Breeding for efficiency in the broiler chicken: A review

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Abstract Artificial selection of broiler chickens for commercial objectives has been employed at an unprecedented magnitude over the recent decades. Consequently, the number of days, total feed and in turn energy, required to raise a broiler to slaughter weight, have decreased dramatically. Feed provision is the poultry industry's biggest environmental hotspot; hence, understanding the interactions between the birds' genetic change and their energy use efficiency forms the necessary starting point for quantifying and predicting and thereby mitigating the future environmental impact of the poultry sector. This review assesses the consequences of artificial selection on the following traits: digestive efficiency, body composition and utilisation of metabolisable energy for growth and metabolic activity. The main findings were (1) the digestive system has been subjected to much physical change due to selection in the recent decades, but this has not led to any apparent change in digestion efficiency. (2) Both the energy intake per day and the metabolic heat production rate have increased in the recent decades whilst (3) the efficiency of utilising energy for growth has also increased; this is due to an increased growth rate, so that broilers reach slaughter weight more quickly and therefore need to allocate less energy overall to metabolic processes, with the exception of growth. (4) There may have been a reduction in the tendency to waste feed through spillage and carry out energetically expensive behaviors. There is a discrepancy in the literature with regards to the influence of selection on body composition and its contribution to feed efficiency. In this review, two scenarios are demonstrated, whereby body composition either has or has not altered via artificial selection. Understanding the effects of artificial selection on the traits that relate to the feed efficiency of the broilers will contribute towards the reduction of the environmental impacts that arise from such systems.

Keywords Broiler · Genotype · Genetic change · Digestive efficiency · Energy use efficiency · Metabolic heat production

Contents

1 Introduction

Modern chicken breeds are the result of billions of years of evolution by means of natural selection, on which artificial selection for commercial objectives has been applied. By far, the greatest progress made in chicken genetics since their domestication has been witnessed in the latter half of the twentieth century, since the advent of industrial scale agriculture (Schmidt et al. 2009). This can be attributed to developments made in quantitative genetics and the success of its commercial application (Siegel and Dunnington 1997).

Broiler breeding methods can be summarised in the following steps: at the highest level, the pure-breeding lines are owned and controlled by the breeding companies. These lines are subjected to full scale selection programs; it is from these

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lines that all of a company's broiler products have descended (Muir and Aggrey 2003). The great-grandparent stocks, which are produced from the pure-bred lines, are subjected to mass selection for selected traits. Growth rate has consistently been the prime selection trait since the 1950s, with more recent emphasis placed on the yield of breast meat, liveability and feed use efficiency (Emmerson 1997; Muir and Aggrey 2003; Laughlin 2007; Renema et al. 2007). Specific grandparent lines are cross-bred to produce the parent stock, which are then distributed to specialist traders and integrated producers. The final step of the intensive artificial selection is the cross-breeding of these hybrids (parent stock) to give rise to the production broilers, which are raised for slaughter by production companies. Much progress has been made in artificial selection technologies over the last century: from mass selection to the use of pedigree charts and hybridisation, to the introduction of selection indices and artificial insemination, to the development of modern breeding value estimation techniques (Rishell 1997; Muir and Aggrey 2003). Consequently, Zuidhof et al. (2014) showed chicken broiler growth rate to have increased by over 400 % between the years of 1950 and 2005 (Fig. 1), when genetically representative birds of those years were grown in identical environments. The consequences of these developments on the broiler traits, in order to increase growth rate and feed use efficiency, form the focus of this review.

The change in the performance of broilers depicted by Fig. 1 can all be attributed to the advancements made in their genetics (Havenstein et al. 2003a, b; Zuidhof et al. 2014) and this has environmental impact implications. For instance, feed provision represents the industry's greatest environmental hotspot (Pelletier 2008; Leinonen et al. 2012, 2013; Prudêncio da Silva et al. 2014); as such, a bird that requires less feed to achieve the same slaughter weight will embody a lower environmental burden. This is a combined result of reduction of environmental impacts related to (1) production of feed (e.g. greenhouse gas emissions from fossil fuels used in crop production and emissions related to agricultural land use changes) and (2) reduced nutrient emissions form poultry manure; the amount of which is also reduced in more feed-efficient birds. Therefore, an investigation into the literature regarding the traits that can affect the feed use efficiency of the birds is justified.

The birds obtain the energy for growth and metabolic functions from their feed in the form of carbohydrates, proteins and fat. Since these components form a majority of the composition of the feed, they therefore strongly determine the total amount of feed consumed. With this in mind, placing selective pressure on increased feed use efficiency is indistinguishable from placing selective pressure on increased energy use efficiency, calculated by dividing the energy retained by the bird (mainly in the form of protein and lipid) by the total energy required to reach a defined live weight. The growth rate, in
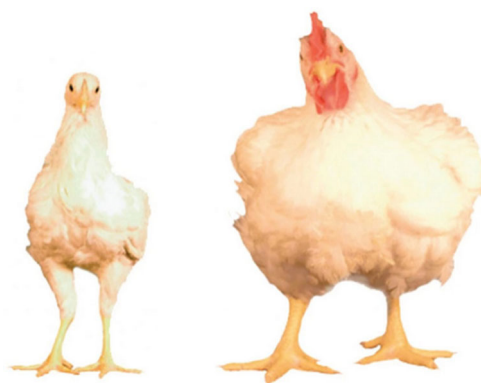

Fig. 1 Photograph showing a commercial broiler genotype produced in the 1950s (*left*) and a commercial broiler genotype produced in 2005 (*right*). Both birds are the same age (56 days) and have been fed on an identical modern diet; they weigh 905 and 4202 g, respectively. Photograph extracted from Zuidhof et al. (2014), copyright license agreement obtained from Oxford University Press in 2015

turn, affects the energy use efficiency because a broiler that reaches slaughter weight quicker needs to allocate less energy overall to the metabolic processes, with the exception of growth during this shorter growth cycle (Emmans 1994, 1997). Energy use efficiency and the growth rate are complex, highly aggregate "composite traits" which by definition are the result of many underlying biological traits (Pym 1990). Thus, identifying these underlying biological traits forms the necessary starting point in quantifying the future environmental impact of the poultry sector. They include behaviour, appetite, digestive efficiency, protein and lipid accretion, and metabolic activity (which includes all life-sustaining biochemical transformations within the cells, such as those related to physical activity, protein turnover and the maintenance of energetically expensive systems, e.g. the digestive system) (Emmerson 1997). The objective of this review is to critically assess the direction and magnitude of the genetic change, which may or may not have taken place in each of these biological traits in the recent decades, in order to understand the genetic potential for future improvements in broiler performance and environmental impact.

The first part of the review is a qualitative investigation into the literature in order to critically assess the potential consequences artificial selection has had on each biological trait and establish how much each of these traits has contributed, if at all, to the changes in energy use efficiency of modern broilers. Narrative summaries have been used to compare studies where experimental data exist but do not provide homogenous quantitative evidence. Studies that give evidence of potential genetic change were especially useful, such as by placing selective pressures on the individual traits of interest and where data could be extracted from comparative studies of different broiler breeds. The second part of the review is quantitative, aiming to determine the metabolisable energy intake of different breeds of broiler and estimate how this energy was

distributed between growth and metabolic heat production. This analysis, in part, focused on the grey literature, such as performance objective tables and nutritional specifications, produced by the breeding companies (Aviagen 2007a, b, 2014a, b; Cobb 2014). These documents provided the information needed to derive typical energy intakes delivering a given performance. On top of genetics, feed formulation has played a crucial role in the improvement of the feed efficiency of production; modern diets have a greater energy density than diets that were fed to broilers 30 years ago, plus they are balanced by an increased content of essential amino acids. It was important not to confound the effects of dietary differences with the potential effects of genetic change in the biological traits.

Much useful information exists in the literature that describes change in poultry genetics in relation to energy efficiency, which is usually expressed as "feed conversion ratio", i.e. the mass of the feed consumed divided by the body mass gain. Data in literature shows that feed efficiency has increased considerably since its adoption into breeding programs in the 1970s (Emmerson 1997; Faraday 2007; Laughlin 2007; Aggrey et al. 2010; de Beer et al. 2011). However, when used to evaluate the changes in the energy efficiency of the birds, such data have no value unless the dietary energy content is known. For this reason, experiments which have compared different breeds on the same diet are of particular interest, from which biological traits such as digestive efficiency and body composition can be compared (Sherwood 1977; Havenstein et al. 2003b; Mussini 2012; Zuidhof et al. 2014). Until now, the consequences of genetic selection on the biological traits aforementioned and ultimately the energy use efficiency of the birds have not been analytically reviewed in such a way as to show how artificial selection has led to an improvement in broiler performance. Therefore, the way in which the information is presented in this review is novel and of high interest to those concerned with poultry genetics.

2 Feed intake, digestion and absorption

Intensive selection pressures placed on broiler performance traits, such as increased body weight and growth rate, have resulted in broilers with an increased appetite and therefore also increased voluntary feed intake per day (Siegel and Wisman 1966; Pym and Nicholls 1979; Havenstein et al. 1994a, 2003b; O'Sullivan et al. 1992b; Schmidt et al. 2009; Howie 2010, 2011) (see also section 5). As well as genetic selection, exogenous factors which influence many physiological and behavioural processes can be carefully controlled to increase feed intake and pre-ingestion efficiency. Light, for instance, is a critical environmental factor for manipulating the feed intake. By artificially increasing the length of time

the bird is subjected to light, its feed intake can be increased; a technique employed in modern poultry systems to favour high growth rates (Olanrewaju et al. 2006; Karakaya et al. 2009). It is possible that improved housing conditions (ambient temperature and humidity, air flow etc.) have reduced the energy requirement of functions other than growth, from thermoregulation to immune responses. This modifies the energy requirements, but also the amino acid requirements of the birds, and could potentially affect feed intake, growth and body composition. However, within experiments discussed in this review, broiler breeds were compared in the same environmental conditions and on the same diet, therefore the differences in performance could only be attributed to genetics.

