likely to benefit from this maintained heterosis. The layer breeding companies have utilised different breeding and selection programmes at different periods of time. In this review strategies followed for the improvement of egg production, feed efficiency, skeletal problems, internal quality of the eggs along with recent molecular genetic studies on these economic traits are discussed.

Breeding goals

All breeding plans for commercial breeding companies have one major objective in common: to increase the genetic potential of the stock to produce saleable, high quality products at minimum cost in a given production system. Breeders of egg-type chickens concentrate on four major objectives. They are:

- Maximum number of saleable eggs per hen housed
- Low feed cost per egg or per kg egg mass
- Optimal internal and external egg quality
- Low mortality and high adaptability to different environments

Layer breeding companies apply selection to improve over 30 traits important for commercial egg production. In general, there are no worldwide or country wise standardised breeding goals set. Differences in economic, social and ecological production environments give rise to different approaches and needs in terms of human welfare and well-being. Breeders today select for (or at least monitor) the age

https://doi.org/10.1017/S0043933910000553 Published online by Cambridge University Press

at sexual maturity, rate of lay, liveability, egg weight, body weight, feed conversion, shell colour, shell strength, albumen height, egg inclusions (blood and meat spots) and temperament. From the early 1980s percentage of solids and lipids in eggs have been added as additional traits (Groen, 2003).

Selection strategies for egg production

Egg production has always been the cornerstone of the selection criteria applied to egg laying stock. A variety of measures are known to contribute to lifetime egg production. Because all hens placed in the laying house contribute to the cost of the flock, many commercial operations base their judgements on hen-housed egg production data. This is the total number of eggs produced divided by the number of hens placed. Hen-housed egg production is a combination of age at first egg, rate of egg production and viability. However, emphasis has been shifting to persistency of lay. As flocks maintain high rates of lay for longer periods of time, they can be kept for advanced ages without being moulted. In recent years there has been an increase in the use of induced moulting to extend the laying life of the hen in many parts of the world.

Traditionally, 'part production record' selection has been advocated by several authors (Bohren *et al.*, 1970) as a means of shortening generation interval to increase genetic progress. Because part record is an integral piece of annual egg production, resulting in a substantial built-in correlation, greater genetic progress in annual egg production has been generally predicted and, in some cases, observed. However, several authors have raised doubts about the validity of this hypothesis (Gowe and Strain, 1963; Muir, 1990). Hence, apart from part-production, annual production is also taken into account for selection decision. However, use of whole production records will double the generation interval. In order to optimise genetic gain per unit of time, multi-stage selection is followed as it reduces the cost and efforts (by discarding inferior birds at early age) and generation interval is minimised (Hicks *et al.*, 1998).

PERSISTENCY OF EGG PRODUCTION

A typical egg production curve for a flock increases rapidly during the first eight or nine weeks of production, maintains a constant production for a certain time, and then decreases slowly. A hen with a flatter egg production curve is considered to be more persistent than a hen with a curve that decreases rapidly after peak production. Persistency of egg production, therefore is an important determining factor for total egg production. Hens with the same total production can exhibit different egg production curves because of differences in persistency. Hens that are more persistent can be more desirable because the producer can depend on a longer period of constant production. The definition for persistency of egg production used in the literature seems to vary. Persistency of production is defined explicitly as 'average weekly or monthly drop in egg production after peak' or 'number of weeks in production until the flock has to be replaced, say 60 per cent of production'. The persistency of egg production is defined commonly as the decline in egg production after peak production and is measured, therefore, by slope of the decline (Grossman *et al.*, 2000).

Grossman and Koops (2001) developed a model for individual egg production in chicken using weekly egg production curve. They concluded that prediction of annual (52-week) egg production based on part-record production (first 22 weeks) might lead to over-prediction because persistency of production lasts longer than the part record. Genetic gain from selection to improve annual production, therefore, might be

https://doi.org/10.1017/S0043933910000553 Published online by Cambridge University Press

increased if selection accounted for persistency of egg production curve, and if data were summarised by 4-week intervals and cumulated.

Anang *et al.* (2001) and Anang *et al.* (2002) investigated the use of monthly production records for genetic evaluation of laying hens using test day model with random regression. The models were compared on the basis of Spearman rank correlations of individual breeding values and sire breeding values estimated from sub-sets of full-sibling split data. The hens which ranked highest on their estimated breeding values from different models were compared phenotypically with their full records. Based on the results, it was concluded that the genetic evaluation based on monthly production may be better than using cumulative production and RRMAS (Random Regression with covariates derived from the regression of Ali and Schaffer) appeared to be the best among the models tested.

CLUTCH LENGTH

Selection for part or whole record egg numbers or laying rate is a normal approach for improving egg production which has shown to yield positive genetic progress. In order to better identify the genetic factors underlying egg production variability, some genetic studies have focused on the time interval between consecutive ovipositions, the mean time of oviposition and the intra-clutch mean lag of oviposition time, in which the view for increasing egg production was ascribed to an increase in the rate of passage of egg through the oviduct and to an increase in the follicular maturation rate. Chen and Tixier-Boichard (2003) studied the correlated effect to long-term selection for clutch length. In response to 16 generations of direct selection for increased average clutch length, other egg production traits such as laying rate and total egg number have been indirectly improved. The clutch length had genetic correlations with egg number (0.777), laying rate (0.863) and clutch number (-0.845). They concluded that selection for clutch length was an effective method for increasing the egg production in which the clutch length was more heritable than laying rate and egg number.

In general, intensive selection for egg production over the decades resulted in a significant reduction in genetic and phenotypic variations in egg number; however the decrease in genetic variation observed in commercial lines are not yet critical. Peak production is approaching the biological limit of one egg a day, but in early (at sexual maturity) and late production (persistency) periods, genetic variation is still high. Including these traits in the selection criteria could improve the egg production in commercial birds. In addition studies have been focused on clutch length and oviposition time. So, in future they will also play an important role in further genetic improvement of layers.

Feed consumption and selection strategy

The trait with most impact on profitability is feed conversion. Feed expenses are the main cost in egg production and account for more than 60% of the production costs in laying hens. The conversion of feed into eggs is primarily a function of egg numbers. It is also influenced by egg size and body weight. Breeders improved feed conversion throughout the 20th century by selection on increased egg mass and smaller body size, and these remain the most important traits involved in variation of the feed consumption (Arthur and Albers, 2003). The most commonly used criteria for feed efficiency in laying hens are daily feed intake per hen, feed intake per egg, feed conversion (kg feed per kg egg mass) and egg income minus feed cost.

https://doi.org/10.1017/S0043933910000553 Published online by Cambridge University Press

RESIDUAL FEED CONSUMPTION (RFC)

Residual feed consumption is the difference between observed and predicted feed intake and has been investigated quite extensively in poultry research with respect to efficiency of feed usage of layers (Bordas *et al.*, 1992; Schulman *et al.*, 1994). RFC is defined as the difference between observed feed intake and expected feed intake based on metabolic body weight, body weight gain and egg mass production. Hence, RFC is the feed consumption corrected for egg mass production, body weight and body weight gain. It measures the remaining part of the variation in feed consumption not accounted for by these three traits. To estimate RFC, feed consumption is measured for individual hens. The expected feed consumption for each hen is calculated from the bird's egg mass and body size using linear model. Hens with high levels of RFC are culled. The linear model for calculating RFC to measure feed efficiency is as follows:

$FI= b_1+BW^{b2}+b_3+\Delta W+e$

Where FI= Feed intake (g/wt), BW=Average body weight between two recordings (g), ΔW=Body weight gain (g/wt), b_1, b_2, b_3 = Partial regression coefficients, e=Error (this is considered to be residual feed intake) (Van Eerden *et al.*, 2004b)

Bordas and Minvielle (1999) studied the pattern of growth and feed intake in divergent lines of laying domestic fowl selected for residual feed consumption and reported that the body weights of males at 28 weeks of age in low intake line (R-) and high intake line (R +) were 2,974 and 2,893 g with feed consumption of 1,228 and 1,411 g respectively. However, in R+ lines the length of wattles was 21% higher and the shanks were 8% longer than those observed in R- line. Van Eerden *et al.* (2004a, b) carried out phenotypic selection for RFC and found no difference in body weight between R- and R+ birds. However, differences in feed intake were pronounced with R+ birds taking significantly more feed than R-birds. Studies on humeral immune responses in growing laying hens between lines revealed that R+ birds had a higher level of non-antigen specific antibodies, as indicated by the higher antibody response to salmonella protein.

Genetic correlations

Luiting and Urff (1991) found a positive genetic correlation between RFC and feed consumption. The genetic correlations between RFC and egg mass, number of eggs, egg weight, age at first egg, body weight and weight gain were all reported to be close to zero. This was further confirmed by Schulman *et al.* (1994). They reported that the genetic correlation between RFC and feed consumption was 0.50 but, as expected, correlations with body weight and egg production were not significant. They also reported a small positive correlation between RFC and body weight gain (0.09) and a small negative correlation between RFC and age at first egg (-0.11). The genetic correlations between RFC and other traits reported by Tixier-Boichard *et al.* (1995) are as follows:

Trait	**Genetic correlation (± S.E)**
Egg number	0.11 ± 0.06
Age at first egg	-0.21 ± 0.08
Egg weight (g)	-0.03 ± 0.06
Body weight (g)	-0.17 ± 0.04
Change in body weight (g)	0.07 ± 0.11
Wattle length (mm)	0.19 ± 0.04

Response to selection

Bordas *et al.* (1992) reported that after 14 generations of selection, the females of the high versus low producers differed by 21g feed/day and the males by 28 g/day during a test period of 33 to 37 weeks. Schulman *et al.* (1994) reported moderate genetic progress

https://doi.org/10.1017/S0043933910000553 Published online by Cambridge University Press

in RFC from 1983 to 1987 due to selection for this trait. The genetic progress was in total -6.13 g/hen/day. This is approximately -1.53 g/hen/day/generation. Bordas *et al.* (1996) reported that feed consumption decreased as a result of selection for RFC; however no change could be found in egg mass, number of eggs, egg weight, age at first egg or body weight. The body weight and egg production parameters of traits divergently selected for RFC are presented *Table 1*.

