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Eddy Decuypere, P.M. Hocking, Kokou Tona, O. Onagbesan, V. Bruggeman, E.K.M. Jones, Sandrine Skiba-Cassy, Nicole Rideau, Sonia Metayer-Coustard, Yves Jégo, et al.

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Broiler breeder paradox: a project report

E. DECUYPERE[1], P.M. HOCKING[2], K. TONA[1], O. ONAGBESAN[1]*, V. BRUGGEMAN[1], E.K.M. JONES, S. CASSY[4], N. RIDEAU[4], S. METAYER[4], Y. JEGO[3], J. PUTTERFLAM[4], S. TESSERAUD[4], A. COLLIN[4], M. DUCLOS[4], J.J. TREVIDY[3] and J. WILLIAMS[4]

[1]Katholieke Universiteit Leuven, Kasteelpark Arenberg 30, Leuven, B-3001, Belgium; [2]Roslin Institute (Edinburgh), Roslin, Midlothian EHS25 9PS, United Kingdom; [13]Hubbard, Le Foeil, BP 159, 22800 Quintin, France; [4]Station de Recherches Avicoles, INRA SRA, 37380 Nouzilly, France
***Corresponding author: Okanlawon.Onagbesan@agr.kuleuven.ac.be**

A first product of this European project was a tool for scoring chick quality. A link was established between chick quality and embryonic physiological parameters such as heat production. Eggs from broiler breeders that give rise to rapidly growing broilers have a different embryonic development that may need modified incubation conditions. Within genotypes, better chick quality induces better liveability and faster growth in broiler production. Extensive data on broiler breeder production were generated. Feed restriction was necessary to maintain welfare and reproduction at acceptable levels in standard broiler breeders. The dw-experimental genotype (E) was more tolerant to *ad libitum* feeding. If an alternative to feed restriction had to be found, the use of a dw genotype with less severe feed restriction could be adopted. Fibre *per se*, or partial feed restriction during the growing period, only compensated to a small extent for the negative effects of early fast growth on later reproduction. The results of the project on behaviour did not support welfare concerns on feed restriction. They confirmed the hypothesis that environmental pecking is a displacement activity rather than a sign of frustration. Factors other than central control by pituitary hormones seem to be involved in the modulation of the laying rate. The local (intra-ovarian) role of growth factors such as Insulin-like Growth Factors (IGFs), Bone Morphogenetic Proteins (BMPs) and leptin are known to modulate the effect of gonadotrophins on ovarian function. For both BMPs and IGFs, feed restriction enhanced the interaction between growth factors and gonadotrophins as well as the proliferation of granulosa cells *in vitro*. Future genetic selection of broiler breeder production might aim at uncoupling the control of growth factors in the ovary from the selection for rapid growth to maintain or increase the growth rate of chicks without further penalising the already poor reproductive performance of broiler breeders. Putative quantitative trait loci for ovulation rate were identified in the project and may eventually facilitate selection by breeding companies for birds that could be fed enough feed to optimise their welfare.

Keywords: broiler breeder; feed restriction; chick quality; growth factors; ovary

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Introduction

The broiler breeder paradox (BBP) concerns the apparent impossibility of reconciling production requirements (good reproductive performance; good health and low mortality of the female broiler breeder; satisfactory growth performance of the offspring) without recourse to severe feed restriction (Remena and Robinson, 2004 for review). Other paradoxes with broiler breeders are low egg production but a hyperactive ovary; and the fact that the welfare of hens is affected by both *ad libitum* and restricted feeding (Hocking *et al.*, 1993, 2001).

These considerations were at the heart of the conception of the BBP European project (Williams *et al.* , 2004) to improve broiler breeder production with the following main objectives:

- To define, understand and improve the relationship between product quality and the genetics and nutrition of breeders.
- To find genetic potential for improving egg production and welfare without decreasing chick-quality production through a deeper understanding of the interaction between reproduction, feed restriction and genotype.
- To adapt feeding regimens more closely to the animals' physiological needs, thus improving welfare.

