

Cuxhaven, December 2006

Editorial

Ladies and Gentlemen,

the first edition of Lohmann Information in its new online format was mailed 25 October 2006 to 922 addresses in 53 countries. We continue to update the address list and are sending this second issue to more than 2000 recipients in 84 countries, with best wishes for personal health and happiness for our readers and successful business in 2007!

We intend to serve our readers by publishing information from scientific research as "food for thought". You as reader are invited to help us in this endeavor by commenting on published articles and by suggesting topics for future issues. In this issue:

1. Under the title "**Performance changes in poultry and livestock following 50 years of genetic selection**", **Prof. Gerald B. Havenstein** reviews the impressive improvement in the efficiency of meat, egg and milk production. The application of quantitative genetic science in poultry and livestock breeding not only enabled the industry to keep up with the growing world-wide demand, but is also a significant contribution to minimize the impact of animal waste on the environment. The author recently retired as head of the Poultry Science Department at the North Carolina State University in Raleigh, NC, USA, which is recognized internationally for its strong research program on animal waste management.
2. **Prof. Jean Noblet** looks at feed efficiency under the title "**Energy evaluation of feeds for pigs: consequences on diet formulation and environment protection**". The author has published extensively on this subject and gave a review at the LAH meeting in November 2005. The proposed NE system provides an energy value which is as close as possible to the "true" energy value of a feed. While its applicability in practice may be discussed, it should help in predicting animal growth and feed conversion more accurately and in evaluating the energy of feed ingredients in terms of requirements of animals for efficient production.
3. Rape seed has long been considered as undesirable in layer feed, because some brown-egg hens may produce eggs with "fishy" taint if rape seed or other critical components are included in the ration. Based on the recent announcement of Lohmann Tierzucht that this problem has been solved by identifying and eliminating a causative gene from its brown-egg strains, nutritionist Mr. **Robert Pottgüter** investigates how feed formulation can benefit from this development. The paper "**New prospects for using rape seed (canola) in layer rations**" includes practical examples for feed formulation with RSM and RSC which may reduce feed cost by 1-3%.
4. Bone fractures in laying hens during their productive lifetime, especially at depopulation, have been the subject of many investigations. Recommendations to reduce their occurrence have focused on optimal nutrition and more exercise in alternative housing systems. In his paper "**Towards the genetic improvement of bone quality in laying hens**", **Dr. R. H. Fleming**, Roslin Institute, reports results of a project in cooperation with Lohmann Tierzucht, which indicate that genetic improvement is possible. Selection for low vs. high bone strength in a highly productive White Leghorn line based on a "bone index" yielded highly significant differences in the incidence of osteoporosis.

With kind regards,



Prof. Dr. Dietmar Flock

Performance changes in poultry and livestock following 50 years of genetic selection

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Introduction

The science of Quantitative Genetics came into existence during the late 1940s and early 1950s, founded on the teachings of individuals such as Jay L. Lush and Arnie Nordskog at Iowa State University, Leon J. Cole and Arthur Chapman at the University of Wisconsin, R. George Jaap at The Ohio State University, Gordon Dickerson at the University of Missouri, Don Warren at Kansas State University, Fred B. Hutt at Cornell University, I. Michael Lerner and Everett Dempster at the University of California, D. S. Falconer and Alan Robertson at the Animal Breeding and Research Organization in Edinburgh, Scotland, and Sewall Wright at the U.S. Department of Agriculture. These individuals, their students, and many others changed the art of animal breeding to a science based on quantitative statistics that can be used for the selection of better performing populations of livestock and poultry. Students of the above individuals were hired to teach and conduct research on quantitative genetics at institutions throughout the U.S. land-grant system, at international agricultural institutions, and at worldwide specialized breeding companies.

Quantitative genetics and breeding procedures have continued to be taught at most agricultural universities since the mid to late 1950s. Those involved in teaching also continued to conduct research and to develop improved mathematical procedures for use in commercial breeding programs. The advent of high speed computers during the 1960s allowed commercial breeding organizations to gather, quickly summarize, and analyze huge amounts of data from their breeding populations. Commercial geneticists then used individual and family information to estimate breeding values for each individual's traits, and an index of those values that predicted the animal's overall genetic merit was then used to select the most meritorious males and females to produce the next generation. Those assessments and selections were done each generation to continue the genetic improvement over time. This process has been used over and over during the past 50 years, and it is the purpose of this paper to provide a brief summary of some of the evidence published over the past 10 – 15 years that demonstrate the changes in the performance of poultry and livestock.

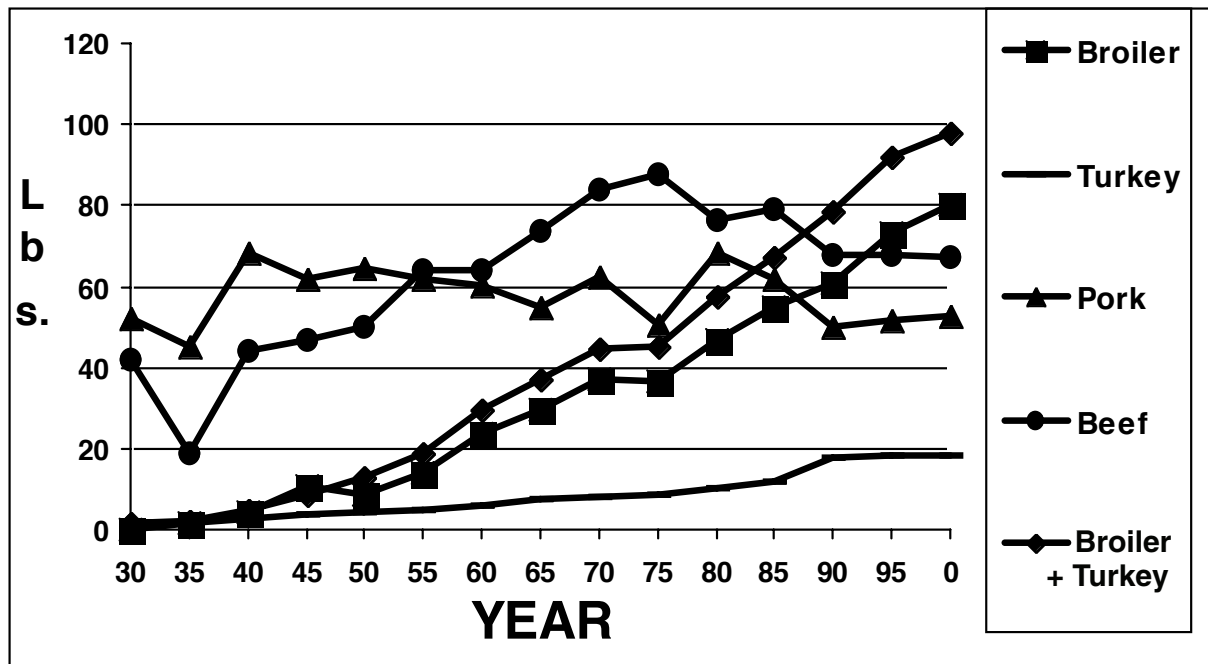
Trends in population growth and consumption of animal products

Not only has the performance of our livestock and poultry changed, but many aspects of the world have changed as well. Before providing evidence as to how quantitative genetics has affected U.S. and worldwide animal production, we need to begin with a little background on the food-animal industries, and specifically how meat and egg consumption has changed over the past half-century, especially in context with the changes in our human population. The animal industries and the types of animals we produce for human food are very different today from what they were 50 years ago. The following summary shows not only how animal production has changed, but also how the human population has changed in terms of the consumption of animal foodstuffs.

The U.S. population doubled from 151 million in 1950 to over 300 million in 2006. If the current trend continues for the next 50 years, the U.S. will have a population of 550 - 580 million people by 2050. Concurrent with the change in the human population is the trend of fewer and fewer people involved in food production. From 1950 to 2000, the percent of the U.S. population engaged in agriculture has dropped from about 10 percent to about 2 percent. At the same time, the number of farms steadily dropped, and the farms producing food have been getting larger and larger, especially during the past 50 years. The number of farms decreased from 6.2 million in 1960 to less than 2 million today.

How do these trends relate to the subject of this paper? Let's take a look at what has happened to per capita meat consumption during this same time period (Figure 1, USDA ERS). The U.S. has experienced a dramatic change during the past 50 years in the types and amounts of meat being consumed, as well as in the types and amounts of animals grown to meet consumer demands. From 1930 to 1950, pork was the meat of choice. During the 1950s through the 1980s beef was the most heavily consumed meat, but from 1985 until today, poultry has become the most consumed meat in the U.S.A. Since about 1993, more broiler meat has been consumed each year than any other type of meat.

Figure 1: U.S. Per Capita Meat Consumption 1930-2000 (Source: USDA)



The estimated change in total meat consumption in the U.S. from 1950 to 2000 is shown in Table 1. Meat consumption tripled during the past 50 years. The increased production and resultant increase in animal waste is a result of the animal industries' response to meet increased consumer demands. If the U.S. human population continues to increase at a similar rate over the next 50 years, input resources will become increasingly taxed and it will become more and more difficult to maintain meat production for this level of demand in the future.

Table 1: Meat Consumption in the U.S. in 1950 and in 2000.

Type of Meat	1950 Per Capita Consumption		1950 Total U.S. Consumption (1000 Tons)	2000 Per Capita Consumption		2000 Total U.S. Consumption (1000 Tons)
	lbs.	kg		lbs.	kg	
Beef	50.1	22.8	4,526	67.0	30.5	9,426
Pork	64.4	29.3	4,862	53.0	24.1	7,457
Broiler	8.7	4.0	657	80.0	36.4	11,256
Turkey	4.1	1.9	310	18.1	8.2	2,546
Total	127.3	57.9	10,355	218.1	99.1	30,686

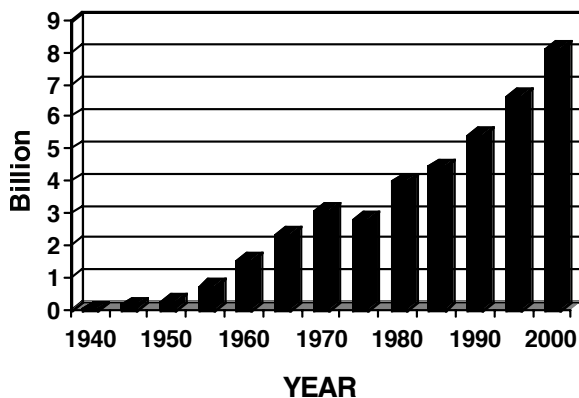
The current level of meat production would have been a lot more difficult if the agricultural community had not applied the scientific information that has come out of our universities and research institutions over the past 50 years to improve the performance of the animals. Science has been used to develop new and improved feedstuffs, it has been used to improve the nutrition and growth rate of the animals, it has been used to prevent devastating animal disease situations, it has been used to improve the general health of the animals, and it has been used to produce environmentally controlled growing facilities which allow us to maximize the growth and efficiency of our livestock and poultry. The greatest single boost to efficiency, however, has been the application of the science of quantitative genetics to select for faster and faster growing meat-type animals, for more efficient egg layers, and for cows with increased milk yield. The following is a brief summary of published data from the scientific literature that support this conclusion.

Several sources of data will be used to illustrate the changes that have taken place in the efficiency of the animal populations currently used for meat, milk and egg production. Changes in efficiency have greatly reduced not only the amount of feedstuffs required to produce a unit of product, but also the amount of waste produced, compared to the inefficiencies in the 1950s.

Broiler data

Almost any food-animal species could be used to demonstrate the changes that have taken place in the efficiency of animal production, but the best example comes from the broiler industry. Figure 2 summarizes the numbers of broilers produced in the U.S. from 1940 through 2000. Broiler production has increased from about 280,000 in 1950 to over 8.2 billion in 2000 (USDA, 2006), and will likely surpass 9 billion in 2006. Many factors have contributed to the development of this agricultural industry, but genetics has played a very major part in the industry’s growth.

Figure 2: U.S. Broiler Production, 1940-2000 (Source, USDA).



A number of studies have been conducted over the past 25 years that clearly document the changes that have taken place in broiler performance (e.g. Sherwood 1977; Havenstein et al. 1994 a,b; Havenstein et al. 2003a,b). These studies used the Athens-Canadian Randombred Control line established in 1957 and modern strains from 1976, 1991 and 2001 to measure growth rate, feed conversion and yield when the broilers were fed 1957 and modern feeds. Body weight data from the Georgia Station (Havenstein et al., 1994a) show that the ACRBC grows exactly the same way today as it grew in 1957 when it was first established as a randombred strain.

Havenstein et al. (2003a,b) summarized the data from two broiler studies carried out in 1991 and 2001, and the growth rate data from their summary is provided in Table 2. The data show that the modern broiler in the year 2001 was nearly five times as large at 42 and 56 days of age as the 1957 randombred broiler, and that the increase in body weight over the 10 year period from 1991 to 2001 was 49.9 and 81.6 grams/year at those two ages, respectively. Edible carcass yield has increased by 12.3 and 13.6 % at 42 and 56 days of age in the 2001 birds in comparison with the yield of the 1957 ACRBC. The data from the Sherwood (1977) and Havenstein et al. (1994a, 2003a) studies consistently show that about 85-90 percent of the change in growth rate has been due to genetic selection, only 10-15 percent of the change is due to improvements in nutrition and nutritional management.

Table 2: Live body weight of modern broilers reared on a modern diet vs. ACRBC broilers reared on a 1957 diet (two studies, 1991 and 2001)^a.

Strain Diet	1991 Comparison		1991 Diff.	2001 Comparison		2001 Diff.	Increase from 1991 to 2001
	Arbor Acres 1991	ACRBC 1957		Ross 308 2001	ACRBC 1957		
Age Days	Body Weight (g)						
21	700	190	510	743	176	567	+57
42	2132	508	1624	2672	539	2133	+509
56	3108	790	2318	3946	809	3137	+819
70	3812	1087	2725	4806	1117	3689	+964
84	4498	1400	3098	5521	1430	4091	+993

^a Adapted from Table 1, Havenstein et al. (2003a)

Because of these changes in growth rate, the feed conversion of broilers at a given age has dropped dramatically over the past 45 years, as shown in Table 3. Feed conversion by age, however, doesn't tell the whole story. The data can be used to project that the modern broiler in 2001 reached 1800 g body weight at about 32 days of age with a feed conversion ratio of 1.46 (Havenstein et al., 2003a), while the ACRBC would have needed an additional 17 days to reach the same BW, and its feed conversion at that age would have been approximately 4.42. Thus, genetics, nutrition and other management changes over the 44 year period from 1957 to 2001 resulted in a broiler that requires approximately 1/3 the time and 1/3 the amount of feed to produce an 1800 g broiler.