Years of advancement in feed distribution technologies and animal husbandry practices have undoubtedly reduced feed spillage to improve the feed use efficiency of the system (Svihus et al. 2004; Howie et al. 2011). Nevertheless, there is anecdotal evidence also to show the involvement of genetics in decreasing feed spillage. For instance, although it was not the aim of the experiment to examine differences in feed spillage between breeds, relatively high feed wastage was observed by Zuidhof et al. (2014) in less selected broiler breeds compared to modern breeds (i.e. birds which have a genotype similar to what could be expected to be grown commercially nowadays). Changing the consistency of the feed can make it less prone to being spilled by old-type breeds (i.e. broilers which are genetically representative of commercial broilers grown in the 1950s), whereas modern breeds show no observable difference in spillage between feeds with different consistencies (Zuidhof et al. 2014). The predisposition of an old-type breed to spill more feed than a modern breed was also observed by Havenstein et al. (1994a) and addressed in the design of later experiments (Havenstein et al. 2003a, b). It can be speculated that breeding birds with increased feed use efficiency has applied selective pressures against temperaments which incur the worst feed handling behaviours thus feed spillage could contribute to the differences in the pre-ingestion efficiency between different breeds.

The gastrointestinal tract's function is to supply the rest of the bird's body, including the digestive organs themselves, with the energy and nutrients needed to survive, grow and reproduce (Jacob 2015). Therefore if limiting, growth and function of the organs that make up the digestive system could be enhanced by selection, better diet and improved husbandry practices in order to change the birds' digestive efficiency and therefore the efficiency with which feed is utilised (Nitsan et al. 1991). Since the nutrients that are not retained by the birds' body are responsible for the eutrophication and acidifying emissions produced by the poultry system (Pelletier 2008; Leinonen et al. 2012), improved digestive efficiency can influence the provision and the excretion of important nutrients, thus affecting the environmental impacts at both ends of the poultry production chain.

Differences in the digestive ability between laying hens and broilers are often reported, which indicates that because both breeds were bred from a common ancestor, digestive efficiency has been altered via artificial selection (Spratt and Leeson 1987; Jackson and Diamond 1996). When young birds representing an egg-laying breed were compared to broilers at a common growth stage, Pishnamazi et al. (2005) showed that the former consistently metabolise a greater amount of energy from their feed. The reason for this may be that in modern broiler breeds, digestive efficiency may have reduced from levels displayed by the egg-laying breed due to the intensified burden (i.e. increased digesta throughput) placed on the digestive system as a result of an increased growth rate and feed intake. However, when placed under selective pressures aiming to improve specific traits, digestive efficiency can actually be improved in broilers. For instance, birds selected for improved feed conversion have been shown to have higher digestive efficiency when compared to birds selected for high growth rate, when fed on the same feed (Doeschate et al. 1993; Carré et al. 2008), whereas no evidence was found within the scope of this review for differences in digestive energy efficiency between divergent lines selected specifically to be lean and fat (Leclercq and Saadoun 1982; Leenstra and Pit 1987; Jorgensen et al. 1990). Furthermore, it is possible to select directly for high protein, lipid and starch digestive efficiency (Mignon-Grasteau et al. 2004; Lopez and Leeson 2008). However, the results of experimental comparisons in digestive efficiency between birds are quite variable and are affected by their size and feeding regime (Zhang and Aggrey 2003; García et al. 2007); for instance, some authors reported large genetic × feed interactions on the digestive efficiency trait (e.g. Mignon-Grasteau et al. 2010), making it unclear as to whether any improvement has been made to this trait in modern commercially grown broilers when compared to old-type breeds.

Selection for higher growth rate has led to a lower degree of maturity at slaughter and this affects the size of different organs at any given age with some organs, such as those that make up the digestive tract, being genetically predisposed to maturing sooner than others (Katanbaf et al. 1988; Mitchell and Smith 1991; Nitsan et al. 1991; Nir et al. 1993). Despite the digestive system maturing more quickly in modern breeds compared to old-type ones, the digestive system has reduced in size relative to body weight at a comparable age. This is reflected in the higher carcass yield (i.e. the proportion of the edible carcass of the total slaughter weight) of modern birds compared to old-type breeds (Havenstein et al. 1994b, 2003a). This might be expected, as maintaining the digestive system requires a high level of metabolic energy (see section 4). Reducing the size of this system relative to body weight therefore will reduce this energy requirement and increase the birds' overall energy efficiency (Mitchell and Smith 1991).

It has been suggested by Ravindran et al. (1999) that the inherently different nutrient utilisation seen between breeds could be due to differences in the structure of the gastrointestinal tract which relate to changes in digestive enzyme output, absorptive capacity and digesta transit time. Poultry rely on enzymatic digestion, more so than other livestock, as their colons are relatively short and largely lack the bacteria that aid other species in digestion. Nir et al. (1993) claimed digestive enzyme production to be the limiting factor in improving broiler digestion, particularly in young birds. Differences in enzyme production between high and low body weight lines have been reported in chickens at the same chronological age (Nir et al. 1987; O'Sullivan et al. 1992a). Elsewhere, it has been found that birds selected for high body weight showed higher intestinal and pancreatic trypsin and amylase levels expressed relative to the intestinal contents (Nitsan et al. 1991; Dunnington and Siegel 1995). Tolkamp et al. (2010) recently provided further evidence in support of the view that enzymatic production can also be altered via selection for growth rate and feed efficiency (Pym 1985; Doeschate et al. 1993) but not by selection for leanness (Leclercq and Saadoun 1982). Investigations by Péron et al. (2007) showed evidence for variation in proventriculus pepsin activity between lines subjected to different selection pressures, which leads to differences in protein digestive efficiency.

A difference in the intestinal absorptive area and capacity between broiler lines subjected to different selection pressures was reported by Bedford (1996). High growth rate lines have a smaller intestine, which has a much greater proportion of muscle by mass than intestinal mucosa, than slower growers relative to body weight when compared at the same age. Despite the actual number of villi decreasing concomitantly with the reduction in the length of the digestive tract, the surface area has increased due to greater intestinal villi size (Mitchell and Smith 1991; Katanbaf et al. 1988; Mussini 2012). Elsewhere, it has been shown that more intestinal membrane transport proteins per unit area can be detected in high body weight genotype embryos compared to a low body weight genotype, but no evidence has been presented to suggest that this has translated into increased absorption posthatch (Mott et al. 2008).

One organ found in the digestive system which seems particularly susceptible to genetic change is the gizzard, responsible for grinding up feed. There is a selective tendency for the gizzard to increase in absolute size when the birds are selected for high digestive efficiency (Maisonnier et al. 2001). This adaptation becomes more pronounced if selection takes place on a diet where the physiochemical properties of the grains make the feed tougher to mechanically breakdown (Péron et al. 2007). Furthermore, the gizzard can be stimulated into growing larger in low digestive efficiency lines when fed on coarse grains, thus improving bird digestive efficiency. This trigger has a much less pronounced reaction in the gizzard of broilers from lines selected for high digestive efficiency

(Rougière et al. 2009). This suggests that the birds which have been specifically selected for high digestive efficiency are genetically predisposed to growing a large gizzard. The gizzard size may also play a vital role in improving digestive efficiencies by increasing the mean digesta retention time, described by some as the greatest influencing factor in the improvement of digestive efficiency (Pym 1985; Maisonnier et al. 2001; Pishnamazi et al. 2005; González-Alvarado et al. 2008; Rougière and Carré 2010). Therefore, should digestive efficiency have increased, the gizzard might be expected to be larger in modern broilers relative to body mass. However, neither the size of the gizzard relative to the body mass nor the digestive efficiency of broilers has been shown to have increased due to commercial breeding programs (Mussini 2012). It would seem that increasing the digestive efficiency of the bird is linked to size increases in the gizzard when digestive efficiency is selected for specifically; such an investment of energy, in contrast, is not placed in the growth of the gizzard when selection pressures are instead placed on energy efficiency more generally.

The digestive efficiency of a modern commercial production breed was shown to be lower than that of a high digestive efficiency line (Carré et al. 2002, 2008; Péron et al. 2007), indicating that selection strategies have not led to the maximum potential digestive efficiency broilers are capable of. In both the experiments carried out by Carré et al. (2002) and Péron et al. (2007), broilers were placed on modern wheat-based diets. When placed on similarly soft wheat grain-based diets (Sideral and Sciphon wheat, respectively), the commercially breed showed moderate digestive efficiencies of protein, starch and lipid when compared with the lines specifically selected for high and low digestion efficiencies. When placed on equally hard wheat grain-based diets (Bastille and Baltimor respectively), starch digestibility was high and lipid and protein digestibility were, again, moderate in a commercial breed compared to high and low digestive efficiency lines. A comparative experiment to determine the digestibility of the same diet between a modern commercial production breed and the high digestibility line would be useful to determine the digestibility potential of broilers. However, these results tentatively suggest that it is unlikely that better overall energy efficiency would be related to the highest potential digestive efficiency, especially in birds selected on feed with high digestibility. In a study by Mussini (2012), it was found that energy digestibility values show very little difference between modern broilers (78.86 %) and birds produced commercially in the 1950s (79.05 %) when placed on a modern corn-based diet. These examples suggest that breeding programs, which aim to improve on overall efficiency, may not have led to significant changes in the overall digestive efficiency of broilers. Thus, most of the genetic gain in energy efficiency might instead come from improved metabolic efficiency in modern breeds selected on high-quality feed.

Differences in resource allocation to digestive organs, observed between the broilers bred for high body weight (Katanbaf et al. 1988; Mitchell and Smith 1991) and for high digestive efficiency specifically (Péron et al. 2006), suggest selecting for digestive efficiency may actually compromise other traits which are incorporated into modern breeding programs and vice versa (Pym et al. 2004). Contrasting correlations in relative organ sizes have been discovered between lines selected for commercial objectives and high digestive efficiency (Carré et al. 2005; Péron et al. 2006; Rougière and Carré 2010; de Verdal et al. 2010). For instance, Mussini (2012) showed that the gizzard is significantly smaller, and the pancreas similar, in modern commercial breeds when compared to old-type breeds fed on the same diet. On the other hand, Péron et al. (2006) found that the gizzard was much larger (correlation = +0.27, +0.82 and −0.05 with protein, starch and lipid digestibility, respectively) and the pancreas much smaller (correlation = −0.22, −0.20 and −0.29 with protein, starch and lipid digestibility, respectively) in the birds selected specifically for high digestive efficiency compared to birds from a control line on the same diet. These observations in organ sizes between the lines indicate that selecting for the maximum energy digestive efficiency generally may not be compatible with selection for high-performance traits. However, experiments carried out by Zhang et al. (2005) showed that selecting for certain digestive efficiencies need not always adversely affect performance traits (e.g. when selecting for phytate phosphorus digestive efficiency). This suggests that it could be at least possible to target specific digestive traits in modern breeding programs. To evaluate conclusively if the selection for high-energy digestive efficiency generally is compatible with high performance for effective incorporation into future breeding programs, the following must be tested: (1) can performances of high digestive efficiency birds be altered compared to that of a control line consisting of a modern commercial breed? And (2) would a combined selection objective, which includes digestive efficiency instead of feed efficiency, generate similar responses to selection as observed in modern breeds? These experiments would fill a gap in the literature; the latter would define whether or not genetic correlations between the traits are as favourable with digestive efficiency as with feed efficiency.

