Demand Driven Productivity in the Egg Business: Combining Advances in Genetics, Health Control and Nutrition to Meet Changing Consumer Preferences

Abstract
Since seven decades, poultry meat and egg consumption in many countries has been accelerating at a faster rate than global population growth. In this review, we will focus on key contributions of applied science and technology which explain the efficiency of today’s production: the change from hatch seasons and egg production in open houses to hatching throughout the year and egg production in environment-controlled houses to supply fresh eggs for urban consumers on demand. Initially, simple mass selection was applied to maximize juvenile growth rate, feed efficiency and carcass value in meat-type chickens, while heterosis effects were exploited to maximize egg production, feed efficiency and egg quality in egg-type chickens. A small number of primary poultry breeders continue to improve the genetic potential for efficient production of poultry meat and eggs and supply licensed hatcheries in many countries with parent stock to multiply the improved efficiency. Electronic data management is used to optimize logistics and the flow of information in a global network of production and marketing. Results of research in poultry pathology are applied to control poultry diseases more effectively, based on diagnostics, eradication and prophylactic vaccination. Modern poultry nutrition is based on least cost feed formulation for individual flocks to minimize feed cost per egg in layer stock, and to minimize feed cost per unit of meat produced in broilers, making best possible use of locally available resources, while minimizing the environmental impact of production.

Introduction
Some developments in our life are easier to understand if we look at them in terms of evolution. Since Darwin shocked the
establishment of his time with his theory of the descent of man, many excellent books have been published on evolution to confirm that evolution is not only the most plausible explanation for past developments, but a continuing process (Weiner, 1994). The same principle holds not only for all species of plants and animals (including man), but also for ecosystems, human societies, ideas and technical inventions: every mutation or invention has to be “better” than previous models to compete successfully against tradition and the establishment.

Evidence for the domestication of chickens has been reported from China as early as 6000 B.C. Initially, people probably enjoyed seeing chickens near their dwellings and attracted them with some feed or left-over food. Shelter and defense against predators was not yet essential as long as they could find an elevated place to roost at night. In the spring, as the days grew longer and warmer, each hen would produce a “clutch” of eggs. She would then become broody and set on them. Three weeks later the chicks would hatch. If people (or other predators) found and consumed the eggs before the chicks hatched, the hen would try to find a better hiding place and lay another clutch of eggs, until the end of the season. Centuries later, people noticed that hens continue to lay eggs in the same nest, as long as one or more eggs are left. Apparently birds can “count” and try to lay a typical number of eggs before they go broody.

We will never know for sure, whether people started to eat eggs before chicken meat, but they must have known that the sex ratio at hatch is about 1:1, and if too many males survive to sexual maturity, they will start to fight and kill each other, until only the most dominant is left. Thus, the practice of growing about 90 percent of the males for human food slowly developed over time. The next step was to develop management procedures to discourage broodiness, and to hatch large numbers of chicks in hatcheries with controlled temperature and humidity. Initially the males were generally raised and sold for human meat consumption, and the females were kept to produce eggs for human consumption. When egg production dwindled to a point where the hens were no longer profitable, they were also slaughtered for food production.

As documented in recent FAO Statistics, chickens in recent years have become the most successful domesticated animal species in terms of the numbers of animals grown (25 billion), as well as in terms of their contribution to human nutrition (67.3 million tons of eggs/yr and 107.5 million tons of poultry meat/yr). These production figures may serve as a reference for governments and NGOs concerned about adequate human nutrition of people currently suffering from starvation or malnutrition. The main obstacles to increased poultry consumption are: (1) traditions and limited purchasing power in developing countries; (2) lack of information on the nutritional value of poultry meat and eggs, compared to other sources of food; (3) objection to products from intensive animal farming by consumers who associate low food prices with poor animal welfare and excessive use of antibiotics. This review will try to explain key factors which have contributed to and accelerated the development of today’s efficient poultry industry.

How broiler breeding started on the East Coast of the USA

For many years, chickens were kept primarily in small flocks to assure self-sufficiency for eggs and chicken meat for the family who owned them, and possibly for a small local market. With increasing urbanization of societies, some farmers began specializing in egg production, others in hatching chicks and selling ready-to-lay pullets, and flock size tended to increase when eggs could be sold at an attractive price. During the 19th and early 20th centuries, poultry organizations were founded to promote information on the husbandry and production of poultry meat and eggs as a means of increasing farm income. During the late 1800s and early 1900s, Poultry departments were established at agricultural schools, colleges and universities, often combining research with teaching and outreach or extension programs.