Table 3: Feed conversion by age of a modern broiler vs. the Athens-Canadian Randombred control in 2001^a

Strain	Study	Feed	Day 21	Day 42	Day 56	Day 70	Day 84
Ross 308	2001	2001	1.32	1.63	1.96	2.26	2.72
ACRBC	2001	1957	1.81	2.34	2.54	3.36	3.84

^a Havenstein et al. (2003a)

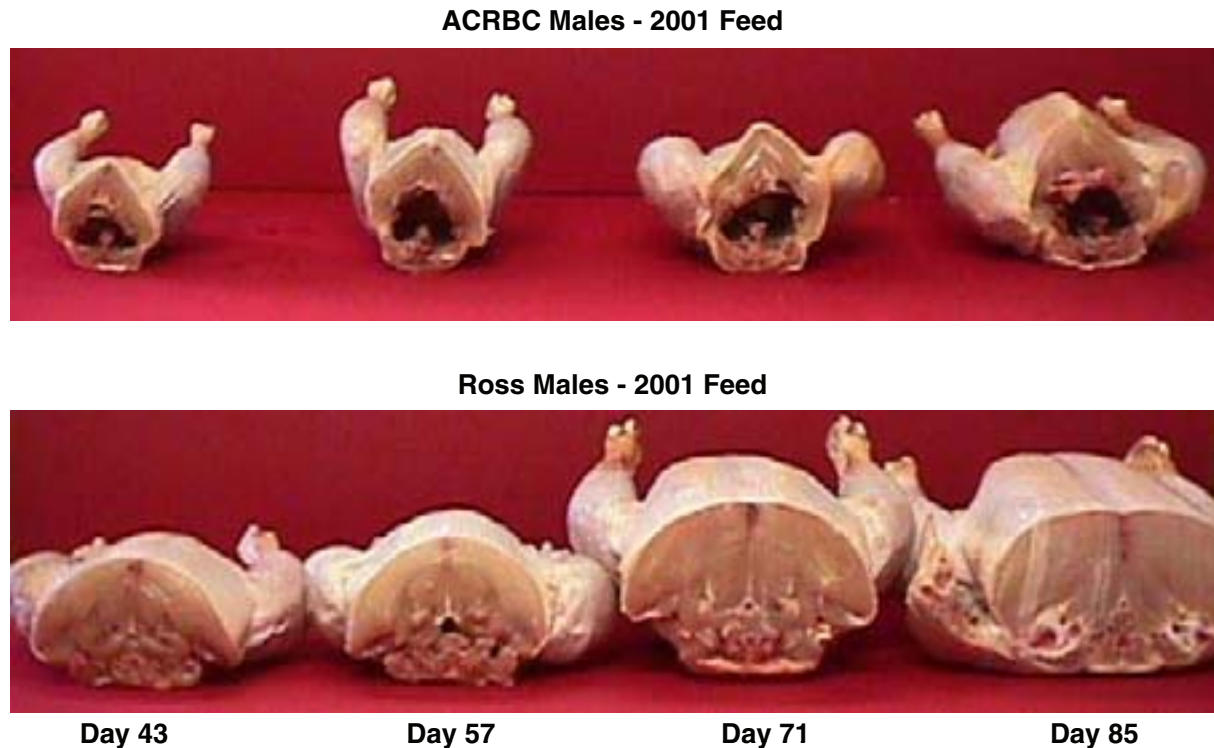
The production of broiler meat today requires roughly one-third the amount of resources (feed, manpower, housing, etc.) and we are producing only about one-third of the waste nutrients that would be produced for the same amount of poultry meat using 1950-type chickens.

Figure 3 demonstrates the incredible difference between 1957 ACRBC and modern-type broilers

Turkey data

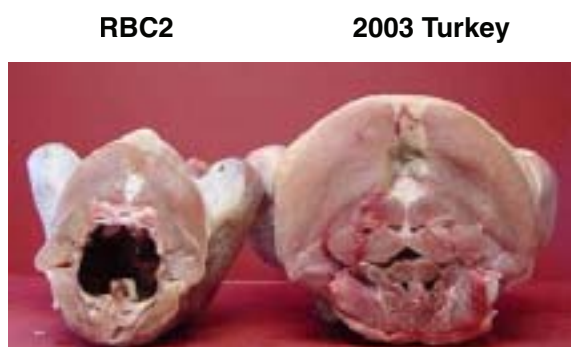
The turkey industry has also applied quantitative genetic selection to its breeding populations. Havenstein et al. (2004a, b; 2007) have recently published a study summarizing the changes that have taken place in the turkey industry from 1966 through 2003. The 2003 turkeys were approximately twice as heavy as the controls representing 1966 turkeys at the four slaughter ages studied. Tom weights increased by 186, 208, 227, and 240 g/year, hen weights by 163, 177, 186, and 204

Figure 3: Broiler carcasses from the Ross 308 and the Control (ACRBC) broilers in the 2001 study (Havenstein et al., 2003a,b)



g/year, at 112, 140, 168, and 196 days of age, respectively, over the past 37 years. Total edible carcass yield increased by 6.5 % over this 37 year period. Feed efficiency to 11 kg of BW for the 2003 toms (2.132 at 98 d of age) was approximately 50 % better than for the 1966 RBC2 toms (4.208 at 196 d of age). The number of days to reach that weight was halved during that period of time. As for the broilers, Figure 4 demonstrates the dramatic difference between modern turkeys and those that were being used by the turkey industry during the mid-1960s.

Figure 4: Turkey carcasses at 196 days of age from the randombred RBC2 strain established in 1966 and maintained at Ohio State University and a modern turkey hatched in 2003 (Source: Havenstein et al., 2004a,b; 2007)



For a number of years nutritionists have been collecting data on the commercial performance of turkeys. Ferket (2003) recently published tables summarizing the average field performance of commercial turkeys from 1966 through 2003. Those data showed that 18 week old turkey toms averaged 8.0 kg in 1966, whereas 2003 toms were nearly double that size at 15.2 kg. Market age to a 15.9 kg body weight for turkey toms was 220 days in 1966, only 133 days in 2003. Feed conversion to 18 weeks improved by 16 % from 1966 to 2003.

Egg-type chickens

Even though the differences between modern egg-type chickens, pigs and dairy cows may not be quite as dramatic as for broilers and turkeys, enormous improvements have been made in the productivity and efficiency of those species as well. For exam-

ple, Anderson (1996) reported that egg production per hen housed was 344 for a 1993 commercial layer strain compared to 267 for the Ottawa randombred control strain (established in 1950) at 82 weeks of age. Average egg weight was 65.0 g/egg for the modern strain vs. 58.1 g/egg for the control, and the combination of improved production and egg size resulted in a 43 % increase in daily egg mass. Efficiency of egg production (egg mass/feed) improved by 32 % over this 43 year period. Body weights of layer strains have been reduced by about 20 percent during the same time, and in combination with the improved productivity, egg-layers require considerably less feed to produce a dozen eggs today than did the birds that were used a half century ago.

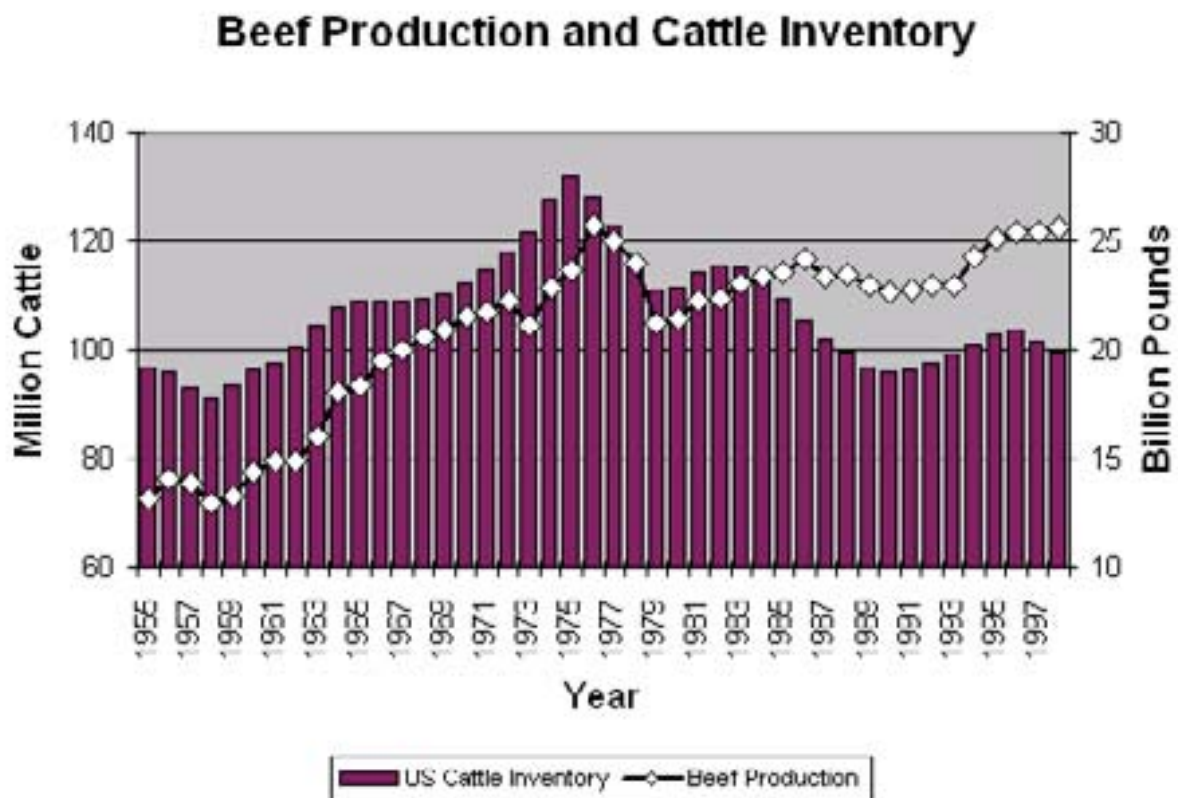
Swine

Performance has also changed dramatically for the swine industry. Although the same types of data are not available for the swine industry as for the broiler and turkey industries, the amount of retail meat per pig has increased by 282 g per year from 1955 to 1997 (Chen et al., 2002). Swine breeders are continuing to improve meat production efficiency by reducing the days to market, reducing the amount of backfat, and by increasing the lean growth rate and loin eye areas of the carcass. All these changes contribute to a reduction of the amount of feed required to produce a unit of marketable meat, and the amount of by-product waste.

Cattle

The beef industry has also greatly improved the output of meat per animal. The number of beef animals on inventory in 1999 (~100 million) is just slightly higher than in 1950 (~97 million), but the amount of beef produced has increased by about 62 percent from about 7.3 million metric tons (MT) in 1950 to over 11.8 MT in 1999. This is largely due to breeding faster growing beef animals. Figure 5 shows the changes in the U.S. beef industry from 1955 to 2000.

Figure 5: Changes in the U.S. beef industry from 1955 to 2000 (Source: USDA)



The dairy industry has been especially successful in improving the efficiency of milk production through the selection of superior performing cows and bulls from summaries of the Dairy Herd Improvement Association. In 1950, the U.S. had 22 million head of dairy cows producing an average of 2,415 kg of milk per year. In 2000, the U.S. dairy industry had 9.2 million cows averaging 8,275 kg milk per year. Total U.S. milk production in 1950 was 53 MT, compared to 76.2 MT in 2000. The dairy industry produced 44% more milk in 2000 with 58 percent fewer cows than in 1950 (Blaney, 2002). Dry matter intake per dairy cow was about 12.3 kg per day in 1950 and had risen to about 20.9 kg per day in 2000 (from DART Ration program of the Dairy Records Management System, based on Brown et al., 1977). Again, these changes are largely the result of genetic selection applying the science of quantitative genetics.

These are but a few examples of the efficiencies that animal scientists and producers have built into the systems used for meat, milk and egg production. This process will continue into the future. The broiler data show that the gains realized in the most recent 10 years were greater than the rates of gain in the preceding decades. This reflects improvements in assessing genetic merit and increased selection pressure applied by primary breeding organizations.

In light of the continuing growth of the world population and increasing per capita demand for food of animal origin, all involved in animal production must continue to focus on both the efficiency of production and the management of by-products in order to keep the food-producing industries viable and to minimize the impact of animal production on the environment.

Conclusions

The take-home message from this review is that our food-animal industries exist to produce food for the human population. Increases in the human population and consumer choice will continue to drive the expansion of these industries. Quantitative genetics has made and will continue to make a major contribution to the efficiency of animal-based food production, and its application has greatly reduced the numbers of animals required to produce our foodstuffs. It has also had a great effect on reducing the amounts of forages and grains required to produce a unit of meat, eggs and milk. As these industries move forward into the future, all involved should not only continue to work toward improving the efficiency of production, but also continue to develop environmentally superior methods for handling by-products from our animal populations.

Consumers, producers, scientists, government officials, environmentalists and ethicists must remember that we are all in this together. Everything possible must be done to develop processes that are both economically sound and environmentally friendly, so that our food animal industries remain viable and sustainable for the future. We cannot return to the past to produce the amount of animal-based foods needed today. The food-animal industries may have a long way to meet all demands of public concern, but continued genetic selection for increased efficiency and application of innovative technologies for animal waste management are contributing in a desired direction, from both a social and an environmental perspective.