Gabarrou *et al.* (1998) reported that divergent selection for RFC resulted in a large difference in feed intake, *i.e.* 41 g/day between high and low lines without causing any changes in body weight and egg production.

Table 1 Body weight and egg production parameters in high and low RFC lines (Bordas *et al.*, 1996).

Trait	Low RFC	High RFC
Body weight -17 weeks (g)	1665.5 ± 24.7	1688.3 ± 22.7
Egg number	109.6 ± 4.5	112.3 ± 4.4
Clutch length (d)	4.3 ± 0.3	5.3 ± 0.4
Egg weight (g)	52.5 ± 0.5	50.4 ± 0.5
Albumen height (mm)	56.9 ± 1.2	51.5 ± 1.0
Shell thickness (mm)	32.9 ± 0.4	31.7 ± 0.3
Wattle length-43 week (mm)	16.9 ± 0.7	28.5 ± 0.6
Shank length (mm)	102.7 ± 0.5	108.7 ± 0.4
Egg mass (g)	1,150.7 ± 26.6	1,199 ± 30.0
Feed intake (g)	2,786.7 ± 59.3	3,656.7 ± 67.3
Residual feed consumption (g)	-329.7 ± 23.6	+437.2 ± 39.7
Feed conversion (Feed intake/Egg mass)	2.44 ± 0.05	3.09 ± 0.07

Shortcuts to reduce feed consumption without direct measurements

Apart from selection for egg mass and body weight to reduce feed consumption, several shortcuts have been suggested to improve feed efficiency without measuring individual feed consumption in large numbers of hens. One of the shortcuts used to reduce feed consumption is the use of sex-linked dwarf gene to lower metabolic body weight and increase egg output per kg body weight. The advantage of using dwarf gene on feed efficiency has been studied by several authors (Cole, 2000; Missohou *et al.*, 2003). The sex-linked dwarf gene (dw) reduces body weight by approximately 30 per cent, as well as egg size primarily due to the reduction in body size. However dwarf layers are more efficient than non-dwarf layers due to their low maintenance requirements.

When a comparison was made between non-dwarf and dwarf hens, enhanced feed efficiency was obtained due to dw gene. A line of brown-egg dwarf layers was developed at China Agricultural University by four repeated backcrosses of the meat type dwarf ISA-Vedette to the female CAU brown-egg layer (Yang *et al.*, 1996). Body weight of this brown-egg dwarf commercial layer at 20 weeks of age was about 1,200g. Total egg numbers up to 72 weeks was approximately 285 with an average egg weight of 56 g. The comparative performance of dwarf (dw) versus brown-egg commercial line is presented in *Table 2*. The brown egg dwarf layers were 30% smaller than the current standard size (2.0-2.1 kg) but had better feed efficiency and shell strength. The possibility of one bird more per cage or two more per m^2 in floor housing system might be economically important in future (Zhang *et al.*, 2005).

https://doi.org/10.1017/S0043933910000553 Published online by Cambridge University Press

Table 2 Comparative performance of dwarf and non-dwarf strain of chicken (Zhang *et al.*, 2005).

Strain	Egg number	Egg weight (g)	Egg mass (g/day)	Body weight		FCR) (kg/kg	Feed (g/day)	Shell strength (N)
				140 day	500 day			
Commercial	287	65.7	52.5	1.83	2.52	2.48	132	37.0
Dwarf	233	61.5	40.0	1.34	1.67	2.40	96	38.7

From majority of the selection experiments reported in the literature and parameters estimated from large commercial populations, it is apparent that a significant residual component of feed intake has been shown to exist, independent of body weight and egg mass output, at different ages. In recent years, because of high heritability and absence of significant negative effect on production parameters, residual feed consumption is used as selection criteria to improve the feed efficiency. Measurement or subjective scoring of correlated traits such as comb size, wattle length, body temperature or activity may produce useful additional data for basic research, but their practical value for line improvement is limited once individual feed consumption data are included (Flock, 1998). As a result of selection, feed conversion in the USA and Canada has improved from 2.95 g feed/g of egg in 1960 to 2.01 g feed/g of egg in 2001. Further continued improvement will be aided by better understanding of the factors influencing feed conversion.

Egg weight

In general egg size averaged 60-61 g across world; however there are regional preferences for egg sizes that can influence the choice of genetic strain. In South Africa, the market preference averages around 58.5 g, whereas Israel and Spain prefer very large eggs (around 70 g and above). This indicates that the weight has been a difficult target to meet, because of varying demand in different markets. Hence, selection emphasis placed on these characteristics varies widely. Most breeders attempt to hold egg weight at current levels and would apply slight upward selection pressure. This is done to offset the tendency of natural selection to reduce egg weight. Because egg weight changes with age, some attention has been given to the shape of the relationship between egg weight and age. This is because, in almost all markets, the lower egg weight categories are less in demand and uneconomic production of over-sized eggs occurs late in the pullet year. Thus it would be advantageous if the age x egg weight curve were altered. Sheldon (2000) reported that selection for reduced variability in egg size would solve this problem. The author also reported that selection of birds with flatter production curves yielded a correlated response of higher egg production. Francesch *et al.* (1997) reported that heritability values for egg weight ranged between 0.20 and 0.33 among different breeds. However, Zhang *et al.* (2005) reported a high heritability value of 0.63 for egg weight.

Breeding chickens to meet egg quality needs

Worldwide, egg customers prefer eggs which have a sound shell, uniform shell colour, freedom from obvious blood and meat spots and a reasonably upright egg white.

https://doi.org/10.1017/S0043933910000553 Published online by Cambridge University Press

However, there are also regional preferences that can strongly influence the choice of genetic type for particular market. The genetic strategies followed for improving different egg quality are discussed below.

EGGSHELL QUALITY

Eggshell quality has received added emphasis as a result of changing commercial practices, with minimising cracked and broken eggs in commercial systems as the eventual target. A variety of techniques have been used to measure the eggshell thickness. Some breeders routinely use direct measurements of shell thickness on eggs sampled from the flock. Other methods include specific gravity, breaking strength, non-destructive deformation and puncture score.

Eggshell thickness

Non-destructive deformation is one of the indicators of eggshell strength. A smaller value means stronger eggshell. Selection has been conducted in the White Leghorn population for increased (weak line) or decreased (strong line) non-destructive deformation. As a result of selection, in generation 10, non-destructive deformation was reduced to 51.9 micro m/kg in the strong line and 100.6 micro m/kg in the weak line. The breaking strength in strong and weak lines was 3.75 kg and 2.17 kg respectively. Non-destructive deformation had a heritability value of 0.33 and genetic correlations were -0.77, -0.89 and -0.94 with breaking strength, shell thickness and percentage of shell in weak line. Selection for non-destructive deformation was effective in improving eggshell strength and selection for strong shell could increase the egg weight but reduce rate of lay (Nirasawa *et al.*, 1998).

Recently, dynamic stiffness (acoustic test used to distinguish between cracked and intact eggs) has been used for eggshell measurement. This trait has high heritability and genetic and phenotypic correlations with other shell quality traits, including eggshell breaking strength. The dynamic stiffness has a correlation of 0.60 with eggshell thickness (De Ketelaere *et al.*, 2000). In another study, De Ketelaere *et al.* (2002) reported that the correlation between dynamic stiffness measurements and eggshell thickness as 0.78. Dunn *et al.* (2005) studied a pedigree population of laying hens which had previously undergone selection for breaking strength and found that the dynamic stiffness had high heritability (0.53) and high genetic and phenotypic correlations with eggshell breaking strength, with the values around 0.50. Bain (2005) reviewed recent advancements in assessment of eggshell quality and reported that the measures including ultrastructural analysis, crystallographic texture and Quasi-static compression tests are more difficult and expensive and, of the methods currently being developed, only the dynamic stiffness measurement could be immediately adopted as a tool in the commercial environment. Zhang *et al.* (2005) reported a heritability value for eggshell index, eggshell thickness (mm) and eggshell strength (kg/cm^2) as 0.40, 0.34 and 0.24 respectively.

In Europe, as a result of proposed changes in legislation concerning laying hens that will see a move from cage to more welfare friendly systems (probably non-cage system) by 2012, there is an increased risk of eggshell breakage. Hence, research emphasis has been focused on improved resistance to breakage using selection of Quasi-static compression, specific gravity or dynamic stiffness measurement. Among these dynamic stiffness measurements better reflect properties of the egg. In future, identification of quantitative trait loci (QTL) and candidate gene will be helpful in further genetic improvement of eggshell quality.

Shell colour

Shell colour is an important characteristic and completely separate breeding programme

https://doi.org/10.1017/S0043933910000553 Published online by Cambridge University Press

exists for the production of white and brown-shelled eggs. The brown-egg type dominates the markets of most of Europe, Southeast Asia, Australia, New Zealand and much of the African and some of the South American countries. Francesch *et al.* (1997) reported that heritability estimates for eggshell colour ranged between 0.27 and 0.49 among different breeds. Zhang *et al.* (2005) reported a heritability value of 0.46 for eggshell colour, hence selection is practised for improvement. Brown eggs are selected for a dark shell and among white egg lines, any hen with tinting in the shell is removed to assure that the commercial line continues to have pure white eggs. The genetic correlations between the eggshell colour with external and internal egg quality traits were low ranging from -0.23 to 0.13, suggesting a minor relationship between shell colour and physical attributes of the shell as well as internal egg quality in brown-egg dwarf layers.