The USA became the leading country in efficient poultry production, based on novel research and the application of theory to practice. Initially, some breeds were placed under a program, called the Registry of Production (ROP) that utilized individual bird production records obtained by trap-nesting. ROP breeders then selected the best performing individuals from their trap-nest records to reproduce the next generation. ROP breeders (like poultry breeders in Europe) were also required to follow breed standards that required that any birds used for breeding had to be totally free of any defects such as crooked toes, cross-beaks, the wrong color of earlobes, the wrong color of the shanks, feathers on the shanks, etc., all of which caused some potentially very promising breeders to be discarded rather than kept to improve the breed’s productivity. Selection for phenotype did not increase productivity significantly. Thus, progress on improving the productivity of a breed under that system was extremely slow, and when they were making
their selections they were not taking into account negative genetic correlations between some of the important traits, such as egg production, egg size and shell quality. For example, improvement in egg number generally resulted in hens that produced smaller eggs.

During the 1940s, Jay L. Lush, I.M. Lerner and a number of their students developed statistical approaches to animal breeding. Those statistical systems, combined with the development of computers that could quickly analyze thousands of records moved the science of animal breeding forward, and the poultry industry responded with the development of a number of major poultry breeding organizations. Kimber Farms in Niles, California, was the first to hire trained geneticists to develop and run their commercial breeding programs. Initially those programs concentrated on finding the best strains of white egg or brown egg chicks, and the breeding stock for those “pure” strains were then selected by utilizing the heritability for each trait, the genetic correlations among the traits, and the economic value of each trait to improve all of the most economically important traits simultaneously.

It was not until 1947, when the Heterosis Conference was held at Iowa State University in Ames, Iowa, USA, that crossbreeding came into the limelight. Some of the breeding companies took the information from that conference to begin breeding programs to utilize the improved performance of strain crosses. As the authors learned during their training at Heisdorf & Nelson Farms, Art Heisdorf was among the participants of the Conference in Ames, and he became fascinated by a paper on recurrent reciprocal selection (RRS), which was subsequently published by Comstock et al. (1950). The theory convinced him to introduce RRS in his White Leghorn lines. Results presented at the European Poultry Conference in Hamburg (Flock, 1980) indicated that the reciprocal crosses exceeded the average of the parent lines by 20% in hen-housed egg production, while the F2 and back-cross combinations were intermediate, as expected from theory. Today, all commercial egg-type chickens are crosses between two or more lines, and they are vastly superior to the strains that were used in the first half of the 20th century.

For a number of reasons, modern meat type chickens have a somewhat different history than do egg type chickens. The primary trait was body weight or juvenile growth rate. Other important traits such as feed conversion, and breast shape and size were generally improved by selecting for body weight. Body weight at a given age was highly heritable, so one could simply choose the fastest growing males and females for reproducing the line. Thus simple mass selection was initially used to improve most of the meat lines.

Initially, males from some of the brown-egg breeds were used for meat production, because those breeds were heavier and faster growing than the white egg breeds. Several breeders from the New England area of the USA rapidly became the suppliers of brown feathered meat-type chickens. Nichols Poultry in New Hampshire had nearly 90 percent of the meat bird market from the mid-1950s to the early 1960s. Most of the brown-egg breeds also had brown feathers, and some of the brown pigment stayed in the skin when the feathers were removed. Because of that, the whole dressed birds that were being sold were not very attractive. Therefore, during the 1950s, geneticists began developing synthetic breeds that carried the dominant white feather gene which produced pure white feathers and a much nicer appearing carcass for the meat-type breeds. Eventually, the broiler market also moved toward the use of dominant white female line breeders and Cornish dominant white male breeders. The Cornish lines produced broader breasted and faster growing birds that were very attractive to consumers. These white feathered meat-type breeds rapidly replaced all of the brown-feathered breeds during the late 1960s.

Reducing the number of days to reach market weight (3 lbs or 1350 grams) was simple and effective with mass selection. All birds were individually weighed and graded for body conformation, the heaviest males and females retained to reproduce the next generation, and the majority sold as broilers. Broiler growth rate has a high heritability, and mass selection reduced age at market weight by one day per year. In subsequent years, primary broiler breeders invested more into their breeding programs: large numbers of fully pedigreed chicks were reared to estimate heritabilities and genetic correlations, and family information was used to estimate breeding values more accurately. Eventually specialized male and female lines were selected on different selection indices to combine divergent traits in the best possible cross.