Zusammenfassung

In den vergangenen 50 Jahren hat sich eine leistungsfähige Industrie entwickelt, um die wachsende Weltbevölkerung mit einem steigenden pro-Kopf Verbrauch an Lebensmitteln tierischen Ursprungs zu versorgen. Intensive Selektion auf hohe Leistung pro Tier und günstige Futtermittelverwertung hat dazu geführt, dass der steigende Bedarf mit immer weniger Tieren bedient werden kann, die Fläche zur Futterproduktion abnimmt und die Umweltbelastung durch Ausscheidung von N und P verringert wird. Mit weiter steigender Nachfrage nach Lebensmitteln tierischen Ursprungs bleibt die produzierende Industrie gefordert, nicht nur die Futtermittelverwertung weiter zu verbessern, sondern auch innovative Lösungen für umweltfreundliche Verarbeitung bzw. Entsorgung der Abfälle zu entwickeln.

Extensive Produktionsverfahren für Nischenmärkte sind keine Lösung für die Welternährung, und es wird keine Rückkehr zu Methoden der „guten alten Zeit“ geben, als 2 Milliarden Menschen auf der Welt lebten, von denen sich wenige regelmäßig Fleisch, Milch und/oder Eier leisten konnten. Verbraucher, Produzenten, Wissenschaftler, staatliche Behörden, Umweltschützer und Ethiker müssen zusammenarbeiten, damit die Produktionsabläufe umweltfreundlicher, gleichzeitig aber Wirtschaftlichkeit und Existenzfähigkeit der Betriebe nicht in Frage gestellt werden. Die landwirtschaftliche Industrie kann nicht alle Forderungen der Öffentlichkeit erfüllen, aber die Selektion auf verbesserte Futterverwertung und die Anwendung moderner Verfahren der Kotaufbereitung gehen in die richtige Richtung als wichtige Beiträge zur Entlastung der Umwelt.

ACKNOWLEDGEMENTS

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Energy Evaluation of Feeds for Pigs: Consequences on Diet Formulation and Environment Protection¹

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Introduction

The cost of feed is the most important cost in pig meat production (about 60%), and the energy component represents the greatest proportion. Therefore, it is important to estimate precisely the energy value of feeds, either for least-cost formulation purposes or for adapting feed supply to energy requirements of animals. Evaluation of energy content of pig feeds is usually based on their digestible (DE) or metabolizable (ME) energy contents. However, the closest estimate of the "true" energy value of a feed should be its net energy (NE) content which takes into account differences in metabolic utilization of ME between nutrients. In addition, NE is the only system in which energy requirements and diet energy values are expressed on a same basis which should theoretically be independent of the feed characteristics. At each step of energy utilization (DE, ME or NE), different prediction methods can be used. An energy system corresponds then to the combination of one step of energy utilization and one prediction method. The objectives of this review paper are 1/ to consider the main factors of variation of digestive and metabolic utilization of energy in pig feeds, 2/ to present the available energy systems for pig feeds with emphasis given to NE systems, 3/ to compare the energy systems and 4/ to evaluate their ability for predicting pigs performance. Methodological aspects of energy evaluation of pig feeds and complementary information have been considered in previous reviews (Noblet and van Milgen, 2004).

Energy utilization

Digestive utilization

For most pig diets, the digestibility coefficient of energy (DCE or DE : gross energy ratio) varies between 70 and 90% but the variation is larger for feed ingredients (10 to 100%; Sauvant et al., 2004). Most of the variation of DCE is related to the presence of dietary fiber (DF) which is less digestible than other nutrients (<50% vs. 80-100% for starch, sugars, fat or protein; Table 1) and reduces the apparent fecal digestibility of other dietary nutrients such as crude protein and fat (Le Goff and Noblet, 2001). Consequently, DCE is linearly and negatively related to the DF content of the feed (Table 2). The coefficients relating DCE to NDF are such that NDF or DF essentially dilute the diet. In other terms, even though DF is partly digested by the young growing pig, it provides very little DE to the animal (Noblet and van Milgen, 2004). The digestive utilization of DF varies with its botanical origin with subsequent variable effects of DF on dietary energy digestibility. The DCE prediction equations presented in Table 2 represent therefore average equations for mixed feeds. They should not be applied to raw materials where specific relationships are to be used (Noblet and Le Goff, 2001; Noblet et al., 2003).

Digestibility of energy can be modified by technological treatments. Pelletting, for instance, increases the energy digestibility of feeds by about 1%. However, for some feeds, the improvement can be more important and depends on the chemical and physical (particle size) characteristics of feeds. In the examples given in Table 3, the improvement in energy digestibility was mainly due to an improved digestibility of fat provided by corn or full-fat rapeseed. Consequently, the energy values of these ingredients depend greatly on the technological treatment. In the specific situation of high-oil corn (7.5% oil), pelletting increased the DE content by approximately 0.45 MJ per kg (Noblet and Champion, 2003); for coarsely ground full-fat rapeseed, the DE values were 10.0 and 23.5 MJ DE/kg DM as mash and after pelletting, respectively.

¹ Adapted from presentations at the Eastern Nutrition Conference organised by the Animal Nutrition Association of Canada, May 2005 in Montreal, Canada and the Nutrition Conference organized by Lohmann Animal Health, November 2005 in Cuxhaven, Germany.

Table 1: Digestibility of fiber fractions and energy in high fiber ingredients in growing pigs (G) and adult sows (S)

	Wheat bran		Corn bran		Sugarbeet pulp	
	G	S	G	S	G	S
Digestibility coefficient (%) of						
Non-starch polysaccharides	46	54	38	82	89	92
Non cellulose polysaccharides	54	61	38	82	89	92
Cellulose	25	32	38	82	87	91
Dietary fiber	38	46	32	74	82	86
Energy	55	62	53	77	70	76

Table 2: Effect of diet composition (g/kg dry matter) on energy digestibility (DCe, %), ME:DE coefficient (%) and efficiency of utilization of ME for NE of mixed diets for growth (k_g %) and for maintenance (k_m %) ^a

Equation	RSD ^b	Source ^c
1 DCe = 98.3 - 0.090 x NDF	2.0	1
2 DCe = 96.7 - 0.064 x NDF	2.2	1
3 ME/DE = 100.3 - 0.021 x CP	0.5	1
4 k_g = 74.7 + 0.036 x EE + 0.009 x ST - 0.023 x CP - 0.026 x ADF	1.2	2
5 k_m = 67.2 + 0.066 x EE + 0.016 x ST	1.9	3

^a CF: Crude Fiber, CP: crude protein, NDF: Neutral Detergent Fiber, EE: ether extract, ST: starch, ADF: Acid Detergent Fiber.

^b Residual standard deviation

^c 1: Le Goff and Noblet (2001) (n=77 diets ; equations 1 and 3 in 60 kg growing pigs and equation 2 in adult sows, respectively) ;

2: Noblet et al. (1994) (n=61 diets ; 45 kg pigs);

3: Noblet et al. (1993) (n=14 diets; maintenance fed adult sows).

Table 3: Effect of pelleting and particle size on digestibility coefficient (%) of fat and energy in growing pigs

	Mash	Pellet
Corn-soybean meal diets ^a		
Fat	61	77
Energy	88.4	90.3
Wheat-soybean meal-full fat rapeseed diets ^b		
Fat	27	84
Energy	73.1	87.4
Wheat-soybean meal-full fat rapeseed diets ^c		
Fat	81	86
Energy	85.5	87.6
Wheat-corn-barley-soybean meal diets: Energy ^d	75.8	77.3

^a Mean of three diets containing 81% corn and 15.5% soybean meal (Noblet and Champion, 2003).

^b One diet containing 60% wheat, 15% soybean meal and 20% full fat rapeseed; rapeseed was coarsely ground (Skiba et al., 2002).

^c One diet containing 60% wheat, 15% soybean meal and 20% full fat rapeseed; rapeseed was finely ground (Skiba et al., 2002).

^d Mean of 4 diets also containing variable amounts of fibre rich ingredients (wheat bran, sugar beet pulp) (unpublished data)

Energy digestibility is affected by other factors than those related to the diet itself. In growing pigs, DCE increases with increasing BW (Noblet et al., 2003). The largest effect of BW is observed when adult sows and growing pigs are compared (Le Goff and Noblet, 2001). In addition, the difference due to BW increase is most pronounced for high fiber diets or ingredients (Equations 1 and 2 in Table 2; Table 4). This improvement in energy digestibility with increasing BW is due to the greater digestibility of the DF fraction (Table 1) related to a greater hindgut digestive capacity in heavier pigs and, more importantly, a slower rate of passage in the digestive tract (Le Goff et al., 2002). The attenuated negative effects of DF on protein and fat digestibility (i.e., reduced endogenous losses) also contribute to the reduced effect of DF on DCE in adult pigs. Therefore, the negative effect of dietary fiber on DCE becomes smaller for heavier pigs or adult sows and the contribution of DF to energy supply becomes largely positive in heavier pigs. From a large data set of measurements (77 diets), Le Goff and Noblet (2001) calculated that one g of NDF provided 3.4 and 6.8 kJ in 60 kg growing pigs and mature sows, respectively. From the same data, it was also shown that the DE difference between adult sows and growing pigs is proportional to the amount of indigestible organic matter as measured in the growing pig (4.2 kJ/g on average; Noblet and Tran, 2004).

The DCE or the DE differences between sows and growing pigs, for a given level of dietary fiber, also depend on the origin of DF or on the physico-chemical properties of DF. This is illustrated in Table 1 where the effects of DF from wheat bran, corn bran and sugar beet pulp are compared. Detailed information on the effect of origin of DF on DCE in both growing pigs and adult sows has been given by Noblet and Le Goff (2001). These results indicate that growing pigs have a limited ability to digest DF with small differences between fiber sources while adult sows digest more efficiently DF but the improvement depends on the chemical characteristics of DF (e.g., level of lignin). The examples presented in Table 4 also illustrate the effect of botanical origin with small differences between physiological stages for Graminae (wheat, barley, wheat bran), Brassicaceae (rapeseed) or Compositae (sunflower) and more pronounced differences for Leguminosae (pea, soybean, lupin), especially for the hull fraction of these grains. The consequence is that the DE difference between adult sows and growing pigs is proportional to indigestible organic matter in growing pigs, but with specific coefficients for each (botanical) family of ingredients (Table 4; Figure 1; Noblet and Tran, 2004).

Table 4: Digestible energy value of some ingredients for growing pigs and adult sows^a

Ingredient	DE, MJ/kg ^b		a ^c
	Growing pig	Adult pig	
Wheat	13.85	14.10	3.0
Barley	12.85	13.18	2.5
Corn	14.18	14.77	7.0
Pea	13.89	14.39	6.0
Soybean meal	14.73	15.61	8.0
Rapeseed meal	11.55	12.43	3.5
Sunflower meal	8.95	10.25	3.5
Wheat bran	9.33	10.29	3.0
Corn gluten feed	10.80	12.59	7.0
Soybean hulls	8.37	11.46	8.0

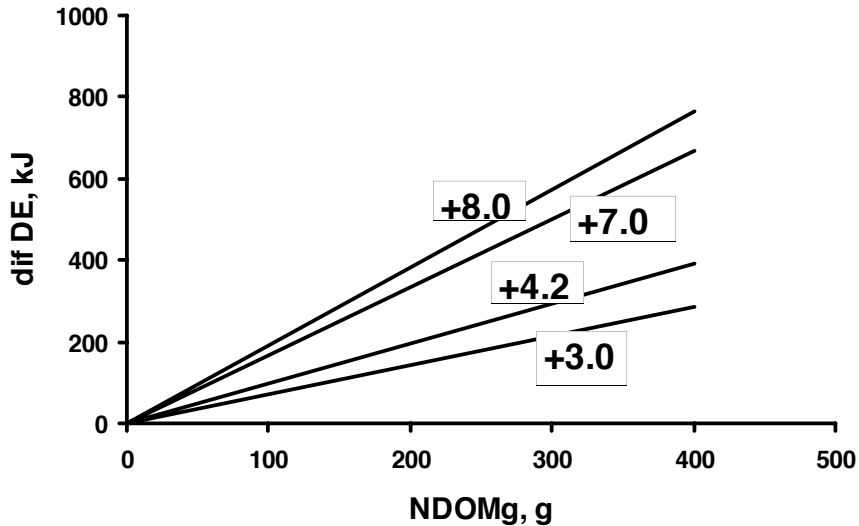
^a Adapted from Sauvant et al. (2004)

^b As fed.

^c kJ difference in DE between adult sows and growing pigs per g of undigestible organic matter in the growing pig (Noblet et al., 2004).

Recent results indicate that DCE in sows is little affected by feeding level (Noblet et al., 2003), which means that values obtained in pregnant sows fed approximately 2.5 kg per day can be extrapolated to lactating sows offered feed ad libitum. An indirect comparison between lactating sows fed above 5

Figure 1: Relationship between DE value in adult sows and DE value in growing pigs (dif DE) and undigestible organic matter in growing pigs (NDOM) for some families of ingredients (adapted from Noblet et al., 2003)



kg/day and pregnant sows fed 2.4 kg per day suggests the same conclusion (Noblet et al., 2003). Little information concerning comparative digestibility in piglets and growing pigs is available. Considering that piglets are usually fed low-fiber diets for which the effect of BW is minimized, piglets can, from a practical point of view, be considered as growing pigs concerning the digestive utilization of energy.

A consequence of the changes of DCE with BW is that digestibility trials should be carried out at approximately 60 kg BW (Noblet et al., 2003) in order to be representative of the total growing-finishing period. A second consequence is that at least two different DE values should be given to feeds: one for growing pigs and one for adult sows (Table 4; Sauvant et al., 2004). This proposal is more justified for fibrous ingredients.

ME:DE ratio

The ME content of a feed is the difference between DE and energy losses in urine and gases (i.e., as methane and hydrogen). In growing pigs, average energy loss in methane is equivalent to 0.4% of DE intake (Noblet et al., 1994). In sows fed at maintenance level, methane production represents a much greater proportion of DE intake (1.5%; Noblet and Shi, 1993) and may reach up to 3% of DE intake in sows fed very high fiber diets (Ramonet et al., 2000). More generally, methane production increases with BW and DF level in the diet. From the compilation of literature data conducted by Le Goff et al. (2002) and unpublished data from our laboratory, Noblet et al. (2004) proposed that methane energy is equivalent to 0.67 and 1.33 kJ per g of fermented DF in growing pigs and adult sows, respectively. Unlike humans, hydrogen production in pigs is rather low and can be neglected.