ALBUMEN HEIGHT

All consumers prefer that the albumen in a broken-out egg is reasonably thick. In the USA, standards are set for minimum acceptable Haugh unit level. The US Department of Agriculture specified that AA quality eggs have a firm, white albumen with a Haugh unit value of 72 or more. Zhang *et al.* (2005) estimated heritability at 0.51 for albumen height, 0.59 for albumen weight and 0.41 for Haugh units. Because of consistent selection for albumen height, Haugh units have increased steadily over time.

As a result of selection for egg quality traits, improvement (*Table 3*) has been noticed between selected (ISA Brown, Babcock) and unselected (Brown leghorn) populations over the years (Silversides *et al.*, 2006).

Table 3 Quality of eggs of three strains of layer (Silversides *et al.*, 2006).

Trait	Selected line		Unselected line
	ISA brown	Babcock	
Egg weight (g)	66.86	64.44	52.45
Albumen height (mm)	6.77	8.82	5.97
Albumen weight (g)	43.34	41.47	33.15
Yolk weight (g)	16.81	16.90	15.44
Shell weight (g)	6.66	6.02	4.79

Considerable research has been made on egg weight, eggshell strength and internal quality of the eggs, and improvements have been made as a result of selection. With the reintroduction of floor systems and consumer interest in processed eggs, in future more emphases have to be given to the eggshell strength and internal quality of the eggs.

Genotype x environment interactions

Poultry production in the unfavourable environment conditions of the tropics mainly suffers from direct and indirect heat stress leading to a general depression in performance, which may not be uniform in all genotypes, revealing significant genotype-environment interactions. A series of experiments was conducted at the Institute of Animal Production, Berlin, over a period of 20 years to explore various aspects of such interactions in layers (Mathur, 2003). Significant genotype-environment interaction may be caused not only by specifically differentiated genotypes such as breed or lines, but also by single major gene effects. Several major genes found in tropical local populations have revealed significant genotype-environment interactions. The naked neck gene (Na) responsible for general

https://doi.org/10.1017/S0043933910000553 Published online by Cambridge University Press

reduction of feathers over the body surface and total loss of feather in the neck region has shown very favourable results under heat stress . The heterozygous naked neck layers had significantly higher egg number, egg weight, egg mass and body weight under constant heat stress. The frizzle gene (F) also revealed its favourable effect on productivity but they were less pronounced than the naked neck gene. The dwarf gene reduces body size and thereby causes a reduction in egg number and egg size but there is a significantly lower depression due to heat stress in dwarf layers than in the normal types. Thus the dwarf gene improves productive adaptability to heat stress. An especially favourable effect of this gene is improvement in feed efficiency.

Horst *et al.* (1995) studied the effect of three major genes (naked neck, frizzle and dwarf) in commercial brown-egg layer line in Turkey, Egypt, Cuba, Burundi, Bolivia and in Malaysia. The effect of naked neck gene was mainly observed on egg number, egg weight, egg mass and productivity index (egg mass production in relation to metabolic body weight). The frizzle gene showed favourable effect on egg production. The dwarf gene had a mainly depressing effect on body weight (ranging from 24 to 36 per cent). This was also associated with reduction in egg number, egg weight and egg mass production. However, considering the productivity index, this gene seems to have very favourable effects.

Chen *et al.* (2002) studied the performance of normally feathered and birds with naked neck gene at high ambient temperature and are presented in *Table 4*. Egg numbers were decreased by 35, 18 and 26% in normally feathered, homozygous naked neck and heterozygous naked neck birds respectively. Both homozygous and heterozygous naked neck genotypes performed better at high ambient temperature with respect to egg number, egg weight, laying rate, clutch length and Haugh units.

Table 4 Performance of normally feathered and naked neck genotypes at two different ambient temperatures (Chen *et al.*, 2002).

Trait	Temperature	Normally feathered (nana)	Homozygous naked neck genotype (NaNa)	Crossbred (Nana)
Age at first egg (day)	22°C	135	142	139
	32°C	134	142	137
Laying rate (%)	22°C	89.7	86.4	88.3
	32°C	58.0	70.8	64.8
Clutch length (day)	22°C	11.8	9.5	11.3
	32°C	4.1	5.3	5.8
Egg number (327 days)	22°C	173	161	167
	32°C	113	132	124
Broken egg (%)	22°C	6.23	5.25	6.75
	32°C	9.54	7.34	6.37
Egg weight (g)	22°C	46.5	49.5	49.4
	32°C	40.0	44.3	42.8
Haugh unit	22°C	81.6	87.3	85.1
	32°C	87.8	91.3	89.9
Shell thickness (mm)	22°C	3.35	3.53	3.49
	32°C	3.11	3.32	3.16
Per cent shell	22°C	8.83	9.30	9.18
	32°C	8.38	8.79	8.44
Yolk/albumen (per cent)	22°C	47.0	43.5	45.4
	32°C	43.5	41.3	41.6
Blood spots (%)	22°C	16.95	9.68	6.98
	32°C	10.64	6.67	7.50
Meat spots (%)	22°C	47.5	41.9	41.9
	32°C	36.2	10.0	22.5

https://doi.org/10.1017/S0043933910000553 Published online by Cambridge University Press

Mahrous *et al.* (2003) studied the effect of naked neck and frizzle gene in hot environmental conditions and reported that naked neck and naked neck frizzle genotypes attained sexual maturity earlier than normally feathered females by about 4.3 and 3.4 days respectively. The presence of naked neck, frizzle and naked neck-frizzle genes significantly increased egg mass, egg number, egg weight, eggshell weight, eggshell percentage and eggshell thickness. They concluded that the effect of Na allele is similar or greater than that of F allele and combination of the two alleles in heterozygous state (NanaFf) results in better performance than those genes considered separately.

Chen *et al.* (2008) investigated the possibility of combining the naked neck gene with a flock with a genetic background that has been optimised for feed efficiency of laying hens in both temperate and sub-tropical environments. Growth performance, anatomical traits, laying traits, and feed efficiency were recorded in each country. The study revealed that the performance was generally lower and mortality of laying hens was higher in Taiwan (11%) than in France (1%). Genotype × environment interactions were rare and were only observed for body weight at 10 weeks of age, and were close to significance for egg weight. Laying performance was significantly decreased in Taiwan by about 25%. The naked neck genotype had a negative effect on body weight and a positive effect of clutch length and egg weight. Based on results they concluded that the introduction of the *NA*NA* mutation appeared to be favourable from the viewpoint of feed efficiency, but it did not improve laying performance in a sub-tropical environment. Other factors rather than temperature, such as diet composition and lighting regimen, may be involved.

Chen *et al.* (2009) compared the laying performance of dwarf laying hen lines segregating for the naked neck mutation (*NA* locus) in two different environmental conditions *i.e.* Taiwan and France. Genetic parameters for laying traits were estimated in each environment and the ranking of sire breeding values was compared between environments. The study revealed that the laying performance for dwarf laying hens was lower and mortality was higher in Taiwan than in France. The line by environment interaction was highly significant for body weight at 16 weeks, clutch length and egg number, with or without using Box-Cox transformations. The selected line was more sensitive to environmental change but in Taiwan it maintained higher egg numbers than the control line. The rank correlations between sire breeding values were low within the selected line and slightly higher in the control line. A few sire families showed good ranking in both environments, suggesting that some families may adapt better to environmental change.

In general, studies by different authors indicated that there is a reduction in performance of layers under high ambient temperature. The results regarding utilisation of the naked-neck and frizzle gene in high ambient temperatures are encouraging. Hence, in future, these genes will play an important role in production of layer lines suitable for high ambient temperature to overcome the genotype-environment interaction.

Skeletal problems in layers and selection strategies

In laying strains, intensive selection for egg production has resulted in birds of low body weight that laid a large number of eggs on low food intakes. Throughout the laying year, the amount of calcium the bird deposit in their shells could be up to 20 times their total body content. Bones act as a store for much of the calcium deposited in shells, and it is perhaps not surprising that stresses in bone formation and resorption can result in skeletal problems in these birds. Bone breakage in layers during production, depopulation and

https://doi.org/10.1017/S0043933910000553 Published online by Cambridge University Press

processing reduces egg production and the value of carcasses of spent hens. Two factors are now causing a rethink in the commercial emphasis on intensive selection for egg production; First, the economic cost of lost egg production in layers resulting from skeletal defects and secondly, increasing concern in many countries regarding the welfare implications of these disorders for the birds. As a result, there is now renewed interest in determining the genetic basis for these disorders, establishing the genetic link between these disorders and egg production and devising genetic or other strategies for minimising the occurrence of severity of the disorders (Whitehead *et al.*, 2003).

MAJOR SKELETAL PROBLEMS

The main skeletal problems in table-egg laying hens are associated with loss of bone mineral during the laying period. The loss of bone mineral may have two causes. They are:

- **Osteomalacia:** This is characterised by defective mineralisation of bone tissue, with a thick seam of poorly, mineralised organic matrix. It is primarily associated with nutritional deficiency of calcium, phosphorus or vitamin D and has not been shown to have a genetic component (Whitehead *et al.*, 2003).
- **Osteoporosis:** It is defined as a decrease in the amount of fully mineralised structural bone, leading to increased fragility and susceptibility to fracture. Unlike osteomalacia, osteoporosis is an altogether more complex problem, has a complex aetiology, with many factors involved (Whitehead and Fleming, 2000; Whitehead *et al.*, 2003). The hallmarks of the osteoporotic bones are increased porosity, fragility and fracture susceptibility caused by a decrease in structural bone content.