Overall, the results found in literature indicate that increasing digestive efficiency is possible; however, there is no clear evidence that breeding for commercial objectives has led to any change in this trait. The morphometries of the internal structures, in particular the organs that comprise the digestive system, are significantly different between high digestive efficiency lines and birds bred for high commercial performance (Carré et al. 2005; Péron et al. 2006; Rougière and Carré 2010). Selecting for high digestive efficiency may conflict with performance traits and this probably goes part way to

explaining why the genetic change witnessed in broilers does not appear to have delivered their full digestive efficiency potential, at least not to the extent it could have had digestive efficiency been the only trait of interest in breeding programs. Artificial selection of broilers for high-performance traits but not specifically for digestive efficiency, whilst fed on feed with high digestibility, has not placed high pressure on increasing digestive efficiency to the highest possible level. Further, selection for high carcass yield prevents the allocation of more resources into the digestive system as it has relatively low economic value. Instead, it has been inadvertently reorganised in such a way as to improve its efficiency per unit of mass and maintain digestive efficiency, whilst digesta daily throughput has augmented due to increased feed intake.

3 Growth and body composition

As mentioned above, faster growth rate of modern broilers compared to older breeds has strongly contributed to the energy efficiency of the birds, as they now reach their slaughter weight in a shorter time and therefore need relatively less energy for metabolic heat production, such as for protein turnover, and physical activity. Furthermore, potential changes in body composition may have also affected the energy dynamics of the birds. The relationship between the amount of protein and lipid in the body can be influenced by diet composition, degree of maturity, sex and genotype (Leclercq and Whitehead 1988). As broiler growth rate has improved, birds reach slaughter weight at decreasing degrees of maturity (Emmans and Kyriazakis 2000). This in turn could lead to reduced carcass fatness, as relative lipid content of the gain increases with the degree of maturity of the animal (Leenstra 1986; Katanbaf et al. 1988). Protein and lipid accretion differ in both energy values and the transfer efficiency of energy from feed to tissue. Fat contains much more combustible energy than protein does (Pym and Solvyns 1979); therefore, any change in the proportion of the retention of these two components will influence the metabolisable energy content of the body and the efficiency of the weight gain.

A modern breed has been shown to be significantly heavier at every age with a significantly increased proportion of breast meat upon reaching slaughter than an old-type breed (Mussini 2012); Schmidt et al. (2009) showed that the growth rate of breast meat has increased twice as fast as the overall body growth rate. Further, in an old-type breed, the breast muscle plateaued at 9 % of the body mass at day 14. In contrast, by day 14, breast muscle constituted 14 % of the body mass of the modern breed; this ratio continued to increase to 18 % by day 35. Apparently, a major difference occurred at day 14; after which, the old-type birds maintained a constant allocation of resources to breast muscle production, whereas the modern

birds continued to incorporate additional resources into this tissue. Similarly, Fleming et al. (2007) reported that the proportion of breast meat by weight at slaughter has increased by 54 % since the 1970s. The relative weight of wing and heart muscle has been shown to have reduced significantly in modern breeds, when compared to breeds grown commercially 50 years ago (Katanbaf et al. 1988; O'Sullivan et al. 1992a; Havenstein et al. 2003a). When compared with the same diet for example, wings were shown to have reduced by 2.2 and 2.0 % relative to bodyweight at the ages of 43 and 57 days, respectively, due to genetics between the 1950s and 2001 (Havenstein et al. 2003a). Meanwhile, the same experiment showed that in the old-type breed, the heart grew to 0.57 and 0.50 % of the body weight at 43 and 57 days of age, respectively; at the same ages, a 2001 breed was shown having a heart that constituted only 0.50 and 0.44 % of its total body weight, respectively (Havenstein et al. 2003a). A lower relative heart weight through the starter period could be in part due to diversion in protein allocation from the heart to the breast tissues (Schmidt et al. 2009). In contrast, heart weight relative to body weight was shown to be similar in old-type and modern breeds in younger broilers by Mussini (2012), but by the age of 28 days, the less selected old-type birds showed significantly larger hearts relative to their overall body mass. Similar disparity exists in scientific reports in the observed change in the relative mass and maturation rates of the liver due to selection (Nir et al. 1978; Katanbaf et al. 1988; O'Sullivan et al. 1992a; Schmidt et al. 2009; Mussini 2012). Contrasting findings in organ growth may be due to differences in the response to selection for high body weight only and the multi-trait breeding programs that have led to modern commercial breeds (Neeteson-van Nieuwenhoven et al. 2013).

Wang et al. (2004) suggested that the modern broiler is actually phenotypically fatter than broilers grown commercially in the 1970s due to their very inactive lifestyles and energy-rich diets. This idea has been perpetuated since (e.g. Roeder 2012) despite there being more evidence to suggest the birds have become leaner over this time (Pym and Solvyns 1979; Remignon and Le Bihan-Duval 2003). This is expected because high carcass fat is considered unfavourable by the customer and has been selected against in breeding programs in order to improve the quality of the product (Muir and Aggrey 2003; Laughlin 2007). There has been more convincing evidence presented in literature to show that, although body fat increased up until the late 1970s in response to selection for greater live weight at a specific age and rapid growth, modern breeds now have significantly reduced fat deposition due to commercial selection pressures (Leclercq and Whitehead 1988; Zuidhof et al. 2014). Fleming et al. (2007) showed body fat content to have reduced from 26.9 % in the 1970s to 15.3 % in commercial breeds used in the last decade, when birds were compared after being reared

on a modern diet. In that study, it was obvious that this fat reduction was due to an increased amount of energy being allocated to the growth of breast meat as discussed above.

In a 2 × 2 factorial design experiment it was found that, when fed on both a modern diet and a 1950s style diet, a modern broiler breed achieved a different body composition compared to an old-type breed, when raised to the same slaughter weight (Havenstein et al. 1994b, 2003a). When placed on the 1950s diet, modern broilers were much smaller but slightly leaner than those placed on the modern diet, nevertheless fatter than the old-type birds. When placed on the more balanced modern diet, which had a higher energy and protein content (Havenstein et al. 1994a, 2003b), the old-type birds became fatter at every age than they did when fed on the 1950s diet. It is likely that the less-balanced 1950s diet did not contain enough nutrients required by the modern breed each day to reach its full genetic potential and so this led to a reduced growth rate. Furthermore, the modern breed had a higher body fat percentage compared to the old-type breed when both breeds were fed on the old diet, probably because energy was overconsumed in order to increase intake of important nutrients (Leeson et al. 1996; Wiseman and Lewis 1998; Swennen et al. 2004; Leeson and Summers 2005; Gous 2007).

Conversely, in other studies, the percentage body fat was similar between the modern and old-type broilers, at least until slaughter weight, when placed on a modern high-protein diet (Mussini 2012; Fancher 2014). Contrary to the findings reported above, these data suggest that there has been little or no overall change in the body composition in commercial breeds due to artifical selection (Aletor et al. 2000). Elsewhere, there has been no difference in body composition found between breeds, when compared at an equivalent body protein weight, even where there has been heavy selection for the yield of specific parts and huge differences in growth rate and mature mass are displayed (Danisman and Gous 2011, 2013). As was highlighted above, modern diets are of higher quality because they contain more energy, more protein and are more balanced compared to diets used in the past. If the reduction in carcass fatness in commercial breeds is the result of considerable improvements made in the nutrition as opposed to genetics, this could, in part, explain the possible peak in carcass fat in the 1970s. This is because 1970s diets contained relatively more energy to protein in an attempt to maximise growth and storing energy as fat is energetically more efficient.

Broilers can be specifically selected for fatness or leanness based on cholesterol levels in the blood plasma (Whitehead and Griffin 1984), resulting in "genetically lean" and "genetically fat" divergent lines. These lean and fat lines were able to achieve the same body composition when the latter was fed on a higher-protein diet (Whitehead and Parks 1988; Whitehead 1990). When fed in such a way that they reach the same body

composition, Whitehead (1990) showed the "genetically lean" birds to have a better energy use efficiency and to retain a higher proportion of the protein that was taken in than the "genetically fat" line. This may be simply explained by the lower growth rate (and therefore longer time and higher metabolic heat production required to reach a certain body weight) achieved by the "genetically fat" birds when grown to a body composition comparable to the "genetically lean" birds. When fed on old diet formulations, growth rate is reduced and the energy use efficiency suffers in "genetically lean" lines, as it does in modern commercial breeds. Therefore, the conclusion drawn by Whitehead (1990) is consistent with the trend presented by both Mussini (2012) and Havenstein et al. (2003a). Since selecting for leanness leads to birds which display greater performance traits (e.g. higher growth rate), selecting for greater performance traits will result in leaner broilers.

Modern commercial broiler body composition is the product of decades of bird and diet coevolution, as breeders and nutritionists have attempted to produce the most efficient birds with the most desirable characteristics, with concomitant advancements made in nutrition. From the data of the experiments discussed here, it would seem that this has led to commercially reared birds that are leaner now than they were half a century ago. However, body composition displays strong genotypic and environmental interactions; the absolute influence on body composition in commercial breeds that can be attributed to each of these factors remains uncertain due to conflicting literature. An interesting example of such interaction is the potential for genetic adaptation to high- and low-protein diets which has been demonstrated in poultry (Sorensen 1985; Marks 1993); when selection takes place on high-protein diets, this results in birds which require such environments for maximum growth, whereas populations selected on low-protein diets do not require high-protein diets for full expression of their genetic potential for growth. Therefore, the body composition of modern broiler breeds can be seen as a culmination of (1) adaptation to a better diet via artificial selection for improved feed use efficiency and this has resulted in a bird which is genetically lean (Whitehead 1990; Mussini 2012; Havenstein et al. 2003a), and (2) genetic change in the body composition irrespective of the dietary changes due to selection pressures placed on reduced fatness (Fleming et al. 2007; Zuidhof et al. 2014).