Energy loss in urine represents a variable percentage of DE since urinary energy depends greatly on the urinary nitrogen excretion. At a given stage of production, urinary nitrogen excretion depends mainly on the (digestible) protein content of the diet. Consequently, the ME:DE ratio is linearly related to the dietary protein content (Table 2). In most situations, the ME:DE ratio of complete feeds is approximately 0.96. However, this mean value cannot be applied to single feed ingredients (Noblet et al., 1993). Consequently, equation 3 in Table 2 cannot be applied beyond the range of typical CP contents of pig diets (10 to 25%) and is therefore not applicable for most ingredients. The most appropriate solution is then to estimate urinary energy (kJ/kg DM intake) from urinary nitrogen (g/kg DM intake). The following equations have been proposed:

$$\text{Urinary energy in pigs} = 192 + 31 \times \text{Urinary nitrogen}$$

$$\text{Urinary energy in sows} = 217 + 31 \times \text{Urinary nitrogen}$$

for growing pigs and adult sows, respectively. For implementing these equations to feed ingredients, it can be assumed that urinary nitrogen represents 50% of digestible nitrogen (Noblet et al., 2003, 2004).

Metabolic utilization of ME

Net energy is defined as ME minus heat increment associated with metabolic utilization of ME and to the energy cost of ingestion, digestion and some physical activity. It is generally calculated as the sum of (estimated or measured) fasting heat production and retained energy. The NE content, as a percentage of ME content (k) corresponds to the efficiency of utilization of ME for NE (Noblet et al., 1994). Apart from variations due to the final utilization of ME (e.g., maintenance, protein gain vs. fat gain vs. milk production), k varies according to the chemical characteristics of the feed since nutrients are not used with the same efficiencies (Noblet et al., 1993, 1994). The variations in k are due to differences in efficiencies of ME utilization between nutrients with the highest values for fat (~90%) and starch (~82%) and the lowest (~60%) for DF and crude protein. These values were confirmed in recent trials (van Milgen et al., 2001; unpublished data). These differences in efficiencies between nutrients also mean that heat increment (per unit of energy) associated with metabolic utilization of energy is higher for crude protein and DF than for starch or ether extract (Noblet et al., 1994; Table 5). Finally, NE measurements conducted in pigs which differ for their BW and the composition of BW gain suggest that the efficiency of ME for NE is little affected by the composition of BW gain, at least under most practical conditions. Similarly, the ranking between nutrients for efficiencies is similar in adult sows fed at maintenance level and in lean fast growing pigs.

Table 5: Energy value of starch, crude protein and fat according to energy systems^a

	Starch	Crude protein ^b	Crude fat ^b
Energy values, kJ/g ^b			
Digestible energy	17.5 (100)	20.6 (118)	35.3 (202)
Metabolizable energy	17.5 (100)	18.0 (103)	35.3 (202)
Net energy	14.4 (100)	10.2 (71)	31.5 (219)
Heat production, kJ/g	3.1	7.8	3.8

^a Adapted from Noblet et al. (1994) (n = 61 diets)

^b Between brackets, energy values as % of starch; crude protein and crude fat are assumed to be 90% digestible; starch is 100% digestible.

The comparison of our results on ME utilization with literature data and the practical consequences on energy evaluation system have been reviewed by Noblet (2000) and Noblet and van Milgen (2004). They have also been validated in recent experiments conducted in our laboratory (Ramonet et al., 2000; van Milgen et al. 2001). They confirm that the increase of dietary crude protein results in an increased HP (Table 6). On the other hand, inclusion of fat contributes to reduction of HP. Diets with low crude protein and/or high fat contents can then be considered as low heat increment diets and are potentially better tolerated under conditions of heat stress (Renaudeau et al., 2001; Le Bellego et al., 2002). However, the effect of DF on HP remains unclear (Noblet and Le Goff, 2001). In some trials, HP is significantly increased when DF is increased (Noblet et al., 1993; 1994; Ramonet et al., 2000; Rijnen et al., 2003) while in other trials, HP remains constant or even decreases (Rijnen et al., 2001; Le Goff et al., 2002). From a biochemical perspective, HP should increase and most results are consistent with this. However, addition of DF may change the behavior of animals (i.e., reduced physical activity) or the overall metabolism, thereby decreasing HP. Furthermore, the effects of DF probably also depend on the nature of DF, and the specific effect of sugarbeet pulp DF (Rijnen et al., 2001) cannot be generalized to other DF sources. Differences in the design of trials and limits of

methodologies may also explain these discrepancies. Finally, another interesting aspect illustrated in the results of van Milgen et al. (2001) concerns the HP associated to the utilization of dietary protein either for protein deposition or for lipid deposition. The data show that the heat increment associated with both pathways is similar and efficiencies are equivalent. From a practical point of view, this means that the NE value of dietary CP is constant, irrespective of its final utilization.

Table 6: Energy utilization of low protein diets

	Trial 1 ^a		Trial 2 ^b	
Crude protein, %	17.4	13.9	21.9-17.4	17.2-12.7
Digestible lysine, g/MJ NE	0.76	0.76	1.05-0.72	1.05-0.72
Energy balance, MJ/kg BW ^{0.60}				
ME intake	2.46	2.46	2.57	2.57
Heat production	1.42 ^x	1.37 ^y	1.40 ^x	1.34 ^y
Energy retained	1.05 ^x	1.09 ^y	1.17 ^x	1.23 ^y
ME/DE, %	95.5 ^x	96.7 ^y	95.7 ^x	96.7 ^y
NE/ME, %	73.2 ^x	75.3 ^y	73.9 ^x	75.9 ^y

^a From Le Bellego et al. (2001); 65-kg pigs; wheat, corn and soybean meal based diets; the low protein diet was supplemented with HCl-lysine (0.43%), methionine (0.11%), threonine (0.16%), tryptophan (0.05%), isoleucine (0.04%) and valine (0.09%); indirect calorimetry method was used for measuring heat production.

^b From Noblet et al. (2003); in 25, 55 and 85 kg pigs; wheat, corn and soybean meal based diets; indirect calorimetry method was used for measuring heat production. Values for CP and lysine levels are given for the 25 and 85 kg pigs; values at 55 kg were intermediary.

^{x,y} Values are significantly different ($P < 0.05$) if different exponents are indicated (within trial).

Energy systems

Digestible and metabolizable energy

Apart from direct measurement on pigs, the DE and ME values of raw materials can be obtained from feeding tables (NRC, 1998; Sauvant et al., 2004). But the utilization of these tabulated values should be restricted to ingredients having chemical characteristics similar or close to those in the tables. As illustrated in the previous section, DCE is affected by BW of the animals. It is therefore appropriate to use DE and ME values adapted to each BW class. However, from a practical point of view, it is suggested to use only two values, one for "60 kg" pigs which can be applied to piglets and growing-finishing pigs and one for adult pigs applicable to both pregnant and lactating sows. Values given in most feeding tables are typically obtained in the 40- to 60-kg pig. The INRA & AFZ feeding tables (Sauvant et al., 2004) provide DE and ME values for these two stages and an illustration is given in Table 4.

The DE content of compound feeds can be obtained by adding the DE contributions of ingredients and assuming no interaction, which is usually the case (Noblet and Shi, 1994; Noblet et al., 2003a). When the actual composition of the feed is unknown, the possibility is to use prediction equations based on chemical criteria (Le Goff and Noblet, 2001) or estimates from near infrared or in vitro methods. Such equations cannot be used for feed ingredients.

Net energy

All published NE systems for pigs combine the utilization of ME for maintenance and for growth (Noblet et al., 1994) or for fattening by assuming similar efficiencies for maintenance and energy retention. The system used in the Netherlands has been adapted from the equations proposed by Schiemann et al. (1972). The "system" used by NRC (1998) for estimating NE values combines results from direct measurements using a questionable animal model (piglet) and estimates from prediction equations. The available NE systems have been described by Noblet (2000). More recently, Boisen and Versteegen

(1998) proposed new concepts for estimating the NE value of pig feeds (so-called physiological energy) and based on the combination of in vitro digestion methods for estimating digestible nutrients and biochemical coefficients for evaluating the ATP potential production from the nutrients. Complementary and theoretical knowledge concerning endogenous secretions could also be included in this approach. Apart from difficulties for implementing the in vitro digestion methods, this approach assumes that energy is used exclusively for ATP production - which is not the case in growing pigs, for instance.

The system proposed by Noblet et al. (1994) and applied in the INRA & AFZ feeding tables (Sauvant et al., 2004) is based on a large set of measurements (61 diets). These results have been validated in recent trials (Le Bellego et al., 2001; Noblet et al., 2001; van Milgen et al., 2001) and its applicability for predicting performance of animals has been demonstrated (see last section). The equations used for predicting NE are given in Table 7. They are all based on information available in conventional feeding tables and are applicable to single ingredients and compound feeds and at any stage of pig production. It has also been demonstrated that these equations can determine a correct hierarchy between feeds for both growing pigs and pregnant or lactating sows. It is important to point out that different DE values or digestible nutrient contents should be used in growing-finishing pigs and adult sows with two subsequent NE values. Reliable information on digestibility of energy or of nutrients is then necessary for prediction of NE content of pig feeds. In fact, this information represents the most limiting factor for predicting energy values of pig feeds.

Table 7: Equations for prediction of net energy in feeds for growing pigs (NEg; MJ/kg dry matter; composition as g per kg of dry matter).

Equation ^a	RSD,%	Source ^b
NEg2a = 0.0113 x DCP + 0.0350 x DEE + 0.0144 x ST + 0.0000 x DCF + 0.0121 x DRes	2.0	1
NEg2b = 0.0121 x DCP + 0.0350 x DEE + 0.0143 x ST + 0.0119 x SU + 0.0086 x DRes	2.4	2
NEg4 = 0.703 x DE - 0.0041 x CP + 0.0066 x EE - 0.0041 x CF + 0.0020 x ST	1.7	1
NEg7 = 0.730 x ME - 0.0028 x CP + 0.0055 x EE - 0.0041 x CF + 0.0015 x ST	1.6	1

^a CF: Crude Fiber, CP: crude protein, EE: ether extract, ST: starch, DCP: digestible CP, DEE: digestible EE, DCF: digestible CF, DRes: digestible residue (i.e., difference between digestible organic matter and other digestible nutrients considered in the equation). The NEg suffix corresponds to the equation number, as given by Noblet et al. (1994).

^b 1: Noblet et al. (1994); 2: Noblet et al. (2004).

INRA-AFZ feeding tables

The INRA-AFZ feeding tables (Sauvant et al., 2004) provide DE, ME and ME values of feeds for pigs as well as digestibility coefficients of major nutrients and organic matter. A lot of effort was put into the estimation of reliable NE values, as it is now agreed that NE content is the best assessment of the "true" energy value for pigs. Two companion articles to the INRA-AFZ tables were produced later on (Noblet et al., 2003; Noblet and Tran, 2004). An Excel spreadsheet has also been produced in order to make available all the equations that were used in the preparation of energy values that are presented in the feeding tables. It must be stressed that the energy values for energy and digestibility coefficients have been obtained only from literature values, thus excluding a "copy/paste" of previous feeding tables. The concepts used originate from studies conducted at INRA over the last 20 years.

Estimation of the energy value of feed ingredients for pigs requires several steps. The first one is the estimation of gross energy (GE); equations are proposed in the tables and in the Excel spreadsheet. In a second step, digestible energy (DE) is calculated as GE multiplied by the apparent faecal digestibility

coefficient for energy (DCe). The energy losses in urine are calculated using the amount of nitrogen excreted in the urine and the losses in the form of gas from degraded cell walls. The metabolizable energy content (ME) is the difference between the DE value and the energy losses in urine and gas. The net energy (NE) value is estimated using the equations proposed by Noblet et al. (1994) that can be applied to both the growing pig and the adult sow. Details on the methods and the calculations for getting the values reported in the tables are given by Noblet et al. (2003; 2004) and Noblet and Tran (2004).

Ingredients presented in the feeding tables have a fixed composition and a corresponding energy value. However, the ingredients composition can be variable in practice, especially for by-products with expected variations in energy values. The basic approach cannot be used routinely for energy evaluation of such feed materials and simplified methods have then been proposed (Noblet et al., 2003; Noblet and Tran, 2004). In brief, for prediction of DE in growing pigs (DEg), prediction equations of GE and DCe have been produced per family of ingredients (Noblet et al., 2003; Noblet and Tran, 2004) and they can be applied for adjusting the DE value according to chemical composition; usually, dietary fiber criteria are used for that correction. For estimating DE in adult pigs (DEs) from DE in growing pigs (DEg), the DEs/DEg ratio cannot be considered as constant when the chemical composition of an ingredient differs from the one in the tables. The following formula:

$$DEs / DEg, \% = 100 + (a / 100) \times (100 - \text{Ash}) \times (100 - b \times DCe) / Deg$$

has been proposed in which "a" represents the amount of additional DE in adult pigs per g of undigestible organic matter in growing pigs (Table 4) and "b" the ratio between organic matter digestibility and energy digestibility. Ash content is in % of dry matter and DCe in %; DEg is expressed in MJ/kg of dry matter. Values of "a" and "b" are listed in the spreadsheet.

The ME/DE ratio of a feed material, for an average catabolism rate of proteins, is assumed to be constant when its chemical composition (nitrogen content) changes within reasonable limits. It is then possible to simplify the estimation of ME content of feed materials by calculating it as DE x (ME/DE). Values for ME/DE of feed materials are listed in the Excel spreadsheet (Noblet and Tran, 2004) or can be obtained from the INRA-AFZ tables per family of ingredients. Like the ME/DE ratio, the NE/ME ratio for a given ingredient does not vary much with the chemical composition. The NE can then be calculated as ME x (NE/ME). Values for NE/ME ratio are listed in the spreadsheet (Noblet and Tran, 2004).