Genetics of osteoporosis

Bone characteristics of osteoporosis were first described in caged laying hens by Couch (1955), who reported a problem termed ‘cage layer fatigue involving bone brittleness, paralysis and death’. Generally, osteoporosis is not so severe as to result in cage layer fatigue, but widespread bone loss can lead to high incidence of fractures at various sites throughout the skeleton. This loss has been shown to start when hens reach sexual maturity and to continue throughout the laying period, so that osteoporosis is most severe in hens at the end of lay. The origin of osteoporosis is not well-defined. It has been suggested that the problem is partly genetic in origin, resulting from the breeding of light weight, energetically efficient birds that maintain a high rate of lay over a prolonged period on a low feed intake (Cransberg *et al.*, 2001). Most modern hybrid strains seem to be susceptible to osteoporosis. However, there is a wide individual variation, with some hens retaining good bone quality at the end of lay. Hence, genetic selection seems to offer the best prospects for improving bone quality and resistance to osteoporosis in hens.

Methods of assessing bone quality

The selection procedure used to date has involved retrospective selection on the basis of hen post-mortem data, but this is not practical for application to commercial breeding programmes. Recently, several newer techniques have been identified. One of the most common techniques used in the past was the determination of bone mineral content by ashing (Hall *et al.*, 2003) followed by measurement of bone calcium content using atomic adsorption spectrophotometry (Cransberg *et al.*, 2001). Bone breaking strength (humerus strength and tibia strength) is a common means of determining functional characteristics of bone as a material. Radiography, digitised fluoroscopy, image analysis and quantitative computer tomography have also been used (Fleming *et al.*, 1998; Korver *et al.*, 2004).

https://doi.org/10.1017/S0043933910000553 Published online by Cambridge University Press

Among the different techniques, ashing, Ca level and breaking strength are necessarily done on post-mortem and radiography requires large doses of radiation and specialised equipment and facilities. Measurement of bone mass using quantitative computer tomography is a new technology, which gives precise answer regarding distribution of mineral density within bone. In addition, amplitude-dependent speed of sound ultrasound and dual-energy X-ray absorptiometry have been used to assess bone quality (Fleming *et al.*, 2004; Hester *et al.*, 2004).

Genetic parameters and response to selection

Bishop *et al.* (2000) studied the inheritance of traits related to osteoporosis over five generations in a commercial pure line of White Leghorns previously selected for high egg production. Measurements were made on a range of morphometric, radiological and strength characteristics of different bones in hens at the end of the laying period to determine the heritabilities for different traits. The heritability values for different traits are as follows:

Character	**Heritability estimate**
Humeral strength (HSTR)	0.34
Tibial strength (TSTR)	0.45
Keel radiographic density (KRD)	0.39

Restricted selection index was monitored to improve bone characteristics by keeping body weight constant with the above three moderately heritable traits. The index was

Bone index= 0.27x KRD+0.37 x HSTR+0.61 x TSTR-0.25 x BW

The three body measurements in the index had moderate to high positive correlations with each other and also with body weight. This indicated that selection for improved strength characteristics alone, without the restriction placed on body weight would have resulted in considerably heavier birds. They reported a heritability of 0.40 for bone index. As a result of selection on bone index, the high and low lines differed by 17% for KRD, 30% for HSTR and 60% for TSTR, in hens after five generations (*Table 5*). Body weight between lines did not differ in either sex. These results indicated that genetically improving the bone strength would decrease the incidence of bone fracture.

Table 5 Bone characteristics and body weight at the end of the laying period in female and male chickens divergently selected for high and low bone index (Bishop *et al.*, 2000).

Character	**Female**		**Male**	
	High line	**Low line**	**High line**	**Low line**
Body weight (kg)	1.80	1.79	2.25	2.21
KRD (mm AI equivalent)	0.41	0.35	0.70	0.62
Tibial strength (kg)	38.2	23.7	60.6	51.0
Humerus strength (kg)	17.9	13.6	36.8	29.2

Whitehead *et al.* (2003) reported that comparisons of tibial cortical thickness at different ages showed that the superior thickness in the high bone index line at the end of the lay was attributable to two factors, namely a greater amount of bone formation during growth and, more importantly, less bone resorption during the laying period. High bone index hens contained more medullary bone and fewer osteoclasts (*Table 6*).

https://doi.org/10.1017/S0043933910000553 Published online by Cambridge University Press

Table 6 Bone characteristics of hens selected for resistance and susceptibility to osteoporosis (Whitehead *et al.*, 2003).

Trait	Age (week)	High bone index line (Resistant line)	Low bone index line (Susceptible line)
Tibia cortical width (mm)	15	0.465	0.448
	25	0.473	0.447
	70	0.422	0.365
Medullary bone content of proximal tarsometatarsus (%)	70	7.83	6.39
Osteoclasts per unit of medulary bone	70	979	1170

Silversides *et al.* (2006) studied the effect of genetics on bone strength in layers and reported that selection has decreased humeral breaking strength rather than tibial strength, resulting in higher incidence of bone fracture in commercial layers.

RELATIONSHIP BETWEEN OSTEOPOROSIS AND OTHER TRAITS

Rennie *et al.* (1997) reported that the correlation between egg production and bone strength ranged between 0.00 and 0.16 and suggested that egg production has little or no effect on bone quality. Bishop *et al.* (2000) also observed no significant difference in mean egg production or egg weight between the high and low bone index lines over a laying year (*Table 7*).

Table 7 Egg production and shell characteristics of resistant and susceptible osteoporosis line.

Character	Resistance line	Susceptibility line
Rate of lay (%)	86.9	87.3
Egg mass (g/hen/day)	51.5	51.8
Feed intake (g/hen/day)	105.2	106.2
Candling cracks (%)	3.1	2.6
Shell weight (mg/cm^2)	79.5	80.5

Various studies by different authors revealed a large individual difference in the bone characteristics of hens at the end of the lay, phenotypically unrelated to egg production in a flock of highly productive hens. This suggests that osteoporosis may be alleviated by genetic selection perhaps without serious consequences for egg productivity (Whitehead *et al.,* 2003; Webster, 2004).

Selection for behaviour in poultry

The strong selection for improved egg production has brought about changes that seem to reduce bird's adaptability. This together with the introduction of specialised production systems has resulted in a range of behavioural problems that reduce well-being. Huber-Eicher (1997) reported that feather pecking in commercial layers is due to redirection of behaviour related to foraging by selection for high production and alteration in husbandry practices. Vaisanen and Jensen (2004) studied behavioural characteristics in jungle fowl and White Leghorns, and reported that the adaptability of the bird to their social and physiological environment may have been influenced by means of selection for increased

https://doi.org/10.1017/S0043933910000553 Published online by Cambridge University Press

production capacity. Leghorns may have greater problems in adapting to new environment. Bessei (1995) reported that selection for egg output might exacerbate feather pecking problems.

Commercial layer lines have been selected in cages for many generations, where the expression of behaviour was restricted. The genetic variation of the behaviour was of little economic importance under these conditions. Increasing concern for animal welfare has resulted in strict legislation concerning animal housing. In poultry industry there is a shift from battery cages to large group housing systems. With the return of husbandry systems for laying hens from conventional cages to floor or aviary systems, behaviour is becoming more important not only with regard to welfare but also to economical aspects. In layers, the major problem is injurious pecking behaviour. Selection for higher production combined with lower body weight has led to higher levels of feather pecking and cannibalism.

FEATHER PECKING

Feather pecking is characterised as picking and pulling of feathers of another bird. In a group of chickens, most members will take part in feather pecking. In pullets and adult hens, close to 50 per cent are observed to feather peck, and in layer chickens, feather pecking has been reported as early as 7 days of age. One or more peaks in feather pecking can be seen at 3 to 15 weeks of age. At the age of 15 weeks to sexual maturity, the level of feather pecking is low. Pecking rises at the onset of laying and this is the time when the risk of cannibalism is greatest. This rise has been attributed to an increase in gonadal hormones (Kjaer and Mench, 2003). There are different forms of feather pecking. The two common types are gentle pecks (mainly directed to tips of feather) and severe feather pecks. Severe feather pecking causes damage to the bird, results in bald patches and is painful. Feather pecking is a serious problem in layers besides impaired animal welfare; feather loss due to feather pecking can lead to heat loss resulting in higher energy requirement (Buitenhuis *et al.*, 2004).

CANNIBALISM

Cannibalism is an extreme form of feather pecking. Feather pecking can result in severe damage of the integument including wounds to the skin. Wounded birds may be pecked to death, which is regarded as cannibalism and is the final phase of feather pecking. There has been a continuous increase in mortality caused by cannibalism in all brown-layer strain crosses tested at the random sample test stations in Germany since the late 1980s, suggesting that selection for higher egg production and lower body weight has led to higher levels of cannibalism. Recent data from German random sample testing stations (*Table 8*) illustrates differences in mortality and other characteristics with or without beak trimming. The changes from conventional cages to floor pens may cost in terms of more mortality and more feed (Flock *et al.*, 2005).

Table 8 Mortality, egg production and feed conversion of commercial layers in different management systems (Flock *et al.*, 2005).

Management system system	Mortality percentage	Egg mass (kg/Hen housed)	Feed conversion (kg/kg)
Conventional cages	5.8	20.35	2.00
Floor (Beak trimmed)	6.9	18.16	2.28
Floor (untrimmed)	17.7	17.03	2.46

https://doi.org/10.1017/S0043933910000553 Published online by Cambridge University Press

GENETICS OF FEATHER PECKING

Feather pecking in layers is a multi-factorial problem, which can be caused by environmental, genetic or nutritional factors. Various measures have been made to control this vicious behaviour. Since management measures (except beak trimming) have failed to effectively control these problems, genetic selection has been put forward as a potential means to improve the situation (Bessei, 2002; Buitenhuis and Kjaer, 2008). Variation among breeds and hybrid lines for feather pecking behaviour and/or feather damage have been reported by different authors (Ambrosen and Peterson, 1997; Kjaer and Sørensen, 1997).

Heritability

Heritability estimates for different measures of feather pecking are presented in *Table 9*. The heritability for actively feather pecking ranged from 0.07 to 0.56 and for receiving feather pecking from 0.15 to 0.25.

Table 9 Heritability estimates for feather pecking behaviour.