4 Metabolic activity

The ingested metabolisable energy that is not stored in the body is released as heat to the environment, and by definition, a more energy-efficient breed would release relatively less metabolic heat than an inefficient one. The effect of the reduced time to reach the slaughter weight on the energy

efficiency of the birds was discussed above, but there has also been discussion on whether the basal metabolic rate (i.e. the metabolic heat produced per day) has changed as a result of genetic selection. There have been attempts to quantify the differences in the metabolic heat production rate between different broiler breeds (e.g. Pym et al. 1984), and it has been suggested that it is lower in breeds selected for high feed efficiency or high weight gain than birds selected for high feed intake. Pym and Farrell (1977) showed the fasting metabolic heat production, indicative of the basal metabolic rate (Noblet et al. 2013), to be 19 % higher in lines selected for high feed consumption when compared to a control line by using respiration chambers to carry out feeding experiments; this led to an estimated 10 % decrease in the feed use efficiency (Carré et al. 2008). This effect supports the view that the basal metabolic rate can be altered when subjected to selection in order to improve the energy use efficiency of broilers, as has been seen in laying hens (Luiting and Urff 1991a, b; Flock 1998). Further evidence presented in literature that indicates that artificial selection can act on the variation in the traits on which the birds' basal metabolic rate is dependant is discussed below.

There is a wide variety of theories in the literature concerning the physiological level (ranging from the cellular level to the locomotive activity of the bird) at which the changes in the bird metabolic rate have potentially occurred. As an extreme example, it has been proposed that genetic predisposition to possessing mitochondria which are more vulnerable to oxidative stress has the potential to lower efficiency due to magnified electron transport chain leak and production of reactive oxygen species (Bottje et al. 2002, 2006; Bottje and Carstens 2009). However, it may seem unlikely, as an overarching factor on which energy use efficiency is dependant, that this would have remained suboptimal after natural selection. Elsewhere, protein turnover has been credited to account for anywhere up to 30 % of broiler heat production, prompting some research into the genetic potential of reducing it (Millward et al. 1976; Muramatsu et al. 1987; Pym et al. 1984). There has been some indication that higher protein accretion rates are achievable through selection by lowering protein degradation rates (Tomas et al. 1988, 1991). However, despite there being some evidence for decreased protein breakdown being genetically predetermined, altered by asserting selection pressure on different traits such as growth rate and feed intake, net protein turnover (i.e. overall protein retention determined by the protein synthesising and degrading processes) does not appear to have been changed as a result of selection for commercial objectives (Pym and Farrell 1977; Whitehead and Griffin 1984; Jorgensen et al. 1990; Pym et al. 2004).

It is unclear how much the artificial selection has been able to change the efficiency of the basic metabolic processes at a cellular or molecular level. However, it is more obvious that selecting for energy efficiency could lead to changes in the proportions of highly energy-demanding tissues, such as in muscle and those found in the digestive system. This in turn can influence the basal metabolic rate. For instance, as mentioned previously, birds with the highest growth rate can be associated with a reduction in the relative amount of mucosa in the small intestine (Mitchell and Smith 1991). It can be postulated that the reduction of this tissue, where cell turnover is high, could lead to a decrease in the energy requirement of the system. Elsewhere, Luiting et al. (1991) suggested the difference between efficient and inefficient laying birds in the unaccounted energy expenditure to be in small part attributed to plumage quality; the evidence to suggest that the birds' basal metabolic rate is greatly affected by interactions between feathering and ambient temperature has been presented by Freeman (1971) and later by Carré et al. (2008). Observable delays in feathering are displayed in birds selected for high feed intake; Deeb and Cahaner (2001) showed that high heat loss is induced by low feathering in a temperate environment which may lead to low feed efficiency. Conversely, in warmer climates, delayed feathering can lead to a decrease in the heat-induced reduction in growth rate. The environments achieved by closed buildings with controlled systems, in which broilers are raised, are designed to alleviate the constraints that the natural environment might apply to the birds' traits, such as on metabolic processes. Adaptations, such as those described above, could result from selection pressures to increase energy use efficiency by means of reducing the overall metabolic energy requirement in such an environment.

As much as 54 % of the difference between efficient and inefficient laying hens in the unaccounted energy expenditure has been attributed to differences in heat production related to physical activity (Luiting et al. 1991). Differences in the locomotive activity of young chicks is significantly influenced by genetics and has been shown to be reduced by 6 % in fast-growing compared to slow-growing broiler breeds (Bizeray et al. 2000; Bokkers and Koene 2003). Fast-growing broilers also showed a lower physical activity level than slow-growing broilers when performing other behaviours such as preening, stretching and ground pecking (Lewis et al. 1997; Siegel et al. 1997; Bokkers and Koene 2003). These behaviours were mostly performed on the spot in a sitting posture in the fast growing breeds resulting in less energy expenditure. Artificial selection for higher growth rate and a more efficient rate of feed conversion has therefore probably favoured birds with reduced subsidiary energy expenditure and subsequently, and perhaps unintentionally, resulted in birds which show reduced physical activity (Weeks et al. 2000). It could also be proposed that reduced physical activity could have led to the reduced observed tendency to spill feed in modern commercial breeds, as was discussed in section 2. It makes sense to select for low physical activity, at least from an energy consumption perspective, if not for the associated animal welfare

concerns (Thorp 1994; Craig and Muir 1998). It should be also noted that contrasting results were found in a study by Skinner-Noble et al. (2003) where it was shown that birds selected for better feed conversion efficiency actually showed a small but significant increase in time spent standing and a decrease in resting behavior. In general, it can be suggested that at least in theory, broilers can be subjected to selection in order to bring down their basal metabolic rate and by extension reduce their metabolic energy expenditure, by selecting for birds which express, above all else, low activity-related heat production (Tolkamp et al. 2010).

5 Quantitative assessment of genetic change in broiler energy efficiency

In order to understand the effect artificial selection has had on the energetic efficiency of broilers, it is necessary to calculate and compare the energy intake of breeds that are representative of those used in industry in the past and present. This can be achieved by calculating the total metabolisable energy that each breed requires to reach a defined live weight, thus determining how efficiently energy is used. This energy requirement of the bird can also be defined as the difference between the combustible energy content of their feed intake and the combustion energy content of their excreta, and methane from enteric fermentation (the latter being minimal in the case of non-ruminant species), and must then be distributed between growth (i.e. the combustion energy content of the protein and lipid retained in the bird's body) and metabolic heat production (Fig. 2). The energy retained in the body as protein and lipid can be quantified based on their heats of combustion, i.e. 23.8 and 39.6 MJ kg^{-1}, respectively (Boekholt et al. 1994; Emmans 1994). These combustion heat values vary slightly throughout literature, probably due to differences in the proportions of the components on which the average properties are determined; however, it cannot be expected that the chemical structure of proteins and lipids (and therefore their combustion heat values) could be altered via artificial selection and so these values were kept constant in our calculations.

The overall protein and lipid that is stored in the body, and their respective energy values, can be used to calculate the overall retained energy; the difference between this stored energy and the metabolisable energy intake is that which is lost as heat. If the metabolic requirements of the birds are lowered, then less feed will need to be consumed in such a condition where energy storage as protein and lipids remains constant.

The model, shown in Fig. 2, was used to assess the genetic change in the broiler energy use efficiency and the partitioning of energy. The total metabolisable energy intake of each bird to reach a defined weight can be calculated when the feed intake and the feed metabolisable energy content are known. In this study, such information was obtained from the industry-provided performance manuals (Aviagen 2007b, 2014b) or in the form of feed conversion ratios in literature (Havenstein et al. 2003b; Mussini 2012; Zuidhof et al. 2014). The growth data were also derived from experimental data found in the literature. The weight at which the breeds were compared was 2 kg. Where the old-type breed did not reach 2 kg before the end of the trial period, the future weight gain was determined through extrapolation using a Gompertz function to relate weight to time (Emmans and Kyriazakis 2000). All the feed intake data used in the calculations were based on the most modern diets applied in these publications. The composition of these diets varied slightly between sources but they all had a known metabolisable energy content. From this, it was therefore possible to calculate the total metabolisable energy requirement of each breed to reach 2 kg by multiplying the metabolisable energy content of the feed by their total intake.

It can be seen in Table 1 that as the growth rate increased (following the trend of genetic changes over recent decades) so too the energy needed for both the growth and the metabolic heat production of the body per day increased (MJ day^{-1}). The growth rate has increased over time, but there are some exceptions to this in the limited data available; notably Mussini (2012) has shown the growth rate to be much greater in the old-type breeds than has been reported for later commercially grown breeds (Havenstein et al. 2003b; Zuidhof
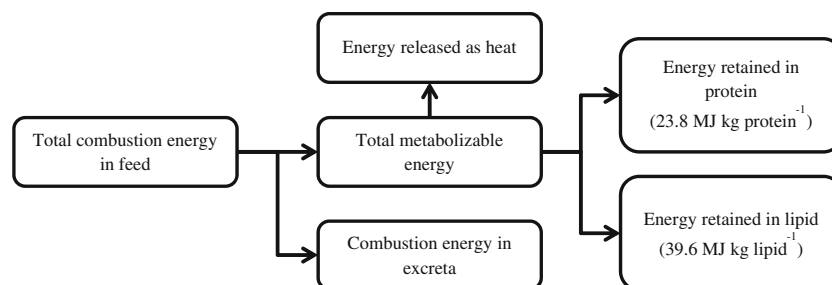

Fig. 2 The main components of energy flow through a broiler chicken as applied in the quantitative data analysis of energy efficiency. The energy contents of protein and lipid were kept constant in the analysis whilst other components (including the mass of protein and lipid within the bird) changed depending on the breed and the scenario

Table 1 Growth rate, total metabolisable energy intake and average metabololisable energy intake rate for each genotype upon reaching 2 kg, as reported in literature

Genotype	1950[1]	1959[2]	1978[3]	2001[2]	2005[3]	2007[4]	2012[1]	2014[4]
Days required to reach 2 kg	55	87	61	34	35	35	33	34
Total metabolisable energy intake (MJ)	51.6	66.5	55.4	38.4	40.5	40.5	42.2	39.9
Average metabolisable energy intake rate (MJ day^{-1})	0.94	0.76	0.91	1.13	1.16	1.16	1.28	1.17

[1] Mussini (2012)

[2] Havenstein et al. (2003a)

[3] Zuidhof et al. (2014)

[4] Aviagen (2007a, b and 2014a, b)

et al. 2014); this can be simply attributed to different growing conditions and feed compositions between experiments. The trend in the energy intake per day (MJ day^{-1}) is to be expected, since modern broilers have an increased feed intake per day resulting in an increased growth rate. However, whilst the energy intake each day increased, the necessary days for growth to slaughter weight decreased in modern breeds. This means that less energy overall was assigned to heat production. Therefore, a downward trend can be seen in the total metabolisable energy intake (MJ) between old-type and modern breeds; this can be seen clearly between the results from the same studies (Table 1).