The experimental work was conducted with three model genotypes of broiler breeders produced by Hubbard-Europe. These include the S (or standard) which is a commercial broiler breeder without the dwarf gene. This genotype represents the largest share of the European production of broiler chicks. S-chicks are slow-feathering breeders that can be feather sexed. The second genotype is the L (or 'Label') type that is a commercial, coloured, dwarf breeder used in Europe for the production of slow growing broiler chicks for the quality market. The third genotype is the E (or experimental), a dwarf genotype under development by Hubbard with the aim of obtaining a new balance between the production of chicks, their viability, the potential for growth (close to that of S-chicks) and the possibility of *ad libitum* feeding of the breeder hens. E-chicks are fast feathering breeders that must be vent sexed.

New results that deserve discussion were obtained in four areas: chick quality, genotype of the breeders, feed dilution and local regulation of the follicular growth.

The chick quality challenge

Embryo physiology, quality of chicks and performance of the broilers from the eggs of the three lines of broiler breeders were compared. All female parent stocks were mated to Cornish males. We developed a quality score for day-old chicks on the basis of physical parameters. Based on information collected from hatcheries and broiler farms on varying physical appearances of day-old chicks, the following criteria were selected for inclusion in the estimation of chick quality physical attributes such as activity, feathering, eyes, conformation of legs, aspect of navel area, yolk absorption, etc. The level of the score for each criterion was related to its importance in the survival of the chick and the severity of any anomaly it may carry. The scores are hedonic in nature and the maximum total score is 100 (Tona *et al.*, 2005b; Bruggeman *et al.*, 2004). From these studies, it appears that the incidence of day-old chicks with sub-normal conditions in the navel area was the highest suggesting that this is a parameter of significant importance in the survival and growth of the chicks. Other subnormal conditions that contributed highly to the number of chicks with low scores included the amount of retracted yolk, remaining membrane, activity, down feathers and general appearance, although these had a lower incidence compared to

defects of the navel area. The combination of these four criteria alone contributed significantly to the downgrading of suboptimal chicks (Tona *et al.*, 2003a, 2004a). Moreover, a positive correlation was found between relative growth up to 7 days (RG) and day-old chick quality. The effects of pre-incubation factors such as egg storage duration, the age of broiler breeders and incubation conditions (especially egg turning duration during incubation) were investigated. There is a greater occurrence of poor quality chicks from eggs stored for longer duration than from eggs stored for shorter duration and this was further exacerbated in eggs from older breeders (Tona *et al.*, 2004b). With respect to egg turning duration, it was shown that, paradoxically, egg turning up to day 18 of incubation depresses relative growth up to 7 days while it improves chick qualitative aspects (Tona *et al.*, 2003c). In a further study, physiological measurements on embryos during incubation, chick quality and growth performance of broiler from S, E and L lines were compared. With regard to embryo physiology, the lowest average egg weight loss during incubation was obtained in the eggs of the E line. Plasma triiodothyroxine (T_3) and T_3/Thyroxine (T_4) ratio were similar between lines at internal pipping stage but corticosterone was higher in the S line. At hatch, T_3/T_4 ratio was higher in the S line compared to the E and L but corticosterone was higher in both S and E lines than L line. Heat production by embryos was different between lines (S>E>L). Partial pressure of CO_2 was also higher in the S line than the E and L lines. These physiological parameters suggest different metabolic rate between lines. Chick quality scores expressed as either percent of high quality chicks or overall average score of each line were not different. However, broiler body weights at 7 and 41 d were different between lines (S>E>L). Chicks of higher quality (score 100) in all lines showed higher body weights than those of lower quality (score < 100). These data suggest a link between levels of embryo metabolism and growth potentials of the lines. The higher growth potential of the S line is related to higher T_3/T_4 ratio (at hatch), higher pCO_2 (at internal pipping) and higher heat production of the embryos.