Trait	Breed	Method of Estimation	Heritability estimates	References
Feather pecking	-	Sire component	0.06[#] 0.14[##] 0.35-0.38[##]	Kjaer and Sørensen (1997)
Being pecked		Sire component	0.15[#]	Kjaer and Sørensen (1997)
Feather/Plumage condition	White Leghorn	Sire component	0.22	Kjaer and Sørensen (1997)
Cannibalistic behaviour	-	-	0.65 ± 0.13[$]	Craig and Muir (1993)

* - Male, ** -Female; # - 6 weeks, ##-38 weeks , ###-69 weeks; + - 42 weeks, ++ - 59 weeks , +++- 67 weeks; $- Realised heritability

Kjaer and Sørensen (1997) reported that the trait performing feather pecking behaviour had an additive genetic variability, with heritability of low to moderate size.

Divergent selection for three generations of feather pecking resulted in a significant difference between high and low lines with regard to feather pecking behaviour. The high pecking hens were on an average heavier than low pecking hens at the age of 27 weeks (1435 g vs. 1371 g). In general, plumage condition was better in low pecking line on the neck, back, wings and tail as well as over the whole body. This indicated that feather pecking could be reduced by selection (Kjaer, 1999; Kjaer, 2001; Kjaer *et al.*, 2001). The generation-wise feather pecking activity is as follows:

Generation	High pecking line (bouts/hour)	Low pecking line (bouts/hour)
Second	3.10	1.37
Third	4.56	0.63

(Source: Kjaer, 2001)

The diurnal rhythm of feather pecking seems to vary between strains. Kjaer (2004) found a rise in feather pecking activity in the last hour of the day in brown shell strains. However, White Leghorns behave significantly differently, with a more even distribution of feather pecking during the day and no rise in feather pecking activity just before dark.

Strain differences in mortality due to cannibalism have been found (Sørensen and Kjaer, 1999). Craig and Muir (1993), Muir and Craig (1998) and Muir (1996, 2003)

https://doi.org/10.1017/S0043933910000553 Published online by Cambridge University Press

were successful in selecting against cannibalistic behaviour in poultry. They reported that group selection has been very effective in reducing the incidence of beak-inflicted injuries in caged hens at high stocking densities and under condition of high social stresses and competition. Commercial breeders have used similar approaches for a number of years, but their results are less spectacular, because most of the commercial strains have a lower initial incidence of cannibalism and selection for multiple objectives requires more time to change additional traits.

So far limited selection pressure has been applied for feather pecking. Direct selection has been shown to be feasible, using individual selection against feather pecking (Kjaer *et al.*, 2001) or group selection against mortality (Craig and Muir, 1993; Muir, 1996).

Measures of feather pecking

Both direct and indirect measures of feather pecking are available. Some of the direct measures include visual observation of feather pecking and scores based on damage as a result of pecking (Kjaer *et al.*, 2001). Plumage condition is an indirect measure of feather pecking and can be biased by abrasion.

Genetic correlations with performance traits

Kjaer and Sørensen (1997) found a negative genetic correlation between feather pecking and body weight of hens at 51 weeks of age. It is a clear indication that small body size, which is desirable in commercial breeding programmes, contributed to the feather pecking problems in laying hens. Hence selection for largest birds will indirectly select against feather pecking; but direct selection will presumably be more effective.

Buitenhuis *et al.* (2004) found a negative phenotypic correlation between gentle feather pecking and egg weight, however no significant genetic correlation was observed. They reported significant additive genetic correlation (0.79) between feather pecking and antibody response to Keyhole Limpet Haemocyanin.

Ground pecking showed a negative correlation with breaking strength of the eggshell at the genetic level meaning that selecting for stronger eggs would reduce ground pecking behaviour. The genetic correlation between ground pecking and eggshell strength at 35, 44 and 50 weeks of age were -0.86, -0.81 and -0.76 respectively. Ground pecking is a foraging behaviour and the commercial laying lines showed less foraging behaviour compared with lines not selected for egg production (Buitenhuis *et al.*, 2004).

Feather pecking is an undesirable behaviour, which causes major problems in non-cage systems. With the phasing out of conventional cages by 2012 (as per EU Council Directive 99/74/EC), more producers are likely to adopt non-cage systems. While national legislation in some countries in Western Europe will ban beak trimming as well. This may lead to increased risk of feather pecking and cannibalism in laying hens. So, methods of reducing the incidence and severity of pecking are urgently needed.

Several authors have identified a hereditary basis of feather pecking behaviour, which is suggested by strain differences. Hence, selection of birds with no or very low tendency to perform feather pecking should reduce the incidence. The trait for receiving feather pecking is probably influenced more by group composition and social organisation, and reported heritability values were low. Hence the trait for receiving feather pecking in selection cannot be recommended. Recently QTL involved in gentle and severe feather pecking have been identified on chicken chromosome two. In future, they may play an important role in reducing feather pecking and cannibalism in commercial layer by way of marker-assisted selection.

https://doi.org/10.1017/S0043933910000553 Published online by Cambridge University Press

Molecular genetic studies

In animal selection and breeding programmes, within each generation geneticists identify and subsequently reproduce those individuals with the best traits. This selection ultimately results in an increase in the frequency of those gene variants that cause desirable effects on the traits under selection. The egg layer industry is particularly challenged, as most of the traits of interest are measurable only in mature females ('female limited traits'). Egg production traits, including age at start of lay and lifetime production, as well as egg quality traits, such as shell strength, shell colour, albumen height, and egg solids can only be measured in females that lay eggs. Both males and females have the gene variants for better egg production, but direct measurement can only be done in females. Indirect selection is done by selecting those males whose sisters or whose daughters have the best traits. This is much less accurate than directly selecting based on individual performance. Molecular genetics allows direct selection to be done in males even for female limited traits. In addition, since the DNA that directs the trait expression is present in the chick at hatch, genetic variation can be measured at day of age, instead of at sexual maturity or even later in life. Thus selection based on DNA can be done at a much earlier age in the lifecycle of the chicken. Accuracy of trait measurement is critical. Without accurate trait information, data will reflect environmental variation.

QUANTITATIVE TRAIT LOCI AND CANDIDATE GENE STUDIES

Body weight

Studies dealing with QTL for body weight using different crosses, such as layer x layer (Tuiskula-Haavisto *et al.*, 2002), broiler x layer (Sewalem *et al.*, 2002) and layer x Red Jungle Fowl (Carlborg *et al.*, 2003) have revealed a number of QTL controlling growth. Tuiskula-Haavisto *et al.* (2002) detected a highly significant QTL on chromosome four for body weight at 40 weeks of age, which mapped to the same area as the QTL for egg weight. The QTL explained 25.8% of the phenotypic variance. Carlborg *et al.* (2003) identified 22 significant loci contributing to the body weight in chickens. Epistasis was more pronounced prior to 46 days of age. Whereas, additive genetic effects explained major portion of the genetic variance later in life. Several of the loci affected either early or late growth but not both. Very few loci affected the entire growth process, which points out that early and late growth, at least to some extent, have different genetic regulation.

Siwek *et al.* (2004) identified three QTLs (On GGA2, GGA3 and GGA9) for body weight at four weeks of age, three QTL (On GGA2, GGA3 and GGA6) for body weight at six weeks of age , one QTL (On GGA7) for body weight at eight weeks of age and one QTL (on GGAZ) for body weight at 12 and 18 weeks of age by half-sibling analysis. The different location of QTL indicated that different sets of genes are involved in the early and late growth.

Jiang *et al.* (2004) reported that a single nucleotide polymorphism in chicken pituitary specific transcription factor (POU1F1) resulted in alterations to codon 299 from AAC to ATC, which substitutes asparagine to isoleucine. The allele (A and T) and genotype (AA, AT and TT) frequencies differed significantly between meat-type chicken (higher frequency of A allele (0.91) and AA genotype (0.84)) and layer-type chickens (frequencies of A allele was ranged from 0.57 to 0.72 and AA genotype was 0.37 to 0.50). Bennett *et al.* (2006) reported that a significant association between IGF1 and osteopontin (SPP1) and five week body weight and between insulin (INS) and 55-week body weight.

https://doi.org/10.1017/S0043933910000553 Published online by Cambridge University Press

Egg production

Schreiweis *et al.* (2005) identified a QTL for egg production from 16 to 25 weeks of age in chromosome four at 20 cm and it explained 6.2% of the phenotypic variation. A QTL affecting age at first egg was found on chromosome Z and explained 4% of the phenotypic variation (Tuiskula-Haavisto *et al.*, 2002).

Feed intake and feed efficiency

Tuiskula-Haavisto *et al.* (2002) detected a QTL for feed intake at 32 to 36 weeks of age in chromosome four and explained 5% of the phenotypic variance.

Chicken insulin-like growth factors 1 and 2 (IGF1 and IGF2) are polypeptide hormones that exert effect on body composition, growth rate and lipid metabolism in poultry. Amills *et al.* (2003) studied the polymorphism in IGF1 and IGF2 and reported that a suggestive associations were found between IGF1-SNP1 and average daily weight gain at 107 days and feed efficiency at 44, 73 an 107 days.

Egg quality traits

Quantitative trait loci affecting Haugh unit at 40 weeks and 60 weeks were detected on chromosome two and they explained 7 and 6% of the phenotypic variance. In addition, a QTL affecting egg white thinning (Haugh unit at 40 weeks) was detected on chromosome four at 215 cm and on chromosome eight at 11 cm. For eggshell quality (breaking strength) at 40 weeks, a QTL at the end of the chromosome Z was detected. It explained 5% of the phenotypic variation and the 90% confidence interval ranged from 97 to 142 cm. A QTL affecting specific gravity of eggs at 40 weeks was detected in chromosome 5 and explained 4% of the phenotypic variation. QTLs for egg weight were found on the chromosome 3, 4 and Z. The QTL at chromosome 4 explained 14.5 to 16% of the phenotypic variation (Tuiskula-Haavisto *et al.*, 2002). Honkatukia *et al.* (2005) also reported two QTL on Chromosome two each for egg quality and egg white thinning.