Energy requirements

Energy requirements are expressed on different bases. In ad libitum fed pigs, they mainly consist in fixing the diet energy density according to regulation of feed intake (appetite), growth potential, climatic factors or economical conditions. In restrictively fed growing pigs or in reproductive sows, it is necessary to define feeding scales according to expected performance (dose response approach). Finally, in more sophisticated or more theoretical approaches (factorial approach or modelling approach), it is necessary to determine the components of energy requirements (requirements, growth, milk production, thermoregulation, etc). Whatever the level of approach, most trials and recommendations were conducted according to DE and ME estimates of feeds and conclusions were expressed as DE or ME values. In addition, the recommendations were obtained with rather conventional feeds, i.e. cereals-soybean meal based diets whose efficiency of ME utilization in growing pigs is close to 74%. This latter value also corresponds to the average efficiency obtained over 61 diets by Noblet et al. (1994). The proposal is then to estimate the NE recommendations (diet energy density, daily energy requirements, components of energy requirements, etc.) as DE or ME requirements multiplied by 0.71 or 0.74, respectively. In the case of reproductive sows, the same approach and the same "correction factors" can be used for estimating their NE requirements but with dietary energy values calculated according to NE values estimated for adult pigs. Finally, for factorial approaches, NE for maintenance can be estimated as 750 kJ/kg BW^{0.60} and 320 kJ/kg BW^{0.75} in growing pigs (Noblet et al., 1994; Le Bellego et al., 2001) and reproductive sows (Noblet et al., 1993), respectively. The NE requirement for growth or milk production is equal to the amount of retained or exported energy.

Comparison of energy systems

DE, ME and NE systems

From the equations reported in Tables 2 and 7, it is obvious that the hierarchy between feeds obtained in the DE or ME systems will vary in the NE system according to the specific chemical composition. Since NE represents the best compromise between the feed energy value and energy requirement of the animal, the energy value of protein or fibrous feeds will be overestimated when expressed on a DE (or ME) basis. On the other hand, fat or starch sources are underestimated in a DE system (Noblet et al., 1993). These conclusions are more clearly demonstrated in Table 8 for a series of ingredients: high fat (animal or vegetable fat, oil seeds) or high starch (tapioca, cereals) ingredients are penalized in the DE system while protein rich and/or fiber rich (meals, fibrous by-products) ingredients are favored. For mixed ingredients, the negative effect of protein or fiber (i.e., protein sources) on efficiency of DE or ME for NE is partly counterbalanced by the positive effect of starch or fat (i.e., energy sources).

Table 8: Relative digestible, metabolizable and net energy values of ingredients for growing pigs^a

	DE	ME	NE	NE/ME ^b
Animal fat	243	252	300	90
Tapioca	101	103	110	81
Corn	103	105	112	80
Rapeseed (full-fat)	160	162	168	78
Wheat	101	102	106	78
Barley	94	94	96	77
Diet	100	100	100	75
Pea	101	100	98	73
Soybean (full-fat)	116	113	108	72
Wheat bran	68	67	63	71
Soybean meal	107	102	82	60
Rapeseed meal	84	80	64	60
Amino acids mixture	148	142	146	78

^a Within each system, values are expressed as percentages of the energy value of a diet containing 67.4% wheat, 16% soybean meal, 2.5% fat, 5% wheat bran, 5% peas, 4% minerals and vitamins and 0.10% of HCl-lysine; the so-called amino acids mixture contains 50% HCl-lysine, 25% threonine and 25% methionine. From Sauvant et al. (2004)

^b As %

Net energy systems

As explained above, several equations (and therefore systems) for prediction of NE of feeds are available (Schiemann et al., 1972: NEs; Just, 1982: NE_j; Noblet et al., 1994: NE_g; CVB, 1994: NE_{nl}). The proposal of NRC (1998) cannot really be considered as a system. These systems were established according to different hypotheses and under different experimental conditions. Therefore, different NE systems do not provide interchangeable estimates and the NE value depends on the choice of the system. For comparing these NE systems, the measured NE_g values of 61 diets (Noblet et al., 1994) have been compared to their calculated NEs, NE_j and NE_{nl} values. Comparison with the system proposed by Boisen and Verstegen (1998) was not possible at this stage. If we consider NE_g as the 100 basis, average NEs, NE_j and NE_{nl} are equivalent to about 94, 83 and 96. As explained by Noblet (2000), these average differences are mainly due to differences in estimates of the fasting heat production. However, this ratio also depends on diet composition. It is slightly decreased for NEs and NE_{nl} when dietary starch content is increased, which means that starch sources are underestimated according to these systems. However, both NE_g and NE_{nl} provide relatively consistent energy values. With regard to NE_j, the NE_j/NE_g ratio is decreased when starch and fat levels are increased and increased for higher levels of crude protein or dietary fiber. It can then be considered that the NE_j

system is close to a ME system and it is progressively replaced by new system in Denmark. Finally, recent trials in which NE value of pig diets has been measured in growing pigs (van Milgen et al., 2001; Le Bellego et al., 2001; Noblet et al., 2001; Le Goff et al., 2002) or in adult sows confirm the accuracy of the NEg system since measured NE values and predicted values according to equations presented in Table 7 were similar.

Energy systems and performance

In diet formulation, chemical and ingredient composition of diets for growing-finishing pigs and reproductive sows is manipulated in order to achieve 1) a minimum level of recommended dietary energy and 2) minimum ratios between lysine and energy, and 3) minimum ratios between essential amino acids and lysine (i.e., ideal protein). These criteria are more relevant to the characteristics of the animal (i.e., BW, genotype, physiological stage) or, in other terms, the nutritional requirements. The expression of nutritional values of feeds should be as consistent as possible with the expression of nutrient requirements. From that point of view, the most consistent expression of energy value and energy requirements is theoretically based on NE. In addition, apart from minimizing the cost of diets, an objective such as minimizing heat dissipation (in heat stressed animals, for instance) can be met when formulating on a NE basis. More generally, the quality of a nutritional evaluation system is given by its ability to predict the performance of the animals and independently of the diet composition (or specific effects of nutrients).

The data presented in Tables 9 and 10 illustrate the relationship between energy system and performance and confirm that NE as calculated according to Noblet et al. (1994a; 2004) is a better predictor of performance than DE or ME. In other words, the NE value is a satisfactory estimate of the energy value of feeds. On the other hand, DE or ME systems overestimate the energy value of high CP diets (Table 11) and underestimate the energy value of fat rich diets. In the specific case of low protein diets which are more and more recommended in order to reduce the impact of pig production on the environment (Le Bellego et al., 2002; Table 9), it is clear that their energy value is underestimated when formulated on a DE or ME basis (Table 11). This may explain the tendency of fatter carcasses when low protein diets are formulated on a DE basis: animals are in fact getting more energy than expected from DE supply (Table 9). This also illustrates the importance of formulation criteria for interpreting performance results and the risks of manipulating the composition of diets according to inaccurate or inappropriate nutritional criteria. The use of ileal digestible (or available) amino acids and NE are then highly recommended.

Table 9: Energy requirements of ad libitum fed growing-finishing pigs according to energy evaluation system)^a

	Diet 1	Diet 2
Diet composition, %		
Crude protein	18.8	14.5
Starch	45.9	50.9
Fat	2.5	2.6
Energy intakes, MJ/d		
DE	38.9 ^a	37.3 ^b
ME	37.1 ^a	36.1 ^b
NE	27.6	27.5
Nitrogen excretion, g/kg BW gain	50.2 ^a	30.9 ^b

^a Performance were measured between 30 and 100 kg at a temperature of 22°C; energy intakes are adjusted by covariance analysis for similar BW gain (1080 g/day) and carcass composition at slaughter; diets had the same ratio between digestible lysine and NE (0.85 and 0.70 g/MJ in the growing and finishing periods, respectively) and the ratios between essential amino acids and lysine were above recommended values; diet composition values represent the mean of the growing diet and the finishing diet. Adapted from Le Bellego et al. (2002).

Table 10: Performance of ad libitum fed growing-finishing pigs according to dietary fat supplementation: comparison of energy systems)^a

Fat supplementation, %	Performance		Relative performance		
	0	0	2	4	6
Feed intake, g/d	2200	100	97.3	97.7	94.1
ME intake, MJ/d	29.7	100	100.0	103.3	102.1
NE intake, MJ/d	22.5	100	100.6	104.3	103.6
BW gain, g/d	737	100	100.5	105.7	106.1
Feed to BW gain:					
kg/kg	2.98	100	96.6	92.3	88.9
MJ ME/kg	40.2	100	99.6	97.8	96.5
MJ NE/kg	30.4	100	100.1	98.8	97.9

^a Between 36 and 120 kg BW; in three successive periods; at each period, the protein:energy ratio (Digestible lysine to NE) was the same for all diets; the protein:energy ratio decreased over successive periods. Protein and energy values of diets (corn/soybean meal/choice white grease) were calculated according to Sauvant et al. (2004).

Table 11: Effect of dietary crude protein level on energy utilization (MJ/kg BW^{0.60}) in growing pigs (adapted from Le Bellego et al., 2001b)¹

	Diet 1		Diet 2
Diet composition, %			
Crude protein	17.4		13.9
Starch	45.0		52.2
At the same DE intake			
Heat production	1.415	**	1.374
Retained energy	1.041	**	1.109
At the same ME intake			
Heat production	1.418	**	1.371
Retained energy	1.051	**	1.098
At the same NEg intake			
DE intake	2.594	**	2.528
ME intake	2.488	**	2.452
Heat production	1.421	**	1.368
Retained energy	1.067	-	1.084

¹ In 65 kg pigs; diets had the same ratio between digestible lysine and NE (0.76 g/MJ) and ratios between essential amino acids and lysine were above recommendations for ideal protein (six amino acids were supplemented in diets 2 and 3). Energy balance results were adjusted by covariance analysis. **: P<0.01

Conclusions

In this review, we have demonstrated that energy value of pig feeds density can be measured according to different criteria (DE, ME or NE) and different systems for each criterion. The most advanced and practically applicable energy evaluation system appears the NE system proposed by Noblet et al. (1994) for which energy values of most ingredients used in pig diets are available (Sauvant et al., 2004); complementary methods have been proposed for evaluating any ingredient that differs in terms of chemical composition from those defined in feeding tables. In addition, these authors have proposed energy values that are different for growing and adult pigs. Technological treatment can also affect the energy value. Unfortunately, current information is insufficient to take this systematically into consideration; it should be an area for future research. This review also indicates that the relative energy density or the hierarchy between ingredients depends on the energy system (DE vs. ME vs. NE) with considerable variation between ingredients or compound feeds when either fat or crude protein contents deviates from values in standard diets. This has also consequences on results of

least-cost formulation with tendencies for lower crude protein diets and higher fat contents when changing from DE to ME and to NE systems. From that point of view, using NE instead of DE or ME is a potential technique for attenuating the negative consequences of pig production on environment by reducing the nitrogen waste. Finally, it can be mentioned that measured or estimated DE, ME or NE values of feeds are indicators of the potential energy value of the feed for meeting the energy requirements of the animals that are dependent on a lot of animal or environment factors. The accuracy of the prediction becomes higher when moving from DE to ME and to NE.

Significant improvements in prediction of energy value of pig feeds will come from an improved knowledge of energy and nutrients digestibility, which depends on chemical characteristics of the feed, (bio)technological treatments, animal factors (body weight) and interactions between these factors. Since DF is the main factor of variation of digestive utilization of the diet, more emphasis should be given to routine techniques that identify the nutritional and physiological "quality" and the role of DF. Improving feed evaluation systems will eventually consist in using more mechanistic approaches based on a nutrient supply (i.e., glucose, amino acids, etc.) which are used for meeting requirements for ATP, protein synthesis, and fat synthesis by the animal. Modeling approaches are then essential for describing both digestion of nutrients and metabolic utilization of nutrients. Energy value (expressed as a caloric value) will then become an auxiliary variable of the model.

Summary

Feeds can be attributed different energy values according to, first, the step considered in energy utilization (DE: digestible energy, ME: metabolizable energy and NE: net energy) and, second, the method used for estimation at each step. Some of the most important dietary (chemical composition, technology) and animal (body weight) factors which affect digestive and metabolic utilization of energy in swine are reviewed. Results indicate that energy digestibility of feeds is negatively affected by dietary fiber content but the negative effect is attenuated with body weight increase. This suggests that feeds should be attributed DE values according to pig BW; in practice, at least two different DE values, one for growing-finishing pigs and one for reproductive sows are recommended. The energy digestibility of pig feeds can also be affected by feed processing (pelletting for instance). Metabolic utilization of ME is dependent on diet chemical composition with efficiencies higher for energy from fat (90%) or starch (82%) than from protein or dietary fiber (60%). The hierarchy between feeds is then dependent on the energy system with overestimation of protein rich feeds and underestimation of starch and/or fat rich feeds in the DE or ME systems. The NE system provides an energy value which is the closest to the "true" energy value of a feed; it predicts more accurately the performance of the pigs and allows implementing safely new feeding approaches.

Zusammenfassung

Der Energiewert eines Futters kann unterschiedlich bestimmt werden, erstens nach der Stufe der Energienutzung (DE: verdauliche Energie; ME: metabolische Energie; NE: Nettoenergie) und zweitens nach der Methode, die auf der jeweiligen Stufe angewandt wird. Die wichtigsten Faktoren im Futter (chemische Zusammensetzung, Technologie) und im Tier (Körpergewicht), welche die verdauliche und nutzbare Energie beim Schwein beeinflussen, werden dargestellt. Ergebnisse von Fütterungsversuchen zeigen, dass die verdauliche Energie mit steigendem Rohfaseranteil sinkt, dass dieser Effekt aber mit steigendem Körpergewicht abnimmt. Deshalb wird vorgeschlagen, für die Praxis unterschiedliche DE-Werte für Mastschweine und Sauen zugrunde zu legen. Die verdauliche Energie eines Futters kann auch durch die technologische Behandlung (z.B. Pelletieren) beeinflusst werden. Die Nutzbarkeit von ME hängt von der chemischen Zusammensetzung ab und ist für Fett (90%) und Stärke (82%) höher als für Protein oder Rohfaser (60%). Die Hierarchie verschiedener Futtermittel hängt vom jeweils benutzten Energiesystem ab und tendiert dazu, den Energiewert in proteinreichen Futtermischungen zu überschätzen und in fett- bzw. stärkereichen Mischungen zu unterschätzen. Das NE System kommt dem wahren Energiewert eines Futters am nächsten. Es erlaubt eine genauere Prognose des Wachstums von Mastschweinen und eine entsprechend sichere Futterformulierung.