The *dw*- alternative

A clear and appealing result of the BBP project has been the extended evaluation of the performance of the so-called 'experimental' E genotype of broiler breeder hens. Consistent resistance to *ad libitum* feeding with relatively diluted diets was observed (Heck *et al.*, 2003b and 2004; Bruggeman *et al.*, 2005). The liveability figures were always better than in standard non-dwarf broiler breeders. The possibilities of using such a genotype in practice will require several complementary validation studies under semi-practical conditions, namely to accurately measure the reproductive performances with males in large flocks. However, even when fed on a diluted diet, the E genotype did not really self-restrict themselves as shown by the comparison of growth curves between restricted and non-restricted E hens (Bruggeman *et al.*, 2005). The delay for offspring to reach market weight (2 to 3 days compared to a S breeder progeny), and the possibly lower breast meat yield call for in depth economic evaluation which must also take into account the expense of extra feed with *ad libitum* feeding. With respect to feeding, a dwarf breeder will always have an advantage upon a non-dwarf due to its lower maintenance requirements. Moreover, besides the dwarfing gene, generations of selection on specific traits (including reproductive fitness and liveability) may also have modified the E genotype's responses to *ad libitum* feeding. However, the *dw* gene has long been known to favour adaptation to *ad libitum* feeding (Hocking *et al.*, 1987, Triyuwanta *et al.*, 1992). Decuypere *et al.*, (1991) have also described the possibility that the dwarfing gene may also favour efficient egg production either in egg-laying type strains or broiler breeder

hens. Awaiting the more prospective genetic approaches that were also developed in the project (Hocking, 2003), the *dw* breeder hens selected with a similar approach as the E genotype might represent a viable alternative to feed restriction on the short term. However the success of the dwarf breeder might be further improved by developing separate feeding programmes for males and females and the possible development of artificial insemination in southern countries (Brillard, 2004). In this project's experiments, the good reproductive performance obtained with the E genotype was largely facilitated by the feeding of diluted feed.

Feed dilution and pecking

Food restricted broiler breeders are more active and spend more time pecking at the environment and at water compared with birds fed *ad libitum*. Two experiments were designed to determine if increased dietary fibre would decrease the prevalence of spot pecking and damaging pecking in food restricted birds and lead to an improvement in their welfare. In the first experiment, three sources of fibre (oat hulls, sugar beet and sunflower) at three concentrations (50, 100 and 200 g/kg) in nutritionally similar rations were assessed for their effect on welfare by measuring changes in behaviour (Hocking *et al.*, 2004). Changes in behaviour and heterophil-lymphocyte ratio were measured at 5, 10 and 15 weeks of age. Body weight at 15 weeks of age decreased in a linear manner with increasing concentrations of the experimental ingredients. Decreased spot pecking was observed in birds fed on the rations containing 50 g/kg of sugar beet pulp and 200 g/kg of oat hulls. The heterophil-lymphocyte ratio was higher in birds fed on the control diet and diets containing 50 g/kg of the high fibre ingredients. Rations containing sugar beet pulp were associated with higher water contents in the gastro-intestinal tract and it was proposed that this improved satiety and welfare (Zaczeck *et al.*, 2003).

However, in a second trial the diet containing 50 g/kg sugar beet was compared with a control diet when fed to food restricted Standard (SR), and Experimental dwarf (ER) broiler breeders, standard birds fed at the same level as the E line (SE) and Label (LA) broiler breeders fed *ad libitum* (Jones *et al.*, 2004a and b). Changes in behaviour, physiology and gut fill were used to assess welfare. Body weights of all birds on the fibre diet were lower, and LA birds ate less than those fed on the control diet. Drinking, litter directed behaviour, resting and standing were affected by a significant group x age interaction with restricted birds showing increased drinking over time and decreased time spent resting compared to the *ad libitum* fed LA birds. The behaviour of ER was comparable with that of the SE broiler breeders. No effects of diet on behaviour and physiological indexes of welfare were observed. With the exception of the crop, the gross composition of the contents of the gut was similar in LA and SR birds.