Fishy-odour in eggs is caused by abnormally high amounts of excreted trimethylamine (TMA). Usually TMA is not excreted because the liver enzyme flavin-containing mono-oxygenase three (FMO3) catalyses oxidation of TMA to odourless trimethylamine N-oxide. Fishy-odour is mainly a problem in brown egg layers. Honkatukia *et al.* (2005) found a missence mutation (T329S) in the chicken FMO3 gene that has been associated with elevated levels of TMA and fishy taint in egg yolks of commercial brown egg layers. In another study, Honkatukia *et al.* (2006) reported that the egg taint disorder and FMO3 gene map to the same location on chicken chromosome eight. Genotyping of the SNP of the FMO3 gene revealed that TT homozygotes expressed high TMA-N content and the AT and AA homozygotes expressed low TMA-N content in the egg yolk.

Schreiweis *et al.* (2005) detected two QTL (230 and 215 cm) on chromosome two for eggshell colour and one QTL on chromosome four at 219 cm and they explained 5 to 5.3% of the phenotypic variation. In addition, chromosome four has multiple QTL for egg weight (204 and 206 cm), albumen weight (206 and 209 cm) and one QTL for shell percentage. The QTL for egg weight accounted for 10.3 to 17.5% of the phenotypic variation. The QTL for albumen weight explained 16.1 to 18.5% phenotypic variation. This indicated that chromosome four harbours multiple genes that contribute to the extreme phenotypic divergence observed among layer, broiler and ancestral chicken populations.

Chicken insulin-like growth factors 1 and 2 (IGF1 and IGF2) are polypeptide hormones that exert effect on body composition, growth rate and lipid metabolism in poultry. Nagaraja *et al.* (2000) reported that an RFLP in 5' end of the IGF1 gene was associated to egg and eggshell weight in White Leghorn chicken. Sazanov *et al.*

https://doi.org/10.1017/S0043933910000553 Published online by Cambridge University Press

(2007) reported that the CR523443 (*Gallus gallus* finished cDNA, clone ChEST985k21) was highly correlated with shell thickness and suggested that it was a candidate gene for shell thickness at 53 weeks of age. This gene is highly correlated (0.85) with shell thickness.

Feather pecking behaviour

Buitenhuis *et al.* (2003 a, b) identified a suggestive QTL on GGA10 for gentle feather pecking at six weeks of age. At 30 weeks of age suggestive QTL were detected on GGA1 and GGA2 for gentle feather pecking. The results indicated that feather pecking behaviour at six weeks of age is regulated by different genes than feather pecking at 30 weeks of age. The results open the possibility to reduce the feather pecking problem and improvement of poultry welfare using molecular genetics.

Skeletal traits

Bennett *et al.* (2006) found a significant association between vitamin D receptors and bone mineral content of the humerus at 35 weeks of age. Bennet *et al.* (2007) found an association between single nucleotide polymorphism in Transforming Growth Factor -β2 gene and bone traits (*Table 10*). In general the CC genotypes had higher bone mineral content, bone mineral density and body weight.

Table 10 Association between Transforming Growth Factor -β2 and bone, egg production and body weight traits (Bennet *et al.*, 2007).

Trait	Age of measurement	Genotype		
	(Week)	TT	TC	CC
Tibial mineral density (g/cm^2)	35	0.238	0.240	0.252
Tibial mineral content (g)	35	4.09	4.17	4.39
Tibial mineral density (g/cm^2)	55	0.316	0.311	0.334
Tibial mineral content (g)	55	5.7	5.7	6.1
Egg production (number of eggs)	46-55	42	39	37
Body weight (g)	1	86.7	88.6	90.1
	2	179	188	190
	3	319	331	339
	4	504	523	537
	5	734	752	770
	6	937	972	990

Chicken lines had previously been successfully selected for shorter shanks because it was considered that the longer shank was a source of leg problems in heavy-bodied chickens. Yu *et al.* (2006) detected eight static QTL affecting shank length from 1 to 12 weeks of age. Strong evidences were found on chromosome two and 23 and explained 5.49 to 6.16% and 4.93 to 8.39% of the phenotypic variation respectively.

The locations of significant QTL for different traits have been reviewed in an elaborate manner by Hocking (2005) and Abasht *et al.* (2006) and they concluded that the Despite differences in experimental conditions and populations used for QTL mapping, independent studies found QTL for similar traits in similar locations in several instances. For millennia improvement of domestic animal species has been done by selection and subsequent breeding of those animals with the more desirable traits. Improvements in traits have been slow and steady. Within the 20th century, progress in performance related traits has improved considerable as better breeding tools were developed. Increased understanding of what controls the traits (*i.e.* genes), realisation of

https://doi.org/10.1017/S0043933910000553 Published online by Cambridge University Press

the environmental influences on gene expression, development of statistical analysis tools and the evolution of rapid computational methods has resulted in the extremely efficient breeding stock that are utilised in production today. Molecular genetics provides yet another set of tools for even more enhanced selection progress and efficiency (Fulton, 2008)

Conclusions

Layer breeding companies have contributed immensely over the decades in the improvement of egg production and feed efficiency. In addition, considerable research has been made on egg weight, eggshell strength and internal quality of the eggs and improvements have been made as a result of selection. Poultry breeding prior to this decade was based mainly on what could be observed or measured at the phenotypic level. Unfortunately those types of traits are also influenced by random environmental factors, such as feed quality, pecking order, temperature and disease. Clearly, random environmental factors are a hindrance to breeding superior genetic stock, however, even greater problems include sex limited traits which can only be measured in one sex, such as egg production, and traits which cannot be measured on either sex in live animals, such as disease resistance and meat quality. In those cases the breeder must rely entirely on information from relatives to make selection decisions. The desire of poultry breeders has always been to get directly at the underlying genetic worth of the bird, free from environmental effects, and on all poultry regardless of sex or ability to measure the phenotype. Modern biochemical techniques allow scientists to probe directly into the genetic code of life. These advances seem to provide the answer to selecting superior animals without the complications of environmental efforts. Recent molecular studies have provided complete genome sequencing, identification of several quantitative trait loci affecting production and reproduction traits and identification of the genes responsible for different phenotypic variation. In future, genomics could well play an important role in unravelling the biological mechanism and supporting breeders in selection programmes.

References

ABASHT, B., DEKKERS, J.C.M. and LAMONT, S.J. (2006) Review of quantitative trait loci in the chicken. *Poultry Science* **85**: 2079-2096

AMBROSEN, T. and PETERSEN, V.E. (1997) The influence of protein level in diet on cannibalism and quality of plumage of layers. *Poultry Science* **76**: 559-563.

AMILLS, M., JIMENEZ, N., VILLALBA, D., TOR, M., MOLINA, E., CUBILO, D., MARCOS, C., FRANCESCH, A., SANCHEZ, A. and ESTANY, J. (2003) Identification of three single nucleotide polymorphisms in the chicken insulin-like growth factor 1 and 2 genes and their associations with growth and feeding traits. *Poultry Science* **82**: 1485-1493.

ANANG, A., MIELENZ, N. and SCHÜLER, L. (2001) Monthly model for genetic evaluation of laying hens 1. Fixed regression. *British Poultry Science* **42**: 2, 191-196.

ANANG, A., MIELENZ, N. and SCHÜLER, L. (2002) Monthly model for genetic evaluation of laying hens II. Random regression, *British Poultry Science* **43**: 384-390.

ARTHUR, J.A. and ALBERS, G.A.A. (2003) Industrial perspective on problems and issues associated with poultry breeding, in: MUIR, W.M. & AGGREY, S.E. (Eds) *Poultry Genetics, Breeding and Biotechnology*, pp. 1-12 (CABI Publishing, CAB International, Wallingford, U.K).

BAIN, M.M. (2005) Recent advances in the assessment of eggshell quality and their future application. *World's Poultry Science Journal* **61**: 268-277.

https://doi.org/10.1017/S0043933910000553 Published online by Cambridge University Press

BENNETT, A.K., HESTER, P.Y. and SPURLOCK, D.E.M. (2006) Polymorphisms in vitamin D receptor, osteopontin, insulin-like growth factor 1 and insulin, and their associations with bone, egg and growth traits in a layer-broiler cross in chickens. *Animal Genetics* **37**: 283-286.

BENNETT, A.K., HESTER, P.Y. and SPURLOCK, D.E.M. (2007) Relationships of a transforming growth factor-β2 single nucleotide polymorphism and messenger ribonucleic acid abundance with bone and production traits in chickens. *Poultry Science* **86**: 829-834.

BESSEI, W. (1995) Proceedings of the 17th World's Poultry Science Congress, Helsinki, Finland. pp.458-469.

BESSEI, W. (2002) Selection for behaviour in poultry. Proceedings of the 7th World Congress on Genetics Applied to Livestock Production, August 19-23, Montpellier, France.

BISHOP, S.C., FLEMING, R.H., MCCORMACK, H.A., FLOCK, D.K. and WHITEHEAD, C.C. (2000) The inheritance of bone characteristics affecting osteoporosis in laying hens. *British Poultry Science* **41**: 33-40.

BOHREN, B.B., KINNEY, T.B, WILSON, S.P. and LOWE, P.C. (1970) Genetic gain in annual egg production from selection on early part-record percent production in the fowl. *Genetics* **65**: 655-667.

BORDAS, A., MERAT, P. and MINVIELLE, F. (1996) Heterosis in egg laying lines under divergent selection for residual feed consumption. *Poultry Science* **75**: 20-24.

BORDAS, A. and MINVIELLE F. (1999) Patterns of growth and feed intake in divergent lines of laying domestic fowl selected for residual feed consumption. *Poultry Science* **78**: 317-323.