In order to determine the distribution in the energy that is stored or released as heat, it was necessary to first understand the body composition at slaughter. Data on body composition of broilers is only sporadically available and is even scarcer when comparing old and modern breeds on the same kind of feed. Only two such sources were identified: Mussini (2012) fed broilers of an old-type breed and a modern breed on the same high-quality modern feed and found no overall significant difference in the body composition between the two. The body composition of the birds presented by Mussini (2012) was similar to the body composition of four modern commercial breeds fed on a high-quality feed by Danisman and Gous (2013). On the other hand, Fleming et al. (2007) have suggested that the body composition in lipid and protein has changed over the last 65 years due to artificial selection, where there has been an increase in protein accretion by slaughter and a much reduced lipid accretion in modern breeds when compared to an old-type breed on a modern diet. It has been suggested that carcass fat content peaked in the 1970s, due to selection for high body weight at an age, and birds are presently at their leanest (Leclercq and Whitehead 1988; Havenstein et al. 2003a). Given this conflicting evidence, it was decided that two contrasting scenarios would be tested to appreciate how bioenergetics may have changed over the recent decades due to genetic selection. The first (scenario 1) was based on evidence presented by Mussini (2012) and assumes no change in body composition due to commercial genetic selection. The second (scenario 2) was based on the findings of Fleming et al. (2007) and assumes body composition has changed considerably over the same time period as discussed above. These two scenarios described above were used to estimate the energy use efficiency (Fig. 3) and the metabolic heat production rate (MJ day^{-1}) (Fig. 4) of the breeds of broiler reported in Table 1. For each breed, the model presented in Fig. 2 was used to calculate the energy retention for the extremes of body composition reported in literature. In order to estimate the body compositions, the ratios of ash to protein and water to protein were assumed to be constant (0.2 and 3.4 kg kg^{-1}, respectively) (Gous et al. 1999). The leanest body composition the birds could achieve in the scenarios had 20.2 % protein and 7.9 % lipid based on the data presented by Mussini (2012); the fattest had 16.1 % protein and 26.9 % lipid based on the data presented by Fleming et al. (2007). Based on these calculations, it was not theoretically possible for the modern breeds to have the fattest body composition because more energy would have to be stored in the body than would be taken in by the birds. In any case, it is consistent with literature that the 2001–2014 breeds are lean; therefore, the fat extreme body composition was not shown for these modern breeds in Figs. 3 and 4.

Scenario 1, where body composition is assumed to have remained unaffected by artificial selection, showed a gradual increase in energy use efficiency (Fig. 3) and in heat production rate (Fig. 4), following the genetic changes towards modern breeds. Since the final weight of the bird remained the same for each breed (2 kg), energy use efficiency relative to body composition has increased in modern breeds when compared to old-type breeds due to a decreased total heat production as a result of a shorter production cycle. Scenario 2, where body composition is assumed to have changed, suggests energy use efficiency peaked in the 1978 breed. The reason for this is that considerably more energy is stored in fat birds and the scenario assumed birds were fattest in the 1970s and leanest in the modern day commercial breed. In both scenarios, the heat production rate has increased, but a much more dramatic increase since the 1970s until now is suggested by scenario 2. Again, this is explained by the fact that considerably more energy can be retained in the body as lipid than as
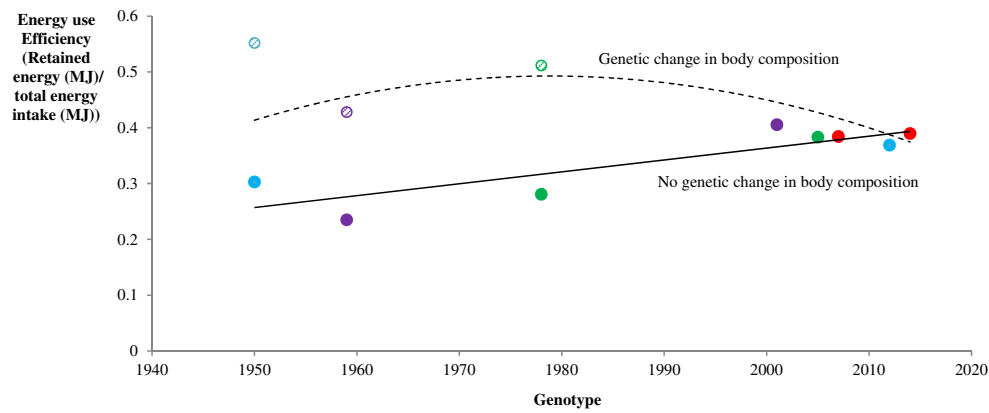
Fig. 3 The genetic trend in energy use efficiency of different broiler genotypes grown commercially from 1950 to 2014 (data in Table 1). The energy use efficiency of each genotype is based on performance data for a broiler grown to 2 kg on a modern diet, provided by Mussini (2012)——●, Havenstein et al. (2003b)——●, Zuidhof et al. (2014)——● and Aviagen (2007a, b and 2014a, b)——●. The *hatched symbols* represent the energy use efficiency for each genotype assuming the leanest potential

body composition (based on Mussini 2012), and the *solid circles* represent the energy use efficiency for each genotype assuming the fattest potential body composition (based on Fleming et al. 2007). The lines represent the overall trends of these two potential scenarios: the *solid line* shows scenario 1 (no genetic change in body composition) and the *broken line* represents scenario 2 (genetic change in body composition)

protein. Therefore, in the scenario where proportionally more protein is stored in the body in modern breeds (scenario 2), a greater fraction of the energy would be lost as heat when the energy intake remains the same. Even where no body composition change is assumed, it can be concluded that genetic selection has resulted in an increased metabolic heat production rate (MJ kg^{-1} day^{-1}) in the recent decades due to the considerable increase in growth rate and the higher energy consumption of metabolic processes related to growth, such as proteinogenesis for example.

It is clear that the total heat produced by broilers to reach a standard slaughter weight has decreased over the decades. However, it is not clear whether all of these can be ascribed

to the short duration of the growth cycle only. Despite artificial selection causing a rise in the heat production rate (MJ kg^{-1} day^{-1}), due to an increased rate of metabolic processes associated with growth, basal metabolic rate related to processes other than growth could still have fallen. Nevertheless, it is impossible to separate the energy needed for metabolic processes specifically associated with the growth of protein and lipid and the energy needed for other metabolic functions. There is other evidence presented here, however, that can support the conjecture that the energy released from metabolic processes excluding growth may have fallen. For instance, it was discussed in the previous section that the lowering of energetically expensive behaviours, in
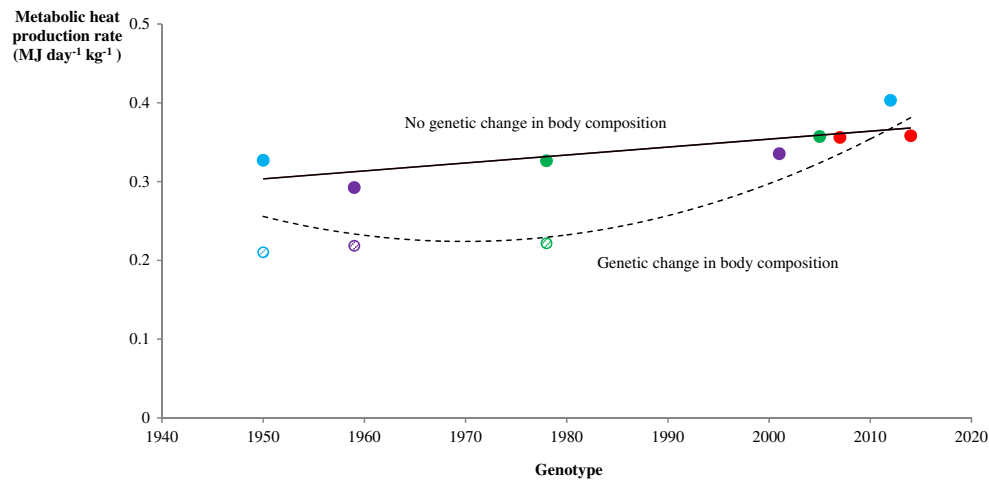

Fig. 4 The genetic trend in the metabolic heat production rate of different broiler genotypes grown commercially from 1950 to 2014. For each genotype this is based on performance data for a broiler grown to 2 kg on a modern diet, provided by Mussini (2012)——●, Havenstein et al. (2003b)——●, Zuidhof et al. (2014)——● and Aviagen (2007a, b and 2014a, b)——●. The *hatched symbols* represent the energy use efficiency for each genotype assuming the leanest potential body composition

(based on Mussini 2012), and the *solid circles* represent the energy use efficiency for each genotype assuming the fattest potential body composition (based on Fleming et al. 2007). The lines represent the overall trends of these two potential scenarios: the *solid line* shows scenario 1 (no genetic change in body composition) and the *broken line* represents scenario 2 (genetic change in body composition)

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particular, has been shown to have occurred in fast-growing birds when compared to slower growers (Bizeray et al. 2000; Bokkers and Koene 2003). A tentative conclusion of this is that, although the overall metabolic rate has increased, the basal metabolic rate may have been reduced to some extent via artificial selection, thus mitigating the increase in the heat production rate (MJ kg^{-1} day^{-1}) due to the increase in growth rate.