It was concluded that the replacement of standard with dwarf broiler breeders may improve the welfare of commercial flocks of broiler breeders by decreasing the severity of food restriction. The welfare benefits of feeding diets containing high concentrations of fibre are negligible and the major role of fibre is to dilute the nutritional value of the ration and increase the mass of food fed to restricted birds. Excessive drinker directed activity in food restricted birds is probably a substitute for foraging rather than an attempt to increase gut fill (Hocking, 2004, Hocking and Jones, 2004).

The behaviour of breeder hens was further studied on S and E breeder hens fed ad libitum (A), restricted at 55% of A (D) or at 30% of A (R) using focal sampling on 144 target hens in total (Picard *et al.*, 2004 a and b). They were videotape recorded after feed distribution and during the afternoon at 6-10 and 10-15 weeks of age. Coding of 383 ten minute files in real time and 107 one minute files for detailed behaviour at slow motion

speed was done using 'The Observer 4.0 video pro'. Time patterns of behavioural sequences were analyzed using 'Theme', software to detect non-random time distances between events. R hens were more active than A and preened more during the afternoon. Pecking at the litter in the afternoon was proportional to feed restriction and expressed in most hens although pecking at an empty trough was expressed in some restricted birds at a high rate. Social behaviours could not be related to feed restriction. E and S genotypes were relatively similar. Several behaviours appeared to be consistently structured in time for all treatments. Others such as "raising the head during a meal" could be either time consistent (detected by Theme) or variable (undetected). Feed restriction seemed to stimulate structured scanning of the environment while eating. Litter pecking is probably the best indicator of feeding motivation in restricted breeders.

The local regulation of follicular growth

The 'erratic oviposition and defective egg syndrome' described early in broiler breeder hens (van Middelkoop, 1972) is associated with *ad libitum* feeding but does not seem primarily related to a systemic hormonal dysregulation (Bruggeman *et al.*, 1998a and b and 1999) or insulin resistance (Rideau *et al.*, 2004). Further confirmation of this was obtained during the project (Onagbesan *et al.*, 2004a). In standard broiler breeder hens fed *ad libitum*, the erratic pattern of oviposition has been related to abnormal regulation of follicle maturation and steroidogenesis in the ovary. Interesting results similar to ours, have been obtained by Lupicki (1994) and Renema and Robinson (2004). Early developing white follicle are less responsive to LH in ad libitum fed birds than in restricted breeders especially at the beginning of the laying period when the abnormal eggs are most frequent.

In the BBP project, an extensive effort to determine the expression of components of the insulin-like growth factors (IGF) and bone morphogenetic proteins (BMP) systems

Table 1 Relative expression of growth factors and their related proteins in the granulosa and Theca of mature yellow follicles in broiler breeder hens aged 32 weeks.

	GRANULOSA	THECA
Insulin-like Growth factors System		
IGF-I	+	+++
IGF-II	+	+++
IGF-Receptor	+++	+
IGF-Binding Protein 1	+	+++
IGF-Binding Protein 2	+	+++
IGF-Binding Protein 3	+	+++
IGF-Binding Protein 4	+++	+
IGF-Binding Protein 5	+++	+
Insulin receptor	**+++**	**+**
Bone Morphogenetic Proteins System		
BMP-2	++	++
BMP-4	+++	+
BMP-7	++	++
BMP-Receptor IA	+	+++
BMP-Receptor IB	+++	+
BMP-Receptor II	+++	+
Leptin Receptor	**+**	**+++**