BORDAS, A., TIXIER-BOICHARD, M. and MERAT, P. (1992) Direct and correlated responses to divergent selection for residual food intake in Rhode Island Red laying hens. *British Poultry Science* **33**: 741-754.

BUITENHUIS, A.J. and KJAER, J.B. (2008) Long term selection for reduced or increased pecking behaviour in laying hens. *World's Poultry Science Journal* **64**: 477-487.

BUITENHUIS, A.J., RODENBURG, T.B., HIERDEN, Y.M.V., SIWEK, M., CORNELISSEN, S.J.B., NIEUWLAND, M.G.B., CROOIJMANS, R.P.M.A., GROENEN, M.A.M., KOENE, P., KORTE, S. M., BOVENHUIS, H. and VAN DER POEL, J.J. (2003a) Mapping Quantitative Trait Loci affecting feather pecking behavior and stress response in laying hens. *Poultry Science* **82**: 1215-1222.

BUITENHUIS, A.J., RODENBURG, T.B., SIWEK, M., CORNELISSEN, S.J.B., NIEUWLAND, M.G.B., CROOIJMANS, R.P., GROENEN, M.A., KOENE, P., BOVENHUIS, H. and VAN DER POEL, J.J. (2003b) Identification of quantitative trait loci for receiving pecks in young and adult laying hens. *Poultry Science* **82**: 1661-1667.

BUITENHUIS, A.J., RODENBURG, T.B., WISSINK, P.H., VISSCHER, J., KOENE, P., BOVENHUIS, H. DUCRO B.J. and VAN DER POEL J.J. (2004) Genetic and phenotypic correlations between feather pecking behavior, stress response, immune response, and egg quality traits in laying hens. *Poultry Science* **83**: 1077-1082.

CARLBORG, Ö., KERJE, S., SCHUTZ, K., JACOBSSON, L., JENSEN, P. and ANDERSSON, L. (2003). A global search reveals epistatic interaction between QTL for early growth in the chicken. *Genome Research* **13**: 413-421.

CHEN, C.F., BORDAS, A. and TIXIER-BOICHARD, M. (2002) Effect of high ambient temperature and naked neck genotype on egg production in purebred and crossbred dwarf brown-egg layers selected for improved clutch length. *Proceedings of the 7th World Congress on Genetics Applied to Livestock Production, August 19-23, Montpellier, France.*

CHEN, C.F. and TIXIER-BOICHARD, M. (2003) Correlated responses to long-term selection for clutch length in dwarf brown-egg layers carrying or not carrying the naked neck gene. *Poultry Science* **82**: 709-720.

CHEN, C.F., HUANG, N.Z., GOURICHON, D., LEE, Y.P., TIXIER-BOICHARD, M. and BORDAS, A. (2008) Effect of Introducing the Naked Neck Gene in a Line Selected for Low Residual Feed Consumption on Performance in Temperate or Subtropical Environments. *Poultry Science* **87**: 1320-1327.

CHEN, C.F., GOURICHON, D., HUANG, N.Z., LEE, Y.P., BORDAS, A. and TIXIER-BOICHARD, M. (2009) Performance comparison of dwarf laying hens segregating for the naked neck gene in temperate and subtropical environments. *Genetics Selection Evolution* 2009, 41:13 doi:10.1186/1297-9686-41-13.

COLE, R.K. (2000) An autosomal dwarfism in the domestic fowl. *Poultry Science* **79**: 1507-1516.

COUCH, J.R. (1955) Cage layer fatigue. *Feed Age* **5**: 55-57.

CRAIG, J.V. and MUIR, W.M. (1993) Selection for reduction of beak-inflicted injuries among caged hens. *Poultry Science* **72**: 411-420.

CRANSBERG, P.H., PARKINSON, G.B., WILSON, S. and THORP, B.H. (2001) Sequential studies of skeletal calcium reserves and structural bone volume in a commercial layer flock. *British Poultry Science* **42**: 260-265.

DE KETELAERE, B., COUCKE, P. and DE BAERDEMAEKER, J. (2000) Eggshell crack detection based on acoustic resonance frequency analysis. *Journal of Agricultural Engineering and Research* **76**: 157-163.

DE KETELAERE, B., GOVAERTS, T., COUCKE, P. DEWIL, E., VISSCHER, J., DECUYPERE, E. and DE BAERDEMAEKER, J. (2002) Measuring the eggshell strength of 6 different genetic strains of laying hens: technique and comparisons. *British Poultry Science* **43**: 238-244.

https://doi.org/10.1017/S0043933910000553 Published online by Cambridge University Press

DUNN, I.C., BAIN, M.M., EDMOND, A., WILSON, P.W., JOSEPH, N., SOLOMAN, S. DE KETELAERE, B., DE BAERDEMAEKER, J., SCHMUTZ, M., PREISINGER, R. and WADDINGTON, D. (2005) Heritability and genetic correlation of measurements derived from resonant frequency analysis; a novel method of determining eggshell quality in domestic fowl. *British Poultry Sciences* **46**: 280-286.

FLEMING, R.H., KORVER, D.R., MCCORMACK, H. and WHITEHEAD, C.C. (2004) Assessing bone mineral density in vivo: Digitized fluoroscopy and ultrasound. *Poultry Science* **83**: 207-214.

FLEMING, R.H., MCCORMACK, H.A., MCTEIR, L. and WHITEHEAD, C.C. (1998) Medullary bone and humeral breaking strength in laying hens. *Research in Veterinary Science* **64**: 63-67.

FLOCK, D.K. (1998) Genetic-economic aspects of feed efficiency in laying hens. *World's Poultry Science Journal* **54**: 225-239.

FLOCK, D.K., LAUGHLIN, K.F. and BENTLEY, J. (2005) Minimizing losses in poultry breeding and production: how breeding companies contribute to poultry welfare. *World's Poultry Science Journal* **61**: 227-237.

FLOCK, D.K. and PREISINGER, R. (2002) Breeding plans for poultry with emphasis on sustainability. *Proceedings of the 7th World Congress on Genetics Applied to Livestock Production*, August 19-23, Montpellier, France.

FRANCESCH, A., ESTANY, J., ALFONSO, L. and ISLESIAS, M. (1997) Genetic parameters for egg number, egg weight and eggshell colour in three Catalan poultry breeds. *Poultry Science* **76**: 1627-1631.

FULTON, J.E. (2008) Molecular genetics in a modern poultry breeding organization. *World's Poultry Science Journal* **64**: 171-176.

GABARROU, J.F., GERAERT, P.A., FEANCOIS, N., GUILLAUMIN, S., PICARD, M. and BORDAS, A. (1998) Energy balance of laying hens selected on residual feed consumption. *British Poultry Science* **39**: 79-89.

GOWE, S.R. and STRAIN, H.J. (1963) Effect of selection for increased egg production based on part-year records in two strains of White Leghorns. *Canadian Journal of Genetics and Cytology* **5**: 99.

GROEN, A.F. (2003) Breeding objectives and selection strategies for layer production, in: MUIR, W.M. & AGGREY, S.E. (Eds) *Poultry Genetics, Breeding and Biotechnology*, pp. 1-12 (CABI Publishing, CAB International, Wallingford, U.K.).

GROSSMAN, M., GOSSMAN, T.N. and KOOPS, W.J. (2000) A model for persistency of egg production. *Poultry Science* **79**: 1715-1724.

GROSSMAN, M. and KOOPS, W.J. (2001) A model for individual egg production in chickens. *Poultry Science* **80**: 859-867.

HALL, L.E., SHIRLEY, R.B., BAKALLI, R.I., AGGREY, S.E., PESTI, G.M. and EDWARDS, H.M. JR. (2003) Power of two methods for the estimation of bone ash of broilers. *Poultry Science* **82**: 414-418.

HESTER, P.Y., SCHREIWEIS, M.A., ORBAN, J.I., MAZZUCO, H., KOPKA, M.N., LEDUR, M.C. and MOODY, D.E. (2004) Assessing bone mineral density in vivo: Dual energy x-ray absorptiometry. *Poultry Science* **83**: 215-221.

HICKS, C., MUIR, W.M. and STICK, D.K. (1998) Selection index updating for maximizing rate of annual genetic gain in laying hens. *Poultry Science* **77**: 1-7.

HOCKING, P.M. (2005) Review of QTL mapping results in chickens. *World's Poultry Science Journal* **61**: 215-226.

HONKATUKIA, M., REESE, K., PREISINGER, R., TUISKULA-HAAVISTO, M., WEIGEND, S., ROITO, J., MAKI-TANILA, A. and VILKKI, J. (2005) Fishy taint in chicken eggs is associated with a substitution within a conserved motif of the FMO3 gene. *Genomics*, **86**: 225-32.

HONKATUKIA, M., REESE, K., PREISINGER, R., WEIGEND, S., ROITO, J., TUISKULA-HAAVISTO, M., MAKI-TANILA, A. and VILKKI, J. (2006) A genetic marker against fishy taint in brown egg layers. *Proceedings of the 8th World Congress on Genetics Applied to Livestock Production, August 13-18, 2006, Belo Horizonte, MG, Brasil*

HORST, P., MATHUR, P.K. and VALLE-ZARATE, A. (1995) Breeding policies for specific tropical environments using appropriate combination of major genes. *Proceedings of the World's Poultry Congress, New Delhi, India*, pp.633-640.

HUBER-EICHER, B. (1997) An experimental study on the development of feather pecking in domestic chicks (*Gallus gallus domesticus*). Inaugural dissertation der Philosophischnaturwissenschaftlichen fakultat der Universitat Bern. Switzerland. pp.1-57.

JIANG, R., LI, J., QU, L., LI, H. and YANG, N. (2004) A new single nucleotide polymorphism in the chicken pituitary - specific transcription factor (POU1F1) gene associated with growth rate. *Animal Genetics* **35**: 344-346.