6 Conclusion and implications

It has been just over a quarter of a century since genetic variation in the complexities of feed utilisation efficiency and growth rate were outlined by Pym (1990), yet until now, the magnitude of the genetic change in these biological traits has not been critically reviewed. Although the contribution of the various biological traits to the improvements made is not well understood, this review provides a more detailed understanding of the interactions between their genetic change and the trends seen in both the energy use efficiency and the heat production rate. This in turn forms the necessary starting point for predicting the future environmental impact of the industry, thereby avoiding unnecessary environmental harm. The results presented in this review demonstrate the fact that the energy use efficiency of broilers has been increased through artificial selection during the last decades, assuming that the scenario according to which there have been no major changes in the body composition of the birds is valid. The results also show that the overall heat production rate (MJ/day) of the birds has increased via genetic selection over the decades, a fact that has previously not been demonstrated as far as the scope of this review could reveal.

There is little doubt that broilers now have a leaner body composition by the time they reach slaughter weight than they did in the recent decades (Whitehead 1990; Havenstein et al. 2003a; Fleming et al. 2007). However, it is unclear how much of an influence genetics has had on this. In reality, it is probable that there has been both a genotypic and nutritional influence on body composition, as birds have been selected for high efficiency and low fatness on ever improving diets. Thus, the genetic progression may actually sit somewhere between the trends proposed by scenarios 1 and 2 in Figs. 3 and 4. In the absence of evidence for genetic improvement made in the broilers' digestive efficiency, the potentially improved energy use efficiency is likely to be mainly the result of a lower total heat production. This, in turn, is the result of increased growth rate, but there may have also been some reduction in the energy consumption of the basal metabolism, which has freed up energy for deposition into growing tissues. Additionally, there is some indication that feed spillage has been reduced in modern breeds compared to old-type breeds,

which may explain part of the apparent increase in energy use efficiency (Zuidhof et al. 2014).

The increased importance placed on global sustainability fits well with the genetic progress made within the poultry industry, which currently has relatively low environmental impacts when compared to other livestock sectors (Williams et al. 2006; Faraday 2007; Laughlin 2007). However, in order to make further progress, it is important to understand how the improvements in energy use efficiency and growth rate have been achieved up until this point. Rising costs of feed, growing global demand for animal protein and greater awareness of the environmental impacts associated with its production will continue to intensify the focus on developing selection strategies that act upon the variation observed in these poultry traits in order to further increase the efficiency of production.

References

Aggrey SE, Karnuah AB, Sebastian B, Anthony NB (2010) Genetic properties of feed efficiency parameters in meat-type chickens. Genet Sel Evol 42(1):1–5. doi:10.1186/1297-9686-42-25

Aletor VA, Hamid II, Niess E, Pfeffer E (2000) Low-protein amino acid-supplemented diets in broiler chickens: effects on performance, carcass characteristics, whole-body composition and efficiencies of nutrient utilisation. J Sci Food Agric 80(5):547–554. doi:10.1002/(SICI)1097-0010(200004)80:5<547::AID-JSFA531>3.0.CO;2-C

Aviagen (2007a) Ross 308 Broiler Nutrition Specifications. http://www.thepoultrysite.com/downloads/vars/a/10/offset/8/. Accessed 8 April 2015

Aviagen (2007b) Ross 308 Broiler Performance Objectives. http://www.thepoultrysite.com/downloads/vars/a/10/offset/8/. Accessed 8 April 2015

Aviagen (2014a) Ross 308 Broiler Nutrition Specifications. http://en.aviagen.com/ross-308/. Accessed 8 April 2015

Aviagen (2014b) Ross 308 Broiler Performance Objectives. http://en.aviagen.com/ross-308/. Accessed 8 April 2015

Bedford M (1996) Interaction between ingested feed and the digestive system in poultry. J Appl Poult Res 5(1):86–95. doi:10.1093/japr/5.1.86

Bizeray D, Leterrier C, Constantin P, Picard M, Faure JM (2000) Early locomotor behaviour in genetic stocks of chickens with different growth rates. Appl Anim Behav Sci 68(3):231–242. doi:10.1016/S0168-1591(00)00105-2

Boekholt HA, Van der Grinten PH, Schreurs VVAM, Los MJN, Leffering CP (1994) Effect of dietary energy restrictions on retention of protein, fat and energy in broiler chickens. Br Poult Sci 35:603–614. doi:10.1080/00071669408417725

Bokkers EAM, Koene P (2003) Behaviour of fast- and slow growing broilers to 12 weeks of age and the physical consequences. Appl Anim Behav Sci 81(1):59–72. doi:10.1016/S0168-1591(02)00251-4

Bottje W, Carstens G (2009) Association of mitochondrial function and feed efficiency in poultry and livestock species. J Anim Sci 87(14_suppl):E48–E63. doi:10.2527/jas.2008-1379

Bottje W, Iqbal M, Tang ZX, Cawthon D, Okimoto R, Wing T, Cooper M (2002) Association of mitochondrial function with feed efficiency within a single genetic line of male broilers. Poult Sci 81(4):546–555. doi:10.1093/ps/81.4.546

Bottje W, Pumford NR, Ojano-Dirain C, Iqbal M, Lassiter K (2006) Feed efficiency and mitochondrial function. Poult Sci 85(1):8–14. doi:10.1093/ps/85.1.8

Carré B, Idi A, Maisonnier S, Melcion J-P, Oury F-X, Gomez J, Pluchard P (2002) Relationships between digestibilities of food components and characteristics of wheats (Triticum aestivum) introduced as the only cereal source in a broiler chicken diet. Br Poult Sci 43(3):404–415

Carré B, Mignon-Grasteau S, Juin H (2008) Breeding for feed efficiency and adaptation to feed in poultry. Worlds Poult Sci J 64(3):377–390. doi:10.1017/S004393390800010X

Carré B, Mignon-Grasteau S, Svihus B, Péron A, Bastianelli D, Gomez J, Besnard J, Sellier N (2005) Nutritional effects of feed form, and wheat compared to maize, in the D+ and D-chicken lines selected for divergent digestion capacity. In: Proceedings of the 15th European Symposium on poultry nutrition, Balatonfüred, Hungary. World's Poultry Science Association (WPSA), pp 42–44

Cobb (2014) Cobb 500. Performance and nutrition supplement. http://www.winmixsoft.com/en/blog/item/cobb500. Accessed 9 March 2015

Craig J, Muir W (1998) Genetics and the behavior of chickens: welfare and productivity. Genetics and the behavior of domestic animals. Academic Press, San Diego, USA

Danisman R, Gous R (2011) Effect of dietary protein on the allometric relationships between some carcass portions and body protein in three broiler strains. S Afr J Anim Sci 41(3):194–208. doi:10.4314/sajas.v41i3.2

Danisman R, Gous R (2013) Effect of dietary protein on performance of four broiler strains and on the allometric relationships between carcass portions and body protein. S Afr J Anim Sci 43(1):25–37. doi:10.4314/sajas.v43i1.3

de Beer M, Elfick D, Emmerson D (2011) Is a feed conversion ratio of 1:1 a realistic and appropriate goal fror broiler chickens in the next 10 years? In: Cronjé P (ed) Recent Advances in Animal Nutrition - Australia, vol 18. Animal Science, University of New England, pp 9–14

de Verdal H, Mignon-Grasteau S, Jeulin C, Le Bihan-Duval E, Leconte M, Mallet S, Martin C, Narcy A (2010) Digestive tract measurements and histological adaptation in broiler lines divergently selected for digestive efficiency. Poult Sci 89(9):1955–1961. doi:10.3382/ps.2010-813

Deeb N, Cahaner A (2001) Genotype-by-environment interaction with broiler genotypes differing in growth rate. 1. The effects of high ambient temperature and naked-neck genotype on lines differing in genetic background. Poult Sci 80(6):695–702. doi:10.1093/ps/80.6.695

Doeschate RT, Scheele C, Schreurs V, Van Der Klis J (1993) Digestibility studies in broiler chickens: influence of genotype, age, sex and method of determination. Br Poult Sci 34(1):131–146. doi:10.1080/00071669308417569

Dunnington EA, Siegel P (1995) Enzyme activity and organ development in newly hatched chicks selected for high or low eight-week body weight. Poult Sci 74(5):761–770. doi:10.3382/ps.0740761

Emmans GC (1994) Effective energy: a concept of energy utilization applied across species. Br J Nutr 71:801–821. doi:10.1079/BJN19940188

Emmans G (1997) A method to predict the food intake of domestic animals from birth to maturity as a function of time. J Theor Biol 186(2):189–200

Emmans G, Kyriazakis I (2000) Issues arising from genetic selection for growth and body composition characteristics in poultry and pigs. BSAS Occasional Publication:39–52

Emmerson D (1997) Commercial approaches to genetic selection for growth and feed conversion in domestic poultry. Poult Sci 76(8):1121–1125. doi:10.1093/ps/76.8.1121

Fancher BI (2014) What is the upper limit to commercially relevant body weight in modern broilers? Aviagen, Huntsville, USA

Faraday G (2007) A study of the scope for the application of research in animal genomics and breeding to reduce nitrogen and methane emissions from livestock based food chains. Project AC0204. Defra, London

Fleming EC, Fisher C, McAdam J (2007) Genetic progress in broiler traits—implications for body composition In: Proceedings of the British Society of Animal Science, Southport, UK p 67

Flock D (1998) Genetic-economic aspects of feed efficiency in laying hens. Worlds Poult Sci J 54(03):225–239. doi:10.1079/WPS19980015

Freeman BM (1971) Body temperature and thermoregulation In: M. BDJFB (ed) Physiology and Biochemistry of the Domestic Fowl, vol 2. Academic Press, London, pp 1115–1151

García V, Gomez J, Mignon-grasteau S, Sellier N, Carré B (2007) Effects of xylanase and antibiotic supplementations on the nutritional utilization of a wheat diet in growing chicks from genetic D+ and D-lines selected for divergent digestion efficiency. Animal 1:1435–1442. doi:10.1017/S1751731107000821