revealed a symmetric distribution between the granulosa and theca tissues of the mature follicle (*Table 1*, Onagbesan *et al.*, 2003a, b and c and 2004b, Metayer *et al.*, 2002, 2004, Heck *et al.*, 2003). Since the F2 and F1 yellow follicles displayed similar endocrine profiles, the preovulatory surge of LH could trigger ovulation of both of these two largest follicles (Onagbesan *et al.*, 1999, 2000; Yu *et al.*, 1992). In the granulosa, insulin and IGF positively regulate steroidogenesis and stimulate growth and differentiation of the chicken ovarian follicle. IGF-I is involved in the regulation of ovarian steroidogenesis in both mammals and birds. IGF-I stimulates progesterone production from avian granulosa cells (Onagbesan *et al.*, 2000). Follicle growth and differentiation is not the result of just one system since both IGF and BMP interact with gonadotrophins (LH and FSH) to regulate follicular growth and differentiation (*Figure 1*). The results were related to the dynamics of follicle turnover and production. All the components screened show a distinct pattern of tissue distribution. Temporal changes related to the maturation of follicles and age of the hens were evident for some components. The tissue localisations of the IGF- and BMP-systems suggest that they could both act in autocrine and paracrine fashions within the follicles. Regulation of the growth and maturation of follicles are not dependent on a single system but the joint results of several systems (BMP, IGF, leptin…). It would therefore be interesting to attempt a 'shotgun' analyses by microarrays (genes) or proteomics (proteins) to look for a wider range of genes and proteins that might change during maturation of follicles. Secondly, varying factors such as diet or genotype could be re-examined using these new approaches targeting specific follicular developmental stages. For example, as the numbers of small white follicles appear sensitive to dietary changes, then tissue localization of differential gene expression in the cells of those small follicles cells using *in situ* hybridisation might open new avenues for the study of follicular maturation.

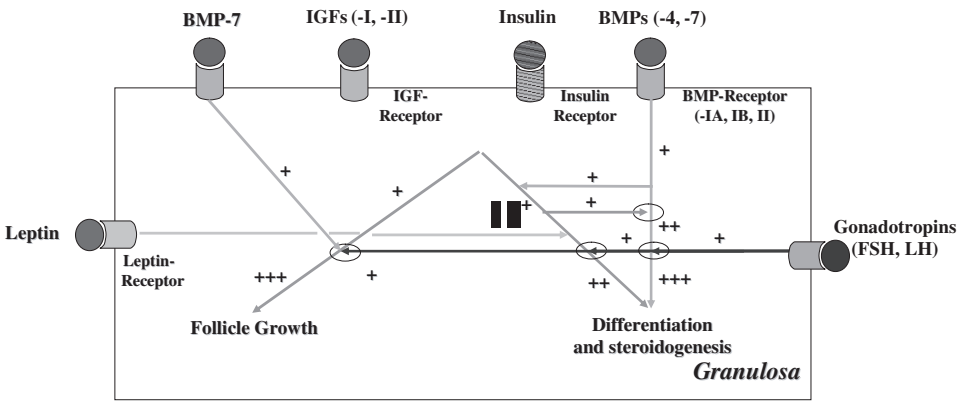

Figure 1: Schematic representation of potential interactions between IGF-, BMP- and leptin-systems in the avian ovarian follicle at 32 weeks of age. ⟲ : synergistic actions; + stimulation; -inhibition. *The negative effect of leptin remains to be demonstrated in hens.

The putative direct action of leptin on the ovary might change during follicular development since the level of expression of its receptor decreased during maturation of the yellow follicle, especially in slow growing L hens and SR hens (Cassy *et al.*, 2004 and b). This suggests further *in vitro* studies of the effects of leptin on granulosa cell steroidogenesis could yield interesting results. No clear influence of glucose/insulin homeostasis was measured during the BBP project. The sensitivity to insulin might be even higher in SA than in SR birds. Further research might involve measurement of cell

signalling and of leptin receptor expression in F4 to F1 follicles, and studies of the kinetics of tolerance to glucose and/or measuring responses to graded doses of exogenous insulin (Rideau *et al.*, 2004).

Conclusions

The results of the BBP project have provided new information in three domains: poultry production, chicken behaviour and physiology of major genotypes of broiler chicks and breeders fed ad libitum or restricted.