When negative genetic correlations between juvenile growth rate and reproductive efficiency became a limiting factor for further progress, specialized sire and dam lines were selected for different performance profiles, combining acceptable egg production of the female parent with maximum growth rate and carcass value of the male parent. During the 1970s the broiler breeding industry had to respond to three different customers: hatchery managers wanted to get as many day-old chicks as
possible out of the parent flocks, at least 140 within 40 weeks of production; processing plant managers wanted uniform body weight and the highest possible breast meat yield; and broiler growers wanted rapid weight gain, efficient feed conversion and minimal mortality. Instead of trying to combine all these goals in one superior cross, breeding companies started to developed different “models” simultaneously. Results of cumulative selection have been documented by Havenstein (2006), details of modern broiler breeding by Laughlin (2007) in Lohmann Information.

How modern breeding of laying hens started in California

Before broilers were “invented” as a more attractive source of poultry meat, it was common to grow cockerels from dual purpose breeds for meat, killing them at an age when they reached a desirable weight. Separating male and female chicks at hatch (chick sexing) became important when interest focused on pullets for egg production, while cockerels became “by-products”, which no longer could recover the feed cost if grown for meat.

Meanwhile, Mendel’s Laws of inheritance had been rediscovered, and geneticists at the University of California used the experimental White Leghorn flock of the Poultry Science Department to demonstrate in a series of selection experiments that egg production can be improved by selection. Egg production was a perfect example to teach students decision making when applying quantitative genetic theory for breed improvement: the major trait to be improved was full-year egg production, which could be measured only in females and required trap-nesting for many months; progeny-testing of males would require pedigree matings and extend the generation interval; egg production of the hens would be affected by broodiness, winter pauses and mortality; disease risks and variable feed quality affected egg production and made comparisons across years difficult. Despite these difficulties, the selection experiment at the University of California (Fig. 1) produced convincing results (Lerner and Hazel, 1947), and poultry companies invested in large-scale breeding programs to benefit from the growing demand for eggs.

From seasonal to year-round supply of eggs

In North America and Europe, egg production used to be more or less seasonal: chicks would hatch in spring, pullets start to lay 5-6 months after hatch, and winter pauses of variable length and intensity resulted in shortage of eggs and correspondingly high egg prices. Producing more eggs around Christmas time was highly desirable. To extend the availability of eggs to full-year, egg producers started to introduce lighting programs and placed flocks twice a year, making double use of their rearing facilities. With unlimited availability and less fluctuation in egg prices, people bought eggs more regularly and included them in their diet as a convenient and attractive part of their diet year round. Research into the mechanisms of light stimulation and the response of chickens to increasing, constant and decreasing day length and light intensity led to the development of specific recommendations for lighting programs to optimize onset of lay and persistent egg production.

From eggs “as laid” on the farm to graded eggs and egg products

Modern consumers like “one-stop-shopping,” and they buy eggs increasingly from discounters. Discounters try to maximize their profit with a strategy of buying a large volume of eggs from a few suppliers at the lowest possible price. They then optimize logistics to keep all outlets supplied with quality eggs at amazingly low prices. Consumers asking how eggs can be produced so cheap without compromising hen welfare and/or egg quality are surprised if they are told that egg producers seldom get more than half of the retail price – unless they invest additional time to sell a small volume on the open market. Discounters also like “one-stop-
shopping" when they load their big trucks at packing stations.

Getting eggs efficiently from the farm to the consumer is a logistic challenge, including the collection, grading and stamping of each egg to identify the country, production system (cage, barn, free range, organic) and a farm code. Most shell eggs are sold in the intermediate weight range, for example grades M (53-63 g) and L (63-73 g) in EU countries. At the beginning of the laying period, most pullets start with an egg weight below 53 g, and egg size increases with age and toward the end of the laying period the shell quality of those XL eggs tends to become a problem.

Eggs that are outside of the “marketable” weight range are generally sold to breaking plants, along with stained eggs and eggs with shell defects, but they generally will not recover their feed cost. Breaking plants are a special part of the egg industry, focused on growing demands by the food processing industry, e.g. bakeries, restaurants, food service units, etc. Some modern breaking plants are connected directly to large egg production units that process eggs from millions of laying hens “online”. Countries like Brazil, with relatively low energy prices, use the egg breaking industry to their advantage to increase their share of the world market for dried egg products, whereas the trade of shell eggs depends more on regional feed prices and differences in poultry welfare requirements.

**Risk management with contributions from avian research**

The growing demand for eggs and poultry meat encourages investment in large units with labor-saving equipment, but the expected return on investment does not always materialize. In a free market, egg prices drop below production cost, if production exceeds demand. The industry may try to get help from the government, e.g. in the form of subsidies for export, but if diseases threaten the industry, avian veterinarians and producers have to join forces to utilize the latest scientific information to safeguard the industry in practice.