González-Alvarado J, Jiménez-Moreno E, Valencia D, Lázaro R, Mateos G (2008) Effects of fiber source and heat processing of the cereal on the development and pH of the gastrointestinal tract of broilers fed diets based on corn or rice. Poult Sci 87(9):1779–1795. doi:10.3382/ps.2008-00070

Gous R (2007) Predicting nutrient responses in poultry: future challenges. Animal 1(1):57–65. doi:10.1017/S1751731107657784

Gous R, Moran E, Stilborn H, Bradford G, Emmans G (1999) Evaluation of the parameters needed to describe the overall growth, the chemical growth, and the growth of feathers and breast muscles of broilers. Poult Sci 78(6):812–821. doi:10.1093/ps/78.6.812

Havenstein G, Ferket P, Scheideler S, Larson B (1994a) Growth, livability, and feed conversion of 1957 vs 1991 broilers when fed "typical" 1957 and 1991 broiler diets. Poult Sci 73(12):1785–1794. doi:10.3382/ps.0731785

Havenstein G, Ferket P, Scheideler S, Rives D (1994b) Carcass composition and yield of 1991 vs 1957 broilers when fed "typical" 1957 and 1991 broiler diets. Poult Sci 73(12):1795–1804. doi:10.3382/ps.0731795

Havenstein GB, Ferket PR, Qureshi MA (2003a) Carcass composition and yield of 1957 versus 2001 broilers when fed representative 1957 and 2001 broiler diets. Poult Sci 82(10):1509–1518. doi:10.1093/ps/82.10.1509

Havenstein GB, Ferket PR, Qureshi MA (2003b) Growth, livability, and feed conversion of 1957 versus 2001 broilers when fed representative 1957 and 2001 broiler diets. Poult Sci 82(10):1500–1508. doi:10.1093/ps/82.10.1500

Howie J (2010) The use of genetic variation in sort-tem feeding behaviour in broiler breeding programmes. PhD Thesis, University of Edinburgh, Edinburgh, Scotland

Howie JA, Avendano S, Tolkamp BJ, Kyriazakis I (2011) Genetic parameters of feeding behavior traits and their relationship with live performance traits in modern broiler lines. Poult Sci 90(6):1197–1205. doi:10.3382/ps.2010-01313

Jackson S, Diamond J (1996) Metabolic and digestive responses to artificial selection in chickens. Evolution 1:1638–1650. doi:10.2307/2410900

Jacob J (2015) Avian digestive system. http://articles.extension.org/pages/65376/avian-digestive-system. Accessed 5 October 2015

Jorgensen H, Sorensen P, Eggum BO (1990) Protein and energy metabolism in broiler chickens selected for either body weight gain or feed efficiency. Br Poult Sci 31(3):517–524. doi:10.1080/00071669008417283

Karakaya M, Parlat S, Yilmaz M, Yildirim I, Ozalp B (2009) Growth performance and quality properties of meat from broiler chickens

reared under different monochromatic light sources. Br Poult Sci 50(1):76–82. doi:10.1080/00071660802629571

Katanbaf M, Siegel P, Dunnington E (1988) Organ growth of selected lines of chickens and their F1 crosses to a common body weight or age. Theor Appl Genet 76(4):540–544. doi:10.1007/bf00260904

Laughlin K (2007) The evolution of genetics, breeding and production. Harper Adams University College, Newport, Shropshire

Leclercq B, Saadoun A (1982) Selecting broilers for low or high abdominal fat: comparison of energy metabolism of the lean and fat lines. Poult Sci 61(9):1799–1803

Leclercq B, Whitehead C (1988) Genetic selection of meat-type chickens for high or low abdominal fat content. In: Leanness in Domestic Birds: Genetic, Metabolic, and Hormonal Aspects pp 25–40

Leenstra F (1986) Effect of age, sex, genotype and environment on fat deposition in broiler chickens. Br Poult Sci 42:12–25. doi:10.1079/WPS19860002

Leenstra FR, Pit R (1987) Fat deposition in a broiler sire strain 2. Comparisons among lines selected for less abdominal fat, lower feed conversion ratio, and higher body weight after restricted and ad libitum feeding. Poult Sci 66(2):193–202. doi:10.3382/ps.0660193

Leeson S, Summers J (2005) Feeding programs for broiler chickens: growth restriction. Commercial poultry nutrition. University Books, Guelph, Ontario

Leeson S, Caston L, Summers J (1996) Broiler response to energy or energy and protein dilution in the finisher diet. Poult Sci 75(4):522–528. doi:10.3382/ps.0750522

Leinonen I, Williams AG, Waller AH, Kyriazakis I (2013) Comparing the environmental impacts of alternative protein crops in poultry diets: the consequences of uncertainty. Agric Syst 121:33–42. doi:10.1016/j.agsy.2013.06.008

Leinonen I, Williams AG, Wiseman J, Guy J, Kyriazakis I (2012) Predicting the environmental impacts of chicken systems in the UK through a life cycle assessment: broiler production systems. Poult Sci 91:8–25. doi:10.3382/ps.2011-01634

Lewis PD, Perry GC, Farmer LJ, Patterson RLS (1997) Responses of two genotypes of chicken to the diets and stocking densities typical of UK and label rouge production systems. I. Performance, behaviour and carcass composition. Meat Sci 45:501–516. doi:10.1016/S0309-1740(96)00084-8

Lopez G, Leeson S (2008) Review: energy partitioning in broiler chickens. Can J Anim Sci 88(2):205–212. doi:10.4141/CJAS07087

Luiting P, Urff E (1991a) Residual feed consumption in laying hens. 1. Quantification of phenotypic variation and repeatabilities. Poult Sci 70(8):1655–1662. doi:10.3382/ps.0701655

Luiting P, Urff E (1991b) Residual feed consumption in laying hens. 2. Genetic variation and correlations. Poult Sci 70(8):1663–1672. doi:10.3382/ps.0701663

Luiting P, Schrama J, Van der Hel W, Urff E (1991) Metabolic differences between White Leghorns selected for high and low residual food consumption. Br Poult Sci 32(4):763–782. doi:10.1080/00071669108417402

Maisonnier S, Gomez J, Chagneau A, Carré B (2001) Analysis of variability in nutrient digestibilities in broiler chickens. Br Poult Sci 42(1):70–76. doi:10.1080/00071660020035082

Marks H (1993) The influence of dietary protein level on body weight of Japanese quail lines selected under high-and low-protein diets. Poult Sci 72(6):1012–1017. doi:10.3382/ps.0721012

Mignon-Grasteau S, Juin H, Sellier N, Bastianelli D, Gomez J, Carré B (2010) Genetic parameters of digestibility of wheat-or corn-based diets in chickens. In: 9th World Congress on Genetics Applied to Livestock Production: 2–6 August 2010; Leipzig, Germany

Mignon-Grasteau S, Muley N, Bastianelli D, Gomez J, Peron A, Sellier N, Millet N, Besnard J, Hallouis J-M, Carré B (2004) Heritability of digestibilities and divergent selection for digestion ability in growing chicks fed a wheat diet. Poult Sci 83(6):860–867. doi:10.1093/ps/83.6.860

Millward D, Garlick P, Reeds P (1976) The energy cost of growth. In: Symposium on 'Nutrition and Growth' vol 03. pp 339–349. doi:10.1079/PNS19760054

Mitchell M, Smith M (1991) The effects of genetic selection for increased growth rate on mucosal and muscle weights in the different regions of the small intestine of the domestic fowl (Gallus domesticus). Comp Biochem Physiol A Physiol 99(1):251–258. doi:10.1016/0300-9629(91)90268-H

Mott C, Siegel P, Webb K, Wong E (2008) Gene expression of nutrient transporters in the small intestine of chickens from lines divergently selected for high or low juvenile body weight. Poult Sci 87(11):2215–2224. doi:10.3382/ps.2008-00101

Muir WM, Aggrey SE (2003) Poultry genetics, breeding, and biotechnology. CABI

Muramatsu T, Aoyagi Y, Okumura J, Tasaki I (1987) Contribution of whole-body protein synthesis to basal metabolism in layer and broiler chickens. Br J Nutr 57(02):269–277. doi:10.1079/BJN19870032

Mussini FJ (2012) Comparative response of different broiler genotypes to dietary levels. University of Arkansas, Fayetteville, North Carolina

Neeteson-van Nieuwenhoven A-M, Knap P, Avendaño S (2013) The role of sustainable commercial pig and poultry breeding for food security. Animal Frontiers 3(1):52–57. doi:10.2527/af.2013-0008

Nir I, Harvey S, Cherry J, Dunnington E, Klandorf H, Siegel P (1987) Growth-associated traits in parental and F1 populations of chickens under different feeding programs 4. Growth and thyroid hormones. Poult Sci 66(1):32–37. doi:10.3382/ps.0660032

Nir I, Nitsan Z, Dror Y, Shapira N (1978) Influence of overfeeding on growth, obesity and intestinal tract in young chicks of light and heavy breeds. Br J Nutr 39(01):27–35. doi:10.1079/BJN19780008

Nir I, Nitsan Z, Mahagna M (1993) Comparative growth and development of the digestive organs and of some enzymes in broiler and egg type chicks after hatching. Br Poult Sci 34(3):523–532. doi:10.1080/00071669308417607

Nitsan Z, Dunnington E, Siegel P (1991) Organ growth and digestive enzyme levels to fifteen days of age in lines of chickens differing in body weight. Poult Sci 70(10):2040–2048. doi:10.3382/ps.0702040

Noblet J, Labussière E, Dubois S, Lange CFM, Barea R, Lasnier J, Rivera V, Warpechowski M, Milgen J (2013) Fasting heat production and metabolic body size in non-ruminant growing farm animals. In: Oltjen JW, Kebreab E, Lapierre H (eds) Energy and protein metabolism and nutrition in sustainable animal production: 4th International Symposium on Energy and Protein Metabolism and Nutrition Sacramento, California, USA 9–12 September 2013. Wageningen Academic Publishers, Wageningen, pp 313–314. doi:10.3920/978–90–8686-781-3_107

O'Sullivan N, Dunnington E, Siegel P (1992b) Correlated responses in lines of chickens divergently selected for fifty-six–day body weight. 1. Growth, feed intake, and feed utilization. Poult Sci 71(4):590–597. doi:10.3382/ps.0710590