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New prospects for using rape seed (canola) in layer rations

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Many people driving through Germany or flying into Frankfurt in spring will recognize rape seed (in many countries better known as canola) as beautiful, yellow blooming fields. Increased demand for rape seed oil and attractive prices relative to other crops helped to expand the cultivation considerably, especially in North-Eastern Germany, but in other regions as well. Rape seed meal (RSM) is a by-product of processing rape seed for oil. RSM, however, does not look as pretty as a blooming canola field, it is dark brown and still has a negative image as a potential ingredient for poultry feed since it has been associated with the occasional “fishy flavor” of some brown eggs.

Why should Lohmann Tierzucht, as a primary breeder of brown-egg type laying hens, now take up this subject and consider RSM in layer rations – instead of repeating the well-known warning against RSM in rations for brown-egg layers? Since consumers tend to quit eating eggs whenever they find an egg with “fishy taint”, breeders of laying hens must have a direct interest to minimize this unpleasant experience to happen. Nutritionists know that RSM can cause “fishy taint” in brown-shelled eggs (seldom also in white eggs from breeds such as Brown Leghorns). However, RSM is generally considered as a good component for ruminant feed. Due to the dark color of RSM, its inclusion may not please conservative egg producers who prefer the light color of a maize-soya feed, but we should focus here on questions of egg quality, adequate nutrition and production cost per egg.

Since the early 1980s, before it was recognized that the cause of “fishy taint” was due to the inability of some hens to metabolize trimethylamin (TMA), Lohmann Tierzucht started to screen brown-egg lines for individual hens laying tainted eggs and to eliminate them before reproduction. While RSM was used in pedigreed test flocks to expose this defect, it was recommended not to use RSM in layer feeds for commercial layers. Unfortunately, many years of conventional selection did not solve the problem completely, and eggs with “fishy taint” still occurred – even if the rations were guaranteed without RSM. Therefore, a more fundamental solution was sought, involving the search for a gene causing this defect. After six years of dedicated research (Honkatukia et al., 2005) and application of results in the breeding program, we can now take a second look at RSM as a useful component of layer feed.

If rape seed meal can be included as a source of protein in layer rations, this will help to reduce feed cost per egg and benefit the whole egg industry. All commercial layers of Lohmann and H&N strains hatched after 2006 should be free of the defect, and we expect that other breeders will use these new tools in their selection programs as soon as possible. RSM has been used successfully as a source of protein in feed for white-egg layers for a long time. However, to minimize possible loopholes in feed logistics for small egg producers with white-egg and brown-egg layers and a single feed silo for all flocks, the conservative approach has been not to include RSM in feed for laying hens in general.

With increasing cultivation of rape seed and its use as renewable energy source in Europe, rape seed meal and rape seed cake (cold-pressed rape seed containing oil residue) are also increasingly available as feed components and included in compound feed. Poultry nutritionists in Germany can refer to successful usage of rape seed protein in compound feed for broilers, turkeys, water fowl, growing pullets, as well as white-egg layers. Efforts of plant breeders to reduce unwanted ingredients in rape seed resulted in “00-rape seed” (0-rape seed = free of erucic acid, 00-rape seed = low in glucosinolate).

The limited usage of RSM in layer feed, especially for brown-egg layers, was due to the component sinapin, which may cause “fishy taint” in some eggs. The residual content of glucosinolate (mustard oil) can be reliably analyzed with the techniques of HPLC and will be further reduced by plant breeders.

German feed laws specify upper limits for glucosinolate contents in RSM to be used in compound feed. Rape varieties rich in erucic acid, which may be cultivated for industrial purposes, are not suitable for use in poultry (and pig) feed.

With about 4.5 million hectares, rape is the most important oil plant in Europe and the second most important worldwide, following soy beans. Rape is a highly productive crop in Europe; rape oil is already an important raw material for the manufacture of margarine and is gaining special interest in human nutrition due to its content of Omega-3 fatty acids. The growing demand for human nutrition also contributes to the increase in the cultivation of rape.

In Germany, 10% of the agricultural cropland is currently being used for rape seed, about 70% of which for the production of Bio-diesel as plant oil fuel. In 2005/2006, the cultivation of rape seed expanded by 10% over the previous fiscal year in the state North Rhein-Westphalia, following a trend throughout Germany which leads to an increase in supply of rape seed meal and rape cake as well as an increase in competitiveness in comparison to soy bean meal, which has to be imported from overseas.

As rape cake contains variable and considerable residual oil content, it is necessary to clarify a few issues in this context. Rape seed oil was never suspected of being a cause of egg taint and has been used in the nutrition of laying hens for a long time. As can be seen from the figures in table 1, rape seed oil has a much lower linoleic acid content than soybean oil or sunflower oil, which can be used in phase feeding to control undesirable increase in egg weight in older hens.

Table 1: Fatty acids (in %) in typical fat and oil components

Fatty acid	Animal fat	Kokos fat	Palm oil	Rape-seed oil	Soybean oil	Sun-flower oil	Poultry fat	Bone fat
Laurin C 12 : 0	0-0.2	48	50	-	-	-	-	-
Palmitin C 16 : 0	23-27	9	7	5	8	6	20	19
Stearin C 18 : 0	14-18	2	2	2	4	4	8	16
Oil C 18 : 1	40-60	7	15	51	28	20	37	47
Linoleic C 18 : 2	7-10	1	1	24	53	70	25	8
Linolenic C 18 : 3	0-1	-	-	6	6	-	4	1

How is rape seed protein used in the nutritionist's program to formulate a specific ration for laying hens? At first, a matrix for all available components with their nutrient and energy content is defined as a unique finger print for every raw material which may be used in the manufacture of a batch of feed. In order to obtain a linear optimization, various raw materials would be allowed to compete. The inclusion in a feed mix is subject to a minimum and maximum limit to be fixed and then optimized on the basis of price and nutritional value of all components. This "price value" of a raw material (e.g. RSM) for a particular feed mix is based on (estimated) nutrient content and current market prices (e.g. in Euro per 100kg). The declaration of the "price value" of a raw material, e.g. RSM in layer mash with 11.4 ME MJ/kg, can be completely different from the actual price on the raw material market: a more expensive raw material with higher nutrient content can be relatively "cheaper" in terms of the feed formulation and in turn contribute to lower feed cost per kg egg mass.

Rape seed meal and rape seed cake (RSC) are good protein sources for poultry nutrition due to their high content of methionine, the most important amino acid in poultry feed. The crude fiber content is high compared to other protein sources, resulting in lower energy content, but this can be balanced in the feed mix with higher fat content, in particular oil. A higher crude fiber content is actually desirable in layer rations. The energy in rape seed cake varies, depending on the residual oil content. Therefore, rape seed cake should be regularly tested for crude fat content.

Table 2: Nutrient content of different raw materials (Source: Degussa and WPSA)

	Soybean meal Hypro	Soybean meal Brasil	Rapeseed cake (5.8%)*	Rapeseed meal (2.0%)*	Sunflower meal Argentina	Peas
Crude protein %	47.8	46.7	34.8	34.0	31.4	20.7
Lysine %	2.86	2.83	1.74	1.81	1.11	1.48
Methionine %	0.65	0.60	0.73	0.68	0.69	0.20
Threonine %	1.85	1.79	1.50	1.47	1.16	0.77
Crude fiber %	3.7	6.2	10.5	12.0	22.3	5.3
ME MJ/kg	10.1	9.8	9.3	7.9	6.7	11.3

* Crude fat

To determine the potential advantage of using RSM or RSC, they were included in optimizing theoretical layer rations. Raw material prices used for the calculations corresponded to actual market prices in Germany in August/September 2006. The compound feed contains the following nutrient specifications: 11.4 ME MJ/kg, 17.5% crude protein, 0.40% methionine, max. 7% crude fat, 3.7% calcium and 0.5% phosphorous. The following table 2 illustrates the compounds which are based on a common German feed for layers containing wheat, maize, soya 48 as well as some sunflower meal extract and wheat by-products.

In table 3, the results of optimizing layer rations with a maximum of 5% or 10% RSM or RSC, respectively, are shown. As expected, the proportion of soybean meal goes down with the inclusion of rape products. Sunflower meal extract and wheat by-products are omitted or reduced, as opposed to wheat, which will increase. When RSM is included, fat is slightly increased, whereas fat content is slightly reduced when RSC is included. The remaining raw materials, i.e. lime stone, mineral nutrients and additional additives remain unchanged. It should be mentioned that the appearance of compounds with rape seed products would naturally be darker in color.

Further consequences result from the optimization. Each % soybean meal is replaced by about 1.4% RSM. Since RSM requires more room in the compound, it suppresses other raw materials which are low in energy. The energy level can be balanced by including a little more fat or oil. Further consequences are a somewhat higher crude fiber content and a lower level of potassium due to reduced soybean meal, both of which are considered favorable for layer feed.

For organic feed, RSC is of special interest, because it is not an "extract". As extracts are not allowed in organic feed, RSC offers a new high-quality source of protein, contributing to a balanced compound at reduced cost.

Table 3: Optimized feed mixtures with rape seed products, compared to a control without RSM or RSC

Parts in %	Control	Mixture 2	Mixture 3	Mixture 4	Mixture 5
Rape seed meal	-	5.0	10.0	-	-
Rape seed cake	-	-	-	5.0	10.0
Wheat	34.0	25.2	37.8	34.6	36.6
Maize	19.0	19.0	19.2	18.6	18.2
Soybean meal 48	20.0	18.3	16.1	17.8	15.1
Fat & Oil	4.7	4.8	4.9	4.6	4.5
Sunflower meal	2.0	-	-	-	-
Wheat by-products	9.5	6.9	1.2	8.6	4.8
Minerals, premix	10.8	10.8	10.8	10.8	10.8

The “value for money” and cost reduction potential of rape seed products in layer feed depends on the actual nutrient ingredients of RSM and RSC and the energy content of the feed. The value of rape seed products is negatively related to the desired energy level. The higher the concentrate in nutrient contents of the remaining raw materials of the feed, the more rape seed products can be included in the feed compound. A higher crude fat content “paves the way” for recipes in higher portions, especially that of RSM. The value of rape seed products depends on the relative prices of other sources of protein, e.g. soybean meal. Since soybean meal is still the most important source of protein for vegetarian rations, rape seed protein offers high value for money especially in Northwest Europe. In the examples calculated it leads to a reduction in cost by up to 3% (0.20 – 0.60 Euro/100 kg) for layer feed.

The following maximum content of rape seed products can be recommended as ‘tried and tested’: 0% in chick starter, 5% in chick feed, 7% in pullet feed, 10% in layer feed. The actual level to be included, however, has to take into account the targeted composition of the final feed mix (e.g. content of specified components).

The practical consequence is that feed compounders may include RSM or RSC in poultry feed for brown-egg strains of LTZ and H&N origin from now on. Until the tainted egg problem has been overcome in all other brown-egg strains in a given market, it will be necessary to continue offering feed without rape seed protein, which will expand the range of products and require special diligence in merchandising different types of feed.

As we know, rape seed is not the only possible cause of egg taint; e.g. some sources of added choline have been suspected of contributing to off-flavor. Also, eliminating the identified major gene from poultry populations does not exclude the possibility that other genes may play a role and will force us to address this topic again at some future point in time. While we benefit from one major achievement due to the application of modern genetic tools, we should not forget that the taste of eggs is influenced by feed quality in many ways. Only raw materials of high quality should be used in layer feed to ensure that consumers can enjoy every egg they eat, whether white or brown.

Summary

Rape seed (better known as canola in some countries) is a highly productive crop, produced primarily for its oil content. Canola oil is used in human nutrition for the production of margarine and as a source of renewable energy (bio-diesel). Rape seed meal (RSM) and rape seed cake (RSC) are by-products which may be used as valuable protein source in animal and poultry nutrition. Until recently, their use

in layer feed has been discouraged, because the occasionally observed "fishy taint" of brown eggs may be due to the inclusion of rape seed products in layer feed. This problem has been solved by identifying the gene which is responsible for the inability of some hens to metabolize trimethylamin (TMA). Lohmann Tierzucht announced that all commercial day-old chicks of Lohmann and H&N origin hatching from January 2007 are free of the genetic defect and can therefore be fed with rations containing rape seed products.

Examples for optimized layer feed including RSM or RSC are given. Rape seed protein has a favorable amino acid profile, with significantly higher methionin level than soybean meal. This makes protein from rape seed especially attractive for organic feed, which is not allowed to contain synthetic amino acids.

Based on actual ingredient prices in Germany in August/September 2006, the cost of compound feed for layers can be reduced by up to 3% (0,20 – 0,60 Euro/100 kg). This shows the high value for money of rape protein and is of great interest in competition with soybean meal, which is still the main protein source in layer feed.

Based on our experience under commercial conditions, we recommend the following levels of RSM in compound feed as safe for efficient production: chick starter 0%, chick mash 5%, pullet developer 7%, layer mash 10%. The optimal level has to be determined on the basis of current prices for all raw materials, in order to maximize egg income over feed cost without compromising egg quality.

Zusammenfassung

Raps ist eine ertragsstarke Feldfrucht. Mit steigendem Anbau für Rapsölproduktion fallen Rapsextraktionsschrot und Rapskuchen in zunehmendem Umfang als Rohstoff für die Tiernahrung an. In der Legehennenfütterung wurden diese kaum genutzt, seitdem ein Zusammenhang zwischen Raps im Futter und dem Auftreten „fischigen“ Geruchs bei Eiern bekannt ist. Die Ursache des „fischigen“ Geruchs ist ein Enzymdefekt einzelner Hennen, die Trimethylamin (TMA) nicht abbauen können. In Zusammenarbeit mit anderen Forschungseinrichtungen ist es der Lohmann Tierzucht gelungen, das Gen für diesen Enzymdefekt zu identifizieren und das Problem durch konsequente züchterische Maßnahmen zu lösen. Mit Beginn des Jahres 2007 können nicht nur Weiße Leghorn, sondern auch braune Legehennen der Herkünfte Lohmann und H&N mit rapshaltigen Rationen gefüttert werden.