Major problems for both the poultry breeding industry and for commercial egg producers in California included respiratory diseases (CRD) and, mortality due to Marek’s disease during pullet rearing and Leucosis during the laying period. During the 1960s, several breeding companies tried to reduce Marek’s mortality by selection, using genetic markers (B21 haplotypes) or exposure of pullets to infection on farms with previous history of high mortality (Beaumont et al., 2003) along with selection for the most resistant families. With the development of Marek’s vaccines and widespread use in commercial hatcheries during the 1970s, these major risks for egg producers were pretty well controlled. But initially, the success of the vaccine resulted in a great reduction in mortality and a large increase in numbers of healthy layers resulting in overproduction of eggs and very low egg prices. It took several years for the industry to scale back the number of layers so that production was back in line with the demand for eggs. Disease risks are minimized today with a combination of bio-security, prophylactic vaccination and monitoring of the health status of our industry flocks. Of major concern today, due to animal welfare requirements, is the control of feather pecking and cannibalism without beak treatment and/or reduction of light intensity.

**Combined efforts of nutritionists and geneticists to reduce feed cost**

Feed accounts for about 60% of egg production cost and is getting major attention whenever focus is on profitability. Based on scientific studies on nutrient requirements of different species of poultry, nutritionists can formulate “least cost” feed for any flock of laying hens, taking the prices of available feed conversion ratio – random sample test 1966-2011 Kitzening.

Fig. 2: Combined effects of genetic selection and management to improve feed efficiency
feed components and the production level of the hens into account. For many years, it had been assumed that laying hens fed a balanced ration ad libitum will eat just enough to satisfy her nutrient needs for maintenance and egg production. If this were true, nutritionists could focus on feed formulation to meet nutrient requirements at minimal feed cost per ton. In the 1970s, when egg prices were low and feed prices high, geneticists started to select more intensely for improved feed efficiency: instead of simply weighing hens to estimate maintenance requirements, individual feed intake was measured to determine “residual” feed consumption and “egg income over feed cost”. Analysis of records from pedigreed hens confirmed that hens with comparable body weight and egg mass production differ more in daily feed intake than previously assumed. Industry data and results of random sample tests confirm that the efficiency of feed conversion has been substantially improved since the 1970s: from about 3 kg to 2 kg feed per kg egg mass (Flock and Heil, 2002; Anderson et al., 2013). At the same time, we have also learned a lot more about the importance of house temperature, water intake, feather cover, feed structure and changing nutrient requirements with age and time of the day.

As recently documented by Damme and Hildebrand (2015), based on results from random sample tests at Kitzingen, feed efficiency has been continuously improved during the last 50 years, but also depends on the management system (Fig. 2). With floor management, behavior traits (nesting behavior, tendency to develop feather pecking and cannibalism) have become more important. Comparisons across years confirm that strains differ in their tendency to develop feather pecking and cannibalism. In anticipation of EU regulations against beak treatment, primary breeders have selected against these behaviors since many years. Egg producers appreciate the experience and advice from independent sources like random sample tests.

**Sustainable breeding of egg-type chickens: co-evolution with human societies**

Several authors have addressed sustainability in this publication before: Hodges (2007) called attention to the importance of family farming in developing countries and criticized negative effects of intensive animal farming on rural employment; Eberz (2009) looked at the increasing demand for food, feed and energy of a growing world population, with focus on research and development to safeguard yields, produce high-quality crops and manage resources efficiently; and Flock (2009) recalled the history of breeding egg-type chickens, with increasing attention to sustainability in terms of “quality of life for egg consumers and producers worldwide, with appropriate attention to bird welfare and natural resources”.

Geneticists in the poultry industry, trained to think in terms of long-term response to selection, review the breeding goals periodically, ideally before each selection cycle, to respond to short-term requirements. For example, selection on feed efficiency started in response to suddenly rising feed prices in the mid-1970s; With single cage management of pedigreed populations this selection was apparently successful and contributed to the increasing market share of brown-egg layers in Europe. Floor management, on the other hand, requires sufficient “feed intake capacity” to meet the nutritional needs in the critical period from sexual maturity to peak production. Fortunately, there is sufficient genetic variation in commercial lines to select for adaptability to different requirements, and management recommendations “from hatch to end of lay” help to translate genetic potential into efficient egg production.

A continuing challenge for poultry breeders in Europe is the strong position of ethicists and animal welfare organizations. When national or regional politicians use the term “sustainability” in the context of agricultural policies, they are more likely to focus on emotions of potential voters than on the global food market. Poultry breeders in Europe have the “benefit” of getting this public pressure first-hand, while international customers of parent stock expect continuous supply of genetic potential for economic egg production under their conditions.