From the producer's stand-point, restriction of standard broiler breeders (S) delayed sexual maturity but improved egg production. S hens fed *ad libitum* exhibited a high mortality rate and low egg production incompatible with a fair economic return for the producer. Slow growing Label-type breeding hens (L) fed *ad libitum* combined early sexual maturity with high production. The comparison of S and L illustrates the incompatibility between reproductive performance and fast growth of offspring. Fibre *per se* or partial feed restriction during the growing period compensate only slightly for the negative effects of early fast growth on later reproduction performance of standard broiler breeders. The dw experimental genotype (E) were more tolerant to *ad libitum* feeding. In other words, if an alternative to feed restriction has to be found, the use of the experimental *dw* genotype with less severe feed restriction could be adopted. Differences in embryonic physiology between broilers from the S, E and L genotypes were observed and point to some very interesting relationships between endocrine parameters, embryonic heat production, and later postnatal growth. Eggs from broiler breeders that give rise to rapidly growing broilers have a different embryonic development that may need modified incubation conditions. Within genotypes, differences in growth rate until slaughter age were related to one-day old chick quality as defined precisely by the BBP project. Differences in chick quality can induce as much as two days' growth retardation in broiler production.

From a behavioural viewpoint, the replacement of S broiler breeders by dwarf broiler breeders (such as E and L) may improve the welfare of commercial flocks by decreasing the severity of feed restriction of the breeders and improving the health status of all the chickens. Restricted birds were more active in general and more immobile before feed distribution. Foraging and searching for food and stereotyped pecking at some environment targets such as an empty feeder or a water nipple were observed more frequently. However, no major signs of frustration and fear were observed. The welfare benefits of fibre *per se* without dilution of the nutrient in the feed are negligible. Dilution of the diet by fibre increases feed consumption and may improve some aspects of welfare. The overall results of the BBP project on behaviour do not lend new support to the welfare concerns of some groups over feed restriction, and tend to confirm the hypothesis that environmental pecking is a displacement activity rather than a sign of frustration.

Physiologists provided a wide range of original results. Different profiles of plasma LH, FSH and oestradiol concentrations in particular, were observed between genotypes and between restricted and *ad libitum* fed birds during the prepubertal period. No between genotype differences in the time of onset of lay were found. Other factors besides central control by pituitary hormones seem to be involved in the modulation of the laying rate. Therefore, the local (intra-ovarian) role of growth factors such as IGFs, BMPs and leptin were extensively studied because they are known to modulate the effect of gonadotrophins on ovarian function. For both BMPs and IGFs, feed restriction enhances the interaction between growth factors and gonadotrophins as well as the proliferation of granulosa cells. The interaction may explain the differential yellow follicle number and (partly) egg

production rate between genotypes, ages, and especially different feed allowances in broiler breeders. However, a certain number of links remain hypothetical and require further verification. Similarly, the leptin receptor fits into this picture of local regulation because leptin antagonises the IGF and insulin stimulating effect on steroidogenesis in mice. In chickens, the high expression of the leptin receptor in small yellow follicles might be related to the lower responsiveness of these follicles to the stimulatory effect of growth factors on steroidogenesis.

A fundamental question remains to be answered: " Is there a causal or functional mechanistic link between fast and efficient growth of the broilers and the observed reproductive problems of broiler breeders? ".

From the results of our project, this question can at least be re-phrased as a more concrete question: "Are the changes in growth related hormones or factors, as a consequence of selection for fast and efficient growth, linked to UNAVOIDABLE changes of these growth factors in the ovary in broiler breeders, resulting in gonadal dysfunction? "

- If the answer is 'NO', then one should extend the selection goals and work with combined selection indices to uncouple the desired and undesired characteristics in breeders.
- If the answer is 'YES', then one should adapt the selection goals to settle for lower bird productivity levels (in broilers) in order to reach acceptable productivity, with acceptable management systems in broiler breeders.

In the first case, the most effective long term strategy for improving the welfare of fast growing standard broiler breeders is genetic selection to decrease the propensity for multiple ovulation that would make it possible to feed more feed without compromising productivity and the sustainability of the European industry. Genetic selection on the basis of DNA markers would make this possible commercially and, as part of the BBP project, we identified two quantitative trait loci (QTL) for yellow follicle numbers in a broiler x layer cross. The results represent a first step in this long-term strategy and are the first evidence that such an approach may be possible.

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