KJAER, J.B. (1999) Genetic parameters of feather pecking and effect of direct selection. *Proceedings of Poultry Genetics Symposium, October 6-8, Mariensee, Germany*, pp.97-103.

https://doi.org/10.1017/S0043933910000553 Published online by Cambridge University Press

KJAER, J.B. (2001) Genetic aspects of feather pecking and cannibalism, in: OESTER , H. & WYSS, C. (Eds) *Proceedings of the 6th European Symposium on Poultry Welfare*, pp. 189-197 (World's Poultry Science Association, Swiss Branch, Druckerei Arm, Bern).

KJAER, J.B. (2004) Diurnal rhythm of feather pecking behaviour and condition of integuments in four strains of loose housed laying hens. *Applied Animal Behaviour Science* **65**: 331-347.

KJAER, J.B. and MENCH, J.A. (2003) Behaviour problems associated with selection for increased production, in: MUIR, W.M. & AGGREY, S.E. (Eds) *Poultry Genetics, Breeding and Biotechnology*, pp. 67-82 (CABI Publishing, CAB International, Wallingford, U.K.).

KJAER, J.B. and SØRENSEN, P. (1997) Feather pecking behaviour in White Leghorns, a genetic study. *British Poultry Science* **38**: 333-341.

KJAER, J.B., SØRENSEN, P. and SU, G. (2001) Divergent selection on feather pecking behaviour in Laying Hens (*Gallus gallus domesticus*). *Applied Animal Behaviour Science* **71**: 229-239.

KORVER, D.R., SAUNDERS-BLADES, J.L. and NADEAU, K.L. (2004) Assessing bone mineral density in vivo: Quantitative computed tomography. *Poultry Science* **83**: 222-229.

LUITING, P. and URFF, E.M. (1991) Residual feed consumption in laying hens. 1. Quantification of phenotypic variation and repeatabilities. *Poultry Science* **70**: 1655-1662.

MAHROUS, M., GALAL, A., FATHI, M.M. and EL-DEIN, A.Z. (2003) Improving productivity of layer chickens in hot environmental condition by introducing naked neck and frizzle genes. *Egyptian Poultry Journal* **23**: 393-408.

MATHUR, P.K. (2003) Genotype-Environment interactions : problems associated with selection for increased production, in: MUIR, W.M. & AGGREY, S.E. (Eds) *Poultry Genetics, Breeding and Biotechnology*, pp. 83-100 (CABI Publishing, CAB International, Wallingford, U.K.).

MISSOHOU, A., DIENG, A., HORST, P., ZARATE, V. A., NESSEIM, T. and TCHEDRE, K. (2003) Effect of dwarf (*dw*) and frizzle (*F*) genes on the performance of layers under Senegalese conditions. *Tropical Animal Health and Production* **35**: 373-380.

MUIR, W.M. (1990) Association between persistency of lay and partial record egg production in White Leghorn hens and implications to selection programmes for annual egg production. *Poultry Science* **69**: 1447-1454.

MUIR, W.M. (1996) Group selection for adaptation to multiple hen cages: Selection program and direct responses. *Poultry Science* **75**: 447-458.

MUIR, W.M. (2003) Indirect selection for improvement of animal well-being, in: MUIR, W.M. & AGGREY, S.E. (Eds) *Poultry Genetics, Breeding and Biotechnology*, pp. 247-256 (CABI Publishing, CAB International, Wallingford, U.K.).

MUIR, W.M. and CRAIG, J.V. (1998) Improving animal well-being through selection. *Poultry Science* **77**: 1781-1788.

NAGARAJA, S.C., AGGREY, S.E., YAO, J., ZADWORNY, D., FAIRFULL, R.W. and KUHNLEIN, U. (2000) Trait association of a genetic marker near the IGF-I gene in egg-laying chickens. *Journal of Heredity* **91**: 150-156.

NIRASAWA, K., NAGAMINE, Y., TAKAHASHI, H., TAKEDA, H., FURUKAWA, T. and TAKEDA (1998) Genetic parameters and the improvement for eggshell strength in domestic fowl. *Proceedings of the 6th World Congress on Genetics Applied to Livestock Production, January 11-16, 1998, Armidale, Australia*. Vol. 24:271-277.

RENNIE, J.S., FLEMING, R.H., MCCORMACK, H.A., MCCORQUODALE, C.C. and WHITEHEAD, C.C. (1997) Studies on effects of nutritional factors on bone structure and osteoporosis in laying hens. *British Poultry Science* **38**: 417-424.

SAZANOV., A.A., STEKOLNIKOVA, V.A., KORCZAK. M., SAZANOVA, A.L., JASZCZAK, K., ZIEBA, G. and MALEWSKI, T. (2007) Expression of positional candidates for shell thickness in the chicken. *Poultry Science* **86**: 202-205.

SCHREIWEIS, M.A., HESTER, P.Y., SETTAR, P. and MOODY, D.E. (2005) Identification of quantitative trait loci associated with egg quality, egg production and body weight in an F2 resource population of chickens. *Animal Genetics* **37**: 106-112.

SCHULMAN, N., TUISKULA-HAAVISTO., M., SIITONEN, L. and MANTYSAARI, E.A. (1994) Genetic variation of residual feed consumption in a selected Finnish egg-layer population. *Poultry Science* **73**: 1479-1484.

SEWALEM, A., MORRICE, D.M., LAW, A.S., WINDSOR, D., HALEY, C.S., IKEOBI, C.O.N., BURT, D.W. and HOCKING, P.M. (2002) Mapping of quantitative trait loci for body weight at 3, 6 and 9 weeks of age in a broiler layer cross. *Poultry Science* **81**: 1775-1781.

SHELDON, B.L. (2000) Research and development in 2000: directions and priorities for the world's poultry science community. *Poultry Science* **79**: 147-158.

SILVERSIDES, F.G., KORVER, D.R. and BUGELL, K.L. (2006) Effect of strain of layer and age at photostimulation on egg production, egg quality and bone strength. *Poultry Science* **85**: 1136-1144.

https://doi.org/10.1017/S0043933910000553 Published online by Cambridge University Press

SIWEK, M., CORNELISSEN, S.J.B., BUITENHUIS, A.J., NIEUWLAND, M.G.B., BOVENHUIS, H., CROOIJMANS, R., GROENEN, M.A.M., PARMENTIER, H.K. and VAN DER POEL, J.J. (2004) Quantitative trait loci for body weight in layers differ from quantitative trait loci specific for antibody responses to sheep red blood cells. *Poultry Science* **83**: 853-859.

SØRENSEN, P. and KJAER, J.B. (1999) Comparison of high yielding and medium yielding hens in an organic system, in: PREISINGER, R. (Ed.) *Proceedings of Poultry Genetics Symposium*, 6-8 October, Mariensee, Germany, p. 145.

TIXIER-BOICHARD, M., BOICHARD, D., GOENEVELD, E. and BORDAS, A. (1995) Restricted maximum likelihood estimates of genetic parameters of adult male and female Rhode Island Red chickens divergently selected for residual feed consumption. *Poultry Science* **74**: 1245-1252.

TUISKULA-HAAVISTO, M., HONKATUKIA, M., VILKKI, J., DE KONING, D.J., SCHULMAN, N.F and MAKI-TANILA, A. (2002) Mapping of quantitative trait loci affecting quality and production traits in egg layers. *Poultry Science* **81**: 919-927.

VAISANEN, J. and JENSEN, P. (2004) Responses of young Red Jungle Fowl (*Gallus gallus*) and White Leghorn layers to familiar and unfamiliar social stimuli. *Poultry Science* **83**: 335-343.

VAN EERDEN, E., VAN DEN BRAND, H., PARMENTIER, H.K., DE JONG, M.C.M. and KEMP, B. (2004b) Phenotypic selection for residual feed intake and its effect on humoral immune responses in growing layer hens. *Poultry Science* **83**: 1602-1609.

VAN EERDEN, E., VAN DEN BRAND, H., DE VRIES REILINGH, G., PARMENTIER, H.K., DE JONG, M.C.M. and KEMP, B. (2004a) Residual feed intake and its effect on *Salmonella enteritidis* infection in growing layer hens. *Poultry Science* **83**: 1904-1910

WEBSTER, A.B. (2004) Welfare implication of avian osteoporosis. *Poultry Science* **83**: 184-192.

WHITEHEAD, C.C. and FLEMING, R.H. (2000) Osteoporosis in cage layers. *Poultry Science* **79**: 1033-1041.

WHITEHEAD, C.C., FLEMING, R.H., JULIAN, R.J. and SØRENSEN, P. (2003) Skeletal problems associated with selection for increased production, in: MUIR, W.M. & AGGREY, S.E. (Eds) *Poultry Genetics, Breeding and Biotechnology* (CABI Publishing, CAB International, Wallingford, U.K.)

YANG, N., NING, Z., WANG, Q., LI, J. and WU, C. (1996) Application of the sex-linked dwarf gene to improving feed efficiency of layers. *Proceedings of the 20th World's Poultry Congress, New Delhi, India*. pp. 447-451.

YU, G., ZHIQIANG, D., XIAOXIANG, H., XUEMEI, D. and NING, L. (2006) Identification of QTL for shank length at different developmental stages in chickens using a genome scan. *Proceedings of the 8th World Congress on Genetics Applied to Livestock Production, August 13-18, 2006, Belo Horizonte, MG, Brasil.*

ZHANG, L.C., NING, Z.H., XU, G.Y., HOU, Z.C. and YANG, N. (2005) Heritabilities and genetic and phenotypic correlations of egg quality traits in brown-egg dwarf layers. *Poultry Science* **84**: 1209-1213.

https://doi.org/10.1017/S0043933910000553 Published online by Cambridge University Press

https://doi.org/10.1017/S0043933910000553 Published online by Cambridge University Press