Genetic theory is applied in large populations to maximize genetic progress, and changes in the performance profile of specific crosses can be predicted with high accuracy. The productivity of commercial layers has been doubled within less than 50 years, from about 150 to more than 300 eggs per year; and the efficiency of feed conversion has been improved from 3 to 2 kg feed per kg egg mass. Most of this improvement has been generated with the introduction of systematic cross-breeding, followed by within-line selection. Large populations assure that the inevitable loss of genetic variation due to intensive selection is kept to a minimum.

**Experimental results to quantify effects of heterosis and inbreeding**

Primary breeding companies have a wealth of internal data on pure-line and cross-line performance of their commercial and experimental lines. To illustrate heterosis effects which may be found in a
superior cross, the results in Table 1 were presented at the European Poultry Conference in Hamburg, 35 years ago. In this case, the two parent lines (P) and reciprocal single crosses (F1) had been directly compared with samples of all four double crosses (F2) and all eight backcrosses (BC) under identical conditions, in single cages. Highly significant heterosis effects were found for hen-housed egg production and egg mass. As expected from theory, about one-half of the superiority of the cross was lost in the F2 and BC combinations. The loss of heterosis in subsequent crosses assures that franchize hatcheries buy new parents every year instead of breeding their own replacements.

The rate of inbreeding in these lines was analyzed from 24 generations of pedigree records, and inbreeding effects were compared with heterosis by regression analysis (Flock et al. 1991). The results in the following table 2 indicate a “loss” of heterosis compared to the earlier study, which was explained as a result of improved pure-line performance.

To remain successful in an ever changing and highly competitive world market, primary breeders continuously monitor the genetic variance in their lines. The focus of genetic improvement will remain on efficient production of “saleable” eggs, but details of the performance profile have changed and will continue to change. The application of genomic selection is expected to contribute significantly to continued progress in all traits of economic significance, and primary breeders of egg-type chickens can offer a wider range of different crosses to meet specific regional demand.

**Changing lifestyles**

The lifestyles and preferences for different sources of food have changed considerably during the last 50 years and will continue to change. The migration of rural people to cities continues in most countries, and there will be more people looking for eggs as a relatively cheap source of high quality food. According to FAO statistics, 107,500 Mio t of poultry meat and 67,300 Mio t of eggs were consumed in 2013. It seems reasonable to assume that the demand for eggs will continue to increase at a faster rate than the growing world population. Eggs could contribute to better nutrition of millions of people currently suffering from starvation or malnutrition. The poultry industry could quickly provide all necessary input for efficient local egg production, if governments or NGOs provide the necessary funding. Governments in developing countries trying to improve the nutrition of pre-school and school children should be aware of the fact that eggs would be a relatively cheap source of valuable nutrients (Yalçın and Yalçın, 2013).

**Summary and Conclusions**

In this review, we recall key factors which helped the egg industry to achieve its strong position in the global food market: (1) the use of lighting programs in environment-controlled houses had two advantages: egg consumption increased, when fresh eggs became available throughout the year, and egg production cost decreased due higher annual egg production per hen and better utilization of facilities; (2) separate selection of meat-type chickens with focus on rapid juvenile growth and egg-type chickens with focus on high egg production accelerated genetic progress in opposite directions, for meat vs. eggs; (3) family selection in pedigreed populations confirmed quantitative genetics theory and generated predictable progress in egg production; (4) theories to explain the phenomenon of hybrid vigor (heterosis) stimulated the development and applica-

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**Table 1:** Estimates of heterosis (h, h'), recombination (r) and selection (s) from a population under long-term RRS (Flock, 1980)

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**Table 2:** Effects of inbreeding and heterosis on reproductive traits and production to 44 weeks of age in commercial lines under long-term RRS (Flock et al. 1991)

**Table 2:** Effects of inbreeding and heterosis on reproductive traits and production to 44 weeks of age in commercial lines under long-term RRS (Flock et al. 1991)
tion of cross-breeding schemes to maximize the utilization of general and specific combining ability of two or more lines; (5) based on research in avian pathology, common poultry diseases were controlled with improved diagnostic tools, eradication of egg-transmitted disease agents and prophylactic vaccination; (6) based on nutrition research and least cost feed formulation from available components, the impact of rising feed cost has been minimized; and (7) global communication and logistics assure the supply of parent stock and exchange of information between primary breeders, multipliers and egg producers to satisfy world-wide demand.

**Literature**