Als Optimierungsbeispiele werden Veränderungen von Legehennenfutter bei Einsatz von Rapsschrot (RSM) bzw. Rapskuchen (RSC) dargestellt. Rapsprotein hat für die Legehennenfütterung ein günstiges Aminosäuremuster mit deutlich höherem Methioningehalt im Rohprotein als Sojaschrot. Dies macht Rapsprotein für die Biofütterung besonders attraktiv, da im Biofutter keine synthetischen Aminosäuren eingesetzt werden dürfen.

Auf Basis aktueller Rohstoffpreise im Zeitraum August/September 2006 in Deutschland reduzieren sich die Kosten eines Standardlegehennenfutters um bis zu ca. 3% (0,20 – 0,60 Euro/100 kg). Dies zeigt die hohe Preiswürdigkeit von Rapsprotein, besonders vor dem Hintergrund, dass Sojaschrot nach wie vor die wichtigste Proteinquelle im Legehennenfutter ist.

Auf der Basis von Praxiserfahrungen können folgende maximalen Einsatzraten von Rapsprotein als unbedenklich empfohlen werden: Kükenstarter 0%, Kükenaufzuchtfutter 5%, Junghennenfutter 7%, Legehennenfutter 10%.

Die exakten Einsatzraten sind im Einzelfall auf Basis einer Optimierung und den Rahmenbedingungen zu erarbeiten, um den bestmöglichen Nutzen hinsichtlich einer Kostenreduzierung bei Absicherung der Eiqualität zu erzielen.

Folien aus einem Vortrag des Autors (Pottgüter, 2006) stehen im Internet.

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Towards the Genetic Improvement of Bone Quality in Laying Hens

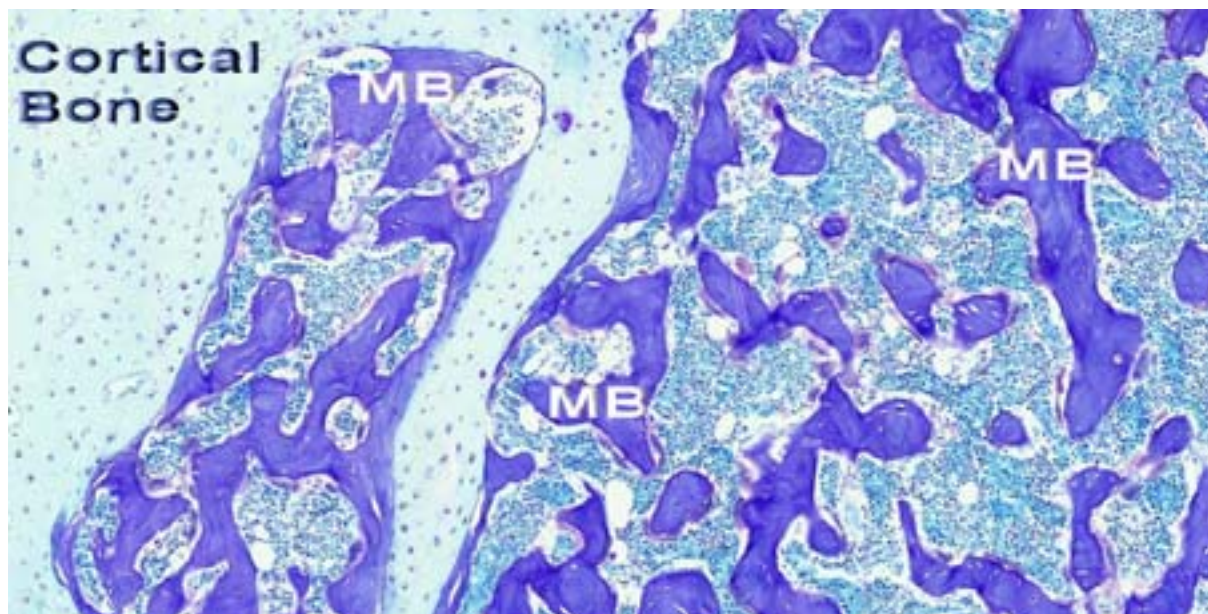
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Introduction

Most poultry workers are well aware of the fragility of bones in end-of-lay hens. The chances of bone fractures occurring in modern hybrids of laying hens are high during their lifetime and extremely high at depopulation. Although this fragility was first identified by COUCH (1955), recent surveys reveal that the problem persists (VAN NIEKERK et al., 1994; BUDGELL and SILVERSIDES, 2004). This skeletal fragility is due largely to loss of structural bone mass throughout the life of the hen, leading to osteoporotic fractures.

Laying hen bones, however, are not like those of mammals; hen long bone marrow cavities contain a woven bone type known as medullary bone (MB). At sexual maturity, hens deposit this bone type as a temporary store of calcium for eggshell formation. At night, when the bird is not taking in dietary calcium, this MB can be utilised as a calcium source. Unfortunately, the increased number of large bone-resorbing cells (osteoclasts) responsible for releasing calcium from the non-structural MB will not discriminate between bone types and structural bone is also lost (see Figure 1). During the laying period, only MB is formed and the missing structural bone is not replaced, leading to increased risk of bone breakage.

Figure 1: Osteoclasts (pink, multinucleated cells) mainly found on medullary bone (MB) during the laying period. Cortical bone (to the left) has also been hollowed out by these cells but the only form of replacement bone formed during lay is MB, weaker in structural terms than cortical bone.



Shortly after it was first identified, it was thought that osteoporosis in hens (also termed Cage Layer Fatigue) must have a genetic component (FRANCIS, 1957). Until very recently, however, research seems to have concentrated upon nutritional and husbandry approaches.

Investigations of osteoporosis in laying hens at Roslin Institute and elsewhere have revealed that good nutrition has a role to play and that adequate levels of Ca, P and Vitamin D are important. However, whilst poor nutrition can exacerbate bone problems, there are very few dietary solutions aside from slight “tweaking” of diets with vitamin K and changing the form of dietary calcium (FLEMING et al., 1998, 2003). The latter is effective because calcium given as either particulate limestone or oystershell can be slowly released overnight, preventing excessive resorption from bone surfaces.

In human bone biology research shows that activity can prevent bone loss through functional loading of the skeleton. When this loading element is removed (as in space flight or prolonged bed rest) bone loss inevitably follows through increased resorption. In hens the introduction of the battery cage and the first reports of severe osteoporosis in the same period were unlikely coincidences. Many researchers have shown that husbandry systems allowing increased activity are beneficial for bone strength (KNOWLES and BROOM, 1990, FLEMING et al., 1994, KEUTGEN et al., 1999). However, there are also disadvantages to the introduction of these systems; apart from the increased chances of pecking and parasitism, the birds often have the chance to fly around, collide and crash-land. Paradoxically the risk of bone fracture is increased in these systems and we should be careful to choose the appropriate hen to stock them with.

Aims

It seemed that most modern hybrid laying hens suffered some degree of bone weakness, particularly towards the end-of-lay. We had to ask ourselves, is there an appropriate hen of sufficient productivity to stock alternative husbandry systems with? HOCKING et al. (2003) demonstrated large genetic variation in bone strength between selected and traditional breeds of laying hen. If we stocked these systems with traditional breeds, certainly they would be less likely to sustain fractures, but production would suffer. In studies of the effects of nutrition and environment on bone strength at Roslin, we noted that there were generally inverse relationships between eggshell and bone quality but there were some birds that did not conform to this relationship; they were productive with good eggs and strong bones. We were therefore hopeful that we could select for bone traits without detriment to production and this was the background to our selection approach for skeletal improvement in layers.

Methods

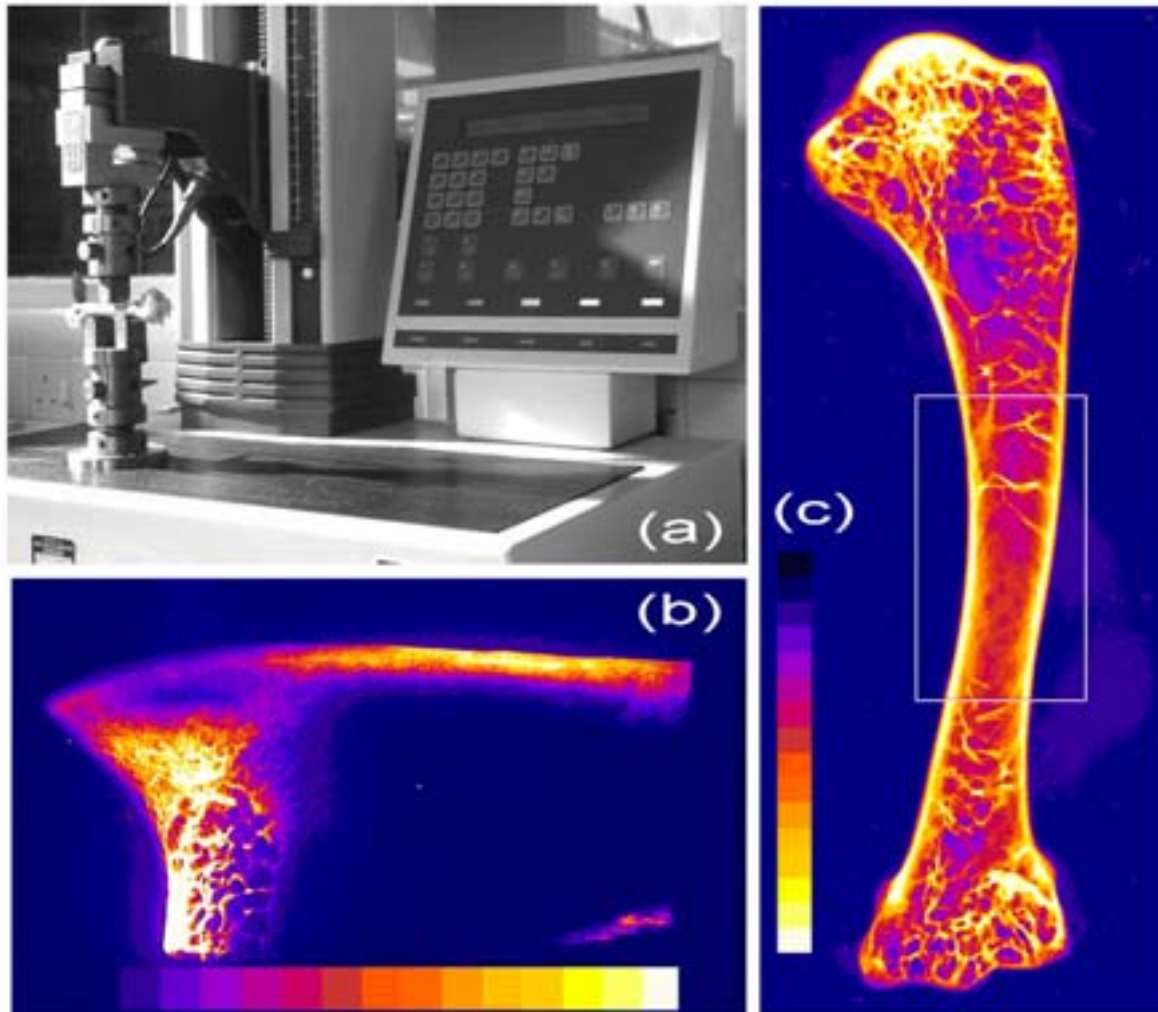
Heritability estimates and segregation of two lines

In 1994, funded partly by the EC and Defra (then MAFF) we began a quantitative selection study initiated by Colin Whitehead (Roslin) and involving groups at Roslin Institute (Steve Bishop, Bob Fleming, Heather McCormack and Lynn McTeir), Lohmann Tierzucht (Dietmar K. Flock and, latterly, Rudolf Preisinger and Matthias Schmutz). For the first 3 years the project also involved ID-DLO Netherlands (Thea Fiks-van Niekerk).

The study began by investigating several post-mortem bone traits in a commercial pure line of Lohmann LSL layers previously selected for high egg production. Figure 2 outlines some measurement methodologies. All bone measurements were made on generation 1 (G1) and G2 hens. Of these measurements, tibia strength (TSTR), humeral strength (HSTR) and keel radiographic density (KRD) were identified as 3 biologically meaningful traits with moderate to high heritabilities.

From G3 onwards, selection was performed retrospectively each year; all birds were hatched from all available hens and selection decisions were made according to the measured post mortem bone characteristics, with entire full sib families being kept or rejected on this basis. A restricted selection index was then devised to improve bone characteristics, using standard selection index theory (CAMERON, 1997). This “Bone Index” (BI) included body weight (BW) - to be held constant - as we did not want to select for heavier birds (body weight and bone strength are known to be strongly related).

Figure 2: Representation of the methodologies used to assess bone quality. (a) 3-point bending test to determine breaking strength of tibiotarsus and humerus, (b) and (c) false colour interpretations of radiographs of keel and humerus respectively, used to determine radiographic density by computerised methods (In the analysis of bone index, humerus radiographic density was not used).



The Index appeared thus:

$$BI = 0.27 \times KRD_s + 0.37 \times HSTR_s + 0.61 \times TSTR_s - 0.35 \times BW_s$$

(where subscript_s indicates that the trait has been standardised to have a standard deviation of 1.0 and a mean of 0.0)

Without initial information on sires, selection began in G3 by assigning birds to High (H) or Low (L) BI line on the basis of their dam's BI value in G2. Common sires were used at this stage. In subsequent generations, sires were used only within the line they were born. Genetic parameters such as heritabilities and genetic and phenotypic correlations between traits were estimated using REML techniques (GILMOUR et al., 1996).

QTL study

Following the establishment of the 2 divergent BI lines, the project continued with the study of quantitative trait loci (QTL) using these 2 lines to locate a potential gene or genes responsible for bone quality. The 2 lines were crossed to eventually produce an F2 reciprocal cross. Twenty five females

and ten males per line were used to produce F1 birds. Retrospective selection was carried out on the basis of post mortem analysis of the parent bones to identify four families whose parents showed the most extreme bone indices. Two males and eight females from each F1 family were selected based on fertility for males and egg production for females. Each male was mated to two females from each of the other families, resulting in 32 families producing F2 birds.