O'Sullivan N, Dunnington E, Larsen A, Siegel P (1992a) Correlated responses in lines of chickens divergently selected for fifty-six–day body weight. 3. Digestive enzymes. Poult Sci 71(4):610–617. doi:10.3382/ps.0710610

Olanrewaju H, Thaxton J, Dozier W, Purswell J, Roush W, Branton S (2006) A review of lighting programs for broiler production. Int J Poult Sci 5(4):301–308

Pelletier N (2008) Environmental performance in the US broiler poultry sector: life cycle energy use and greenhouse gas, ozone depleting, acidifying and eutrophying emissions. Agric Syst 98(2):67–73. doi:10.1016/j.agsy.2008.03.007

Péron A, Gomez J, Mignon-Grasteau S, Sellier N, Besnard J, Derouet M, Juin H, Carré B (2006) Effects of wheat quality on digestion differ between the D+ and D-chicken lines selected for divergent digestion capacity. Poult Sci 85(3):462–469. doi:10.1093/ps/85.3.462

Péron A, Svihus B, Gabriel I, Bérot S, Tanguy D, Bouchet B, Gomez J, Carré B (2007) Effects of two wheat cultivars on physico-chemical properties of wheat flours and digesta from two broiler chicken lines (D+ and D−) differing in digestion capacity. Br Poult Sci 48(3):370–380. doi:10.1080/00071660701341963

Pishnamazi A, Pourreza J, Edriss M, Samie A (2005) Influence of broiler breeder and laying hen breed on the apparent metabolizable energy of selected feed ingredients. Int J Poult Sci 4(3):163–166

Prudêncio da Silva V, van der Werf HMG, Soares SR, Corson MS (2014) Environmental impacts of French and Brazilian broiler chicken production scenarios: an LCA approach. J Environ Manag 133:222–231. doi:10.1016/j.jenvman.2013.12.011

Pym RAE (1985) Direct and correlated responses to selection for improved feed efficiency. British poultry Science, Edinburgh, Scotland

Pym RAE (1990) Nutrition genetics. In: R C (ed) Poultry Breeding cind Genetics Elsevier, Amsterdam, pp 209–237

Pym R, Farrell D (1977) A comparison of the energy and nitrogen metabolism of broilers selected for increased growth rate, food consumption and conversion of food to gain. Br Poult Sci 18(4):411–426. doi:10.1080/00071667708416381

Pym R, Nicholls P (1979) Selection for food conversion in broilers: direct and correlated responses to selection for body-weight gain, food consumption and food conversion ratio. Br Poult Sci 20(1):73–86. doi:10.1080/00071667908416551

Pym R, Solvyns A (1979) Selection for food conversion in broilers: body composition of birds selected for increased body-weight gain, food consumption and food conversion ratio. Br Poult Sci 20(1):87–97. doi:10.1080/00071667908416552

Pym R, Leclercq B, Tomas F, Tesseraud S (2004) Protein utilisation and turnover in lines of chickens selected for different aspects of body composition. Br Poult Sci 45(6):775–786. doi:10.1080/00071660400012774

Pym R, Nicholls P, Thomson E, Choice A, Farrell D (1984) Energy and nitrogen metabolism of broilers selected over ten generations for increased growth rate, food consumption and conversion of food to gain. Br Poult Sci 25(4):529–539. doi:10.1080/00071668408454894

Ravindran V, Hew L, Ravindran G, Gill R, Pittolo P, Bryden W (1999) Influence of xylanase supplementation on the apparent metabolisable energy and ileal amino acid digestibility in a diet containing wheat and oats, and on the performance of three strains of broiler chickens. Crop Pasture Sci 50(7):1159–1163

Remignon H, Le Bihan-Duval E (2003) Meat quality problems associated with selection for increased production. In: M. MW, E. AS (eds) Poultry Genetics, Breeding and Biotechnology. Cabi, Wallingford, UK, pp 53–66

Renema R, Rustad M, Robinson F (2007) Implications of changes to commercial broiler and broiler breeder body weight targets over the past 30 years. Worlds Poult Sci J 63(03):457–472. doi:10.1017/S0043933907001572

Rishell W (1997) Breeding and genetics—historical perspective. Poult Sci 76(8):1057–1061. doi:10.1093/ps/76.8.1057

Roeder M (2012) Sustainable food vol 2. The Stationery Office, London, UK

Rougière N, Carré B (2010) Comparison of gastrointestinal transit times between chickens from D+ and D− genetic lines selected for divergent digestion efficiency. Animal 4(11):1861–1872. doi:10.1017/S1751731110001266

Rougière N, Gomez J, Mignon-Grasteau S, Carré B (2009) Effects of diet particle size on digestive parameters in D+ and D− genetic chicken lines selected for divergent digestion efficiency. Poult Sci 88(6):1206–1215. doi:10.3382/ps.2008-00408

Schmidt C, Persia M, Feierstein E, Kingham B, Saylor W (2009) Comparison of a modern broiler line and a heritage line unselected since the 1950s. Poult Sci 88(12):2610–2619. doi:10.3382/ps.2009-00055

Sherwood DH (1977) Modern broiler feeds and strains: what two decades of improvement have done. Feedstuffs 49:70

Siegel P, Dunnington E (1997) Genetic selection strategies—population genetics. Poult Sci 76(8):1062–1065. doi:10.1093/ps/76.8.1062

Siegel P, Wisman E (1966) Selection for body weight at eight weeks of age 6. Changes in appetite and feed utilization. Poult Sci 45(6):1391–1397. doi:10.3382/ps.0451391

Siegel PB, Picard M, Nir I, Dunnington EA, Willemsen MHA, Williams PEV (1997) Responses of meat-type chickens to choice feeding of diets differing in protein and energy from hatch to market weight. Poult Sci 76:1183–1192. doi:10.1093/ps/76.9.1183

Skinner-Noble D, Jones R, Teeter R (2003) Components of feed efficiency in broiler breeding stock: is improved feed conversion associated with increased docility and lethargy in broilers? Poult Sci 82(4):532–537. doi:10.1093/ps/82.4.532

Sorensen P (1985) Influence of diet on response to selection for growth and efficiency. In: Poultry Genetics and Breeding. British Poultry Science Ltd. Longman Group, Harlow, England, pp 85–95

Spratt R, Leeson S (1987) Determination of metabolizable energy of various diets using leghorn, dwarf, and regular broiler breeder hens. Poult Sci 66(2):314–317. doi:10.3382/ps.0660314

Svihus B, Juvik E, Hetland H, Krogdahl Å (2004) Causes for improvement in nutritive value of broiler chicken diets with whole wheat instead of ground wheat. Br Poult Sci 45(55–60). doi:10.1080/00071660410001668860

Swennen Q, Janssens G, Decuypere E, Buyse J (2004) Effects of substitution between fat and protein on feed intake and its regulatory mechanisms in broiler chickens: energy and protein metabolism and diet-induced thermogenesis. Poult Sci 83(12):1997–2004. doi:10.1093/ps/83.12.1997

Thorp BH (1994) Skeletal disorders in the fowl: a review. Avian Pathol 23(2):203–236. doi:10.1080/03079459408418991

Tolkamp B, Wall E, Roehe R, Newbold J, Zaralis K (2010) Review of nutrient efficiency in different breeds of farm livestock. Defra, UK

Tomas F, Jones L, Pym R (1988) Rates of muscle protein breakdown in chickens selected for increased growth rate, food consumption or efficiency of food utilisation as assessed by Nτ-methylhistidine excretion. Br Poult Sci 29(2):359–370. doi:10.1080/00071668808417061

Tomas F, Pym R, Johnson R (1991) Muscle protein turnover in chickens selected for increased growth rate, food consumption or efficiency of food utilisation: effects of genotype and relationship to plasma IGF-I and growth hormone. Br Poult Sci 32(2):363–376. doi:10.1080/00071669108417361

Wang YQ, Thomas B, Ghebremeskel K, Crawford MA (2004) Changes in protein and fat balance of some primary foods: implications for obesity. In: 6th Congress of the International Society for the Study of Fatty Acids and Lipids, Brighton, UK

Weeks CA, Danbury TD, Davies HC, Hunt P, Kestin SC (2000) The behaviour of broiler chickens and its modification by lameness. Appl Anim Behav Sci 67(1–2):111–125. doi:10.1016/S0168-1591(99)00102-1

Whitehead CC (1990) Responses of body composition, growth and food efficiency to dietary protein in genetically lean and fat broilers up to seven weeks of age. Br Poult Sci 31(1):163–172. doi:10.1080/00071669008417242

Whitehead C, Griffin H (1984) Development of divergent lines of lean and fat broilers using plasma very low density lipoprotein concentration as selection criterion: the first three generations. Br Poult Sci 25(4):573–582. doi:10.1080/00071668408454899

Whitehead C, Parks J (1988) The growth to maturity of lean and fat lines of broiler chickens fed diets of different protein content: evaluation of a model to describe growth and feeding

characteristics. Anim Prod 46(03):469–478. doi:10.1017
/S0003356100019085

Williams AG, Audsley E, Sandars DLD (2006) Determining the environ-
mental burdens and resource use in the production of agricultural
and horticultural commodities. Research Project IS0205. Cranfield
University and Defra, Bedford, UK

Wiseman J, Lewis C (1998) Influence of dietary energy and nu-
trient concentration on the growth of body weight and of
carcass components of broiler chickens. J Agr Sci 131(03):
361–371

Zhang W, Aggrey S (2003) Genetic variation in feed utilization efficiency
of meat-type chickens. Worlds Poult Sci J 59(3):328. doi:10.1079
/WPS20030020

Zhang W, Aggrey S, Pesti G, Bakalli R, Edwards H (2005) Correlated
responses to divergent selection for phytate phosphorus bioavail-
ability in a randombred chicken population. Poult Sci 84(4):536–
542. doi:10.1093/ps/84.4.536

Zuidhof MJ, Schneider BL, Carney VL, Korver DR, Robinson FE (2014)
Growth, efficiency, and yield of commercial broilers from 1957, 1978,
and 2005. Poult Sci 93(12):2970–2982. doi:10.3382/ps.2014-04291