The F2 birds were hatched in nine batches. Female offspring from families were retained for analysis. DNA was collected from F0 and F1 parents, and F2 progeny. At 60 weeks of age, birds from families where there were at least 20 hens were killed and bone characteristics were assessed to allow calculation of bone index for each bird.

Hens laying less than 230 eggs were omitted in the final analysis because periods of non-laying allow structural bone to be deposited. After parentage checking and genotyping edits 372 hens were available for analysis. The QTL mapping method of HALEY et al. (1994) was implemented using QTL Express software (SEATON et al., 2002). Experiment wide significance thresholds using all genotypes were estimated using 1000 iterations and were 8.1 for P=0.05 and 9.8 for p=0.01.

Results

Heritabilities and segregation of Lines

Heritabilities of the traits included in the Bone Index, and for the Index itself, for all measurements from birds up to G5 are shown in Table 1. All traits were moderately to highly heritable. Genotypic and phenotypic correlations are also shown in Table 1.

Table 1: Heritabilities (in bold), phenotypic (above diagonal) and genetic correlations (below diagonal) calculated from all birds (n=1306) up to G5 (from Bishop et al., 2000)

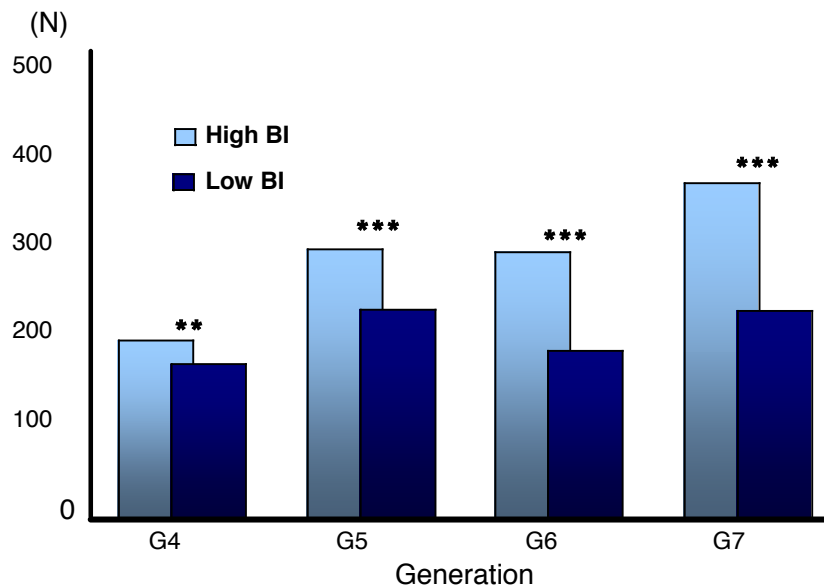
	BW	KRD	HSTR	TSTR	BI
BW	0.49	0.28	0.21	0.29	-0.10
KRD	0.36	0.39	0.33	0.51	0.58
HSTR	0.26	0.49	0.30	0.50	0.66
TSTR	0.33	0.66	0.77	0.45	0.81
BI	-0.12	0.67	0.76	0.84	0.40

The response to selection for all traits up to G5 was rapid, and is well documented by BISHOP et al. (2000). For the most highly heritable trait (breaking strength of the tibiotarsus) selection response has been monitored up to G7 and is shown in Figure 3.

Following G7, selection pressure for bone characteristics was relaxed and birds were crossed randomly within each line. The lines have been monitored since and an almost two-fold difference in tibia strength still exists, with no difference in body weight. In the H line, keel deformities were reduced in G4, G5 and G6, and eliminated completely in G7 hens (FLEMING et al., 2004). This is of particular relevance to the use of alternative husbandry systems.

A recent study of genetic, nutritional and environmental effects utilising these lines demonstrated that nutrition and husbandry improvements in G9 birds from both the H and L lines were simply additive (FLEMING et al., in press, 2006). In this study there were no detrimental effects on egg production or shell quality in H line hens compared to L line hens, suggesting that we have been successful in selecting hens with improved bone status without affecting eggshell quality and production. The mechanisms behind the differences appear to be due to (i) an increase in peak bone mass prior to

Figure 3: Selection for Bone Index (BI) Response in tibia strength (N)

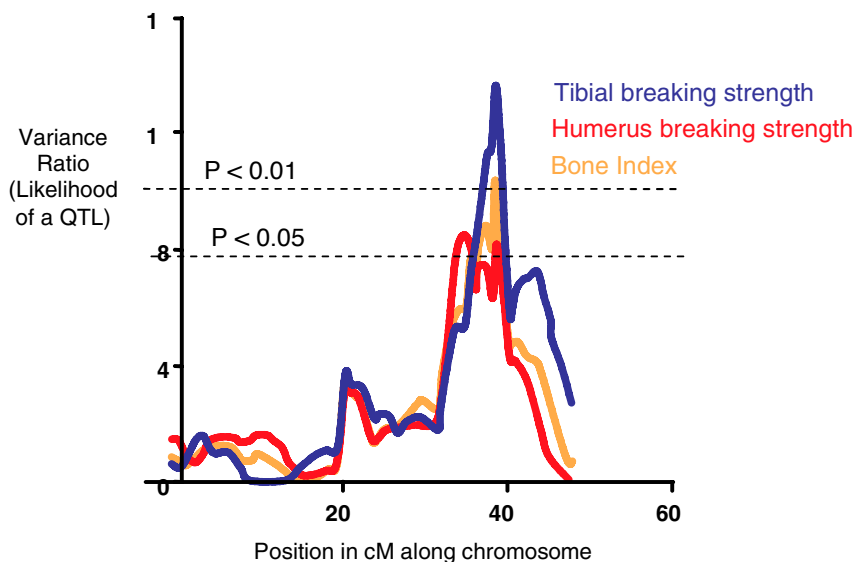


lay in the H line and (ii) a reduced number of active osteoclasts in the H line during lay, leading to less overall bone resorption. There also appear to be some qualitative differences in bone collagen structure (SPARKE et al., 2002). The lines were still well segregated, and base populations of each line remain at Wursterheide Farm for future research.

QTL analyses

A detailed account of the QTL investigation is provided by DUNN et al. (in press, 2007). The evidence for a QTL affecting bone index on chromosome 1 (see Figure 4) was strong ($P < 0.05$). This region also contained significant QTL for humeral and tibiotarsal breaking strength.

Figure 4: Interval mapping of QTL on chromosome 1 (from Dunn et al., 2007 - in press)



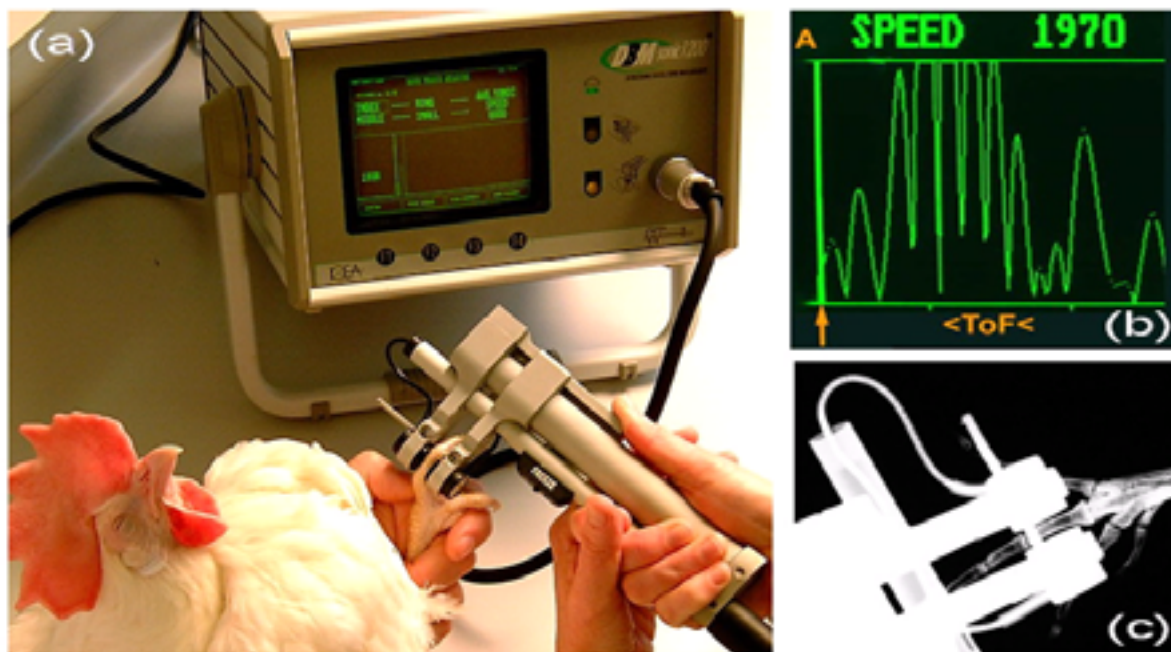
The QTL region on chromosome 1 at 370 cM (198 to 393 CM interval) accounted for a large proportion of the difference between the founder strains for tibiotarsal (18%) and humeral breaking strength (27%) and the bone index. There was also some indication that this QTL has a correlated effect on egg shell strength at 60 weeks of age as evidenced by a non-significant QTL at 366 cM on chromosome 1.

Further Studies

For further molecular genetic studies we hope to make use of material from the previous QTL study, and also new material from the selected lines and other commercial pedigree populations of laying hens. The primary objective will be to identify single nucleotide polymorphism (SNP) marker(s) that could be used in practical selection for improved bone quality traits in laying hens.

The phenotypic analyses so far have been based on post mortem measurements. Obviously, this is not ideal and we have been developing the application of ultrasound measurements on hen toe bones as a means of predicting bone quality (see Figure 5). Previous studies utilising ultrasound have revealed that the measurement is a moderately heritable trait and is related to our existing post-mortem bone measurements (FLEMING et al., 2004). In the proposed studies, ultrasound measurements will be assessed further.

Figure 5: The use of Amplitude dependent Speed-of-Sound (Ad-SoS) technology to determine bone quality in the laying hen toe. (a) In live, conscious hens, the probe and detector are applied to the 3rd tarsal; (b) output trace showing the “time-of-flight” principle – the more bone there is, and the more “connected” it is, and the faster and stronger the trace is. The mean velocity (in ms-1) is displayed for the small bone peaks furthest to the left of the trace; (c) radiograph showing probe position.



The specific objectives of our further studies are:

- A To establish a panel of SNP markers which segregate with the bone index trait in the F2 population
The QTL will be fine mapped to give a density of around 1 SNP marker per cM. Markers will be derived from databases and genotyped using Affymetrix targeted genotyping platform.

- B** To determine segregation of SNP markers with the bone index trait in the founder line of the H and L lines
The selected SNP markers will be genotyped in 2000 birds of the current generation of the founder line (a White Leghorn-type bird) of the H and L lines to confirm that the QTL is still segregating. The birds will also be phenotyped for tibia strength. The markers or combinations of the markers (haplotypes) that segregate with the bone trait will then be defined.
- C** To test the universality of the results in three pedigree lines of laying hens.
To determine whether the markers identified in Objectives A and B are also valid in other populations, three lines of pedigree Lohmann laying hens will be tested.
- D** To test the relevance of markers in line of commercial hens
1000 end-of-lay hens will be assessed for bone quality by ultrasound. 200 hens in each of the high and low bone quality categories will be taken for genotyping and tibia strength measurement.

Summary

The chances of bone fractures occurring in modern hybrid laying hens are high during their lifetime and extremely high at depopulation. This skeletal fragility is due largely to loss of structural bone mass throughout the life of the hen, leading to osteoporotic fractures.

While investigations of osteoporosis in laying hens at Roslin Institute and elsewhere revealed that good nutrition and exercise in alternative housing systems are helpful in minimizing the incidence of bone fractures, interest in genetic differences continues.

In a cooperative research project, Roslin Institute and Lohmann Tierzucht developed two White Leghorn lines with low and high incidence of osteoporosis, respectively. This article reports on cumulative differences between these two lines and consequences for future breeding approaches to reduce this problem in laying hens.

Tibia strength (TSTR), humeral strength (HSTR) and keel radiographic density (KRD) were identified as biologically meaningful traits with moderate to high heritabilities. Negative correlations between bone strength and shell strength, found in preliminary analyses, are apparently not serious enough to preclude improved bone strength while maintaining adequate shell quality.

Zusammenfassung

Bei modernen Legehybriden steigt im Laufe der üblichen Nutzungsdauer die Gefahr von Knochenbrüchen und ist vor allem beim Verladen von Schlachthennen ein tierschutzrelevantes Problem. Die Bruchanfälligkeit der Knochen hängt mit dem Abbau von strukturierter Knochenmasse bei der Eischalenbildung zusammen, was dann zu osteoporotischen Brüchen führen kann.

Die meisten Untersuchungen zu diesem Thema haben sich mit optimaler Fütterung und Haltung beschäftigt, genetische Unterschiede in der Anfälligkeit gegen Knochenbrüche sind für nachhaltige Verbesserungen von besonderem Interesse.

In Zusammenarbeit zwischen dem Roslin Institute und der Lohmann Tierzucht wurden zwei Versuchslinien der Rasse Weiße Leghorn mit hoher Legeleistung und niedriger bzw. hoher Anfälligkeit gegen Knochenbrüche entwickelt. In dieser Arbeit werden genetische Parameter und der kumulative Selektionsfortschritt dargestellt und Möglichkeiten für weitere züchterische Maßnahmen vorgestellt.

Die Bruchfestigkeit von Tibia (TSTR) und Humerus (HSTR) sowie Dichte des Brustbeins (KRD) wurden als drei biologisch sinnvolle Merkmale mit mittlerer Heritabilität ermittelt, aus denen ein Knochenindex (BI) als Selektionsmerkmal berechnet werden kann. Die in ersten Untersuchungen festgestellte negative Korrelation zwischen Knochenstärke und Schalenstabilität ist offenbar keine unüberwindliche Hürde; bessere Knochenstabilität lässt sich auch ohne Verlust an Schalenqualität erreichen.

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