The broiler breeder paradox from an ethical, genetic and physiological perspective and suggestions for solutions

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Summary

Due to intensive selection, broiler chickens became the most efficient meat producing animals because of their fast growth, supported by a virtually unlimited voluntary feed intake. These characteristics cause a lot of problems in the management of broiler breeder hens, since a negative correlation between muscle growth and reproduction effectiveness is observed. This problem, namely the ‘fast muscle growth versus reproduction health’-paradox induces another paradox, namely: ‘acceptable reproduction and health versus hunger stress and impaired welfare’ because broiler breeder hens require dedicated programs of feed restriction to a) maximize egg and chick production and b) to avoid metabolic disturbances and mortality in broiler breeders.

Given that poultry selection is a global large-scale business and since chickens are prolific species, the only improvement in profit can be obtained by selecting on feed conversion and/or higher breast meat percentage which will intensify the broiler breeder paradox. New feeding strategies are being studied, but it is questionable if the paradox can be solved by management tools alone. Since breeding and selection are long-term processes, involving animals, farmers, consumers, industry, environment..., a more sustainable breeding goal needs to be determined by pluridisciplinarity and an open debate between several actors in the discussion. Using dwarf broiler breeder hens could be one alternative, because dwarf hens combine a relatively good reproductive fitness with ad libitum feeding. Another possibility is to accept lower broiler productivity by assigning economic values to welfare and integrity-traits included in an extended breeding goal.

Introduction about the nature of the problem

World increase of consumption of animal products is estimated at ± 7% per year between 2005 and 2015 and a similar increase is expected until 2025 or later. This is true for animal food production in general and may be even more pronounced for chicken meat production as this sector is growing relatively faster than that of the other meat species. At the top of the animal production pyramid, animal breeding and reproduction play an influential role on the animals that are available for food production (Fabre technology platform, 2005). Genetic selection has increased production levels and efficiency, but animals that have been selected for high production efficiency seem to be more at risk for behavioural, physiological and immunological problems. Genetic selection is often still a black box if we do not understand the underlying physiological processes and may lead to loss of homeostatic balance, resulting in the occurrence of pathologies and consequently in impaired welfare (Rauw et al., 1998). Our efforts to breed for higher production efficiency may raise concerns regarding both animal welfare and animal integrity. The reflection on the
ethical significance of breeding goals can help us to evaluate these breeding goals according to their potential to affect animal welfare and integrity (Mepham, 1995). This may force us to recognize our moral responsibility and to discuss the limits of acceptability. Applied and practical ethics provide us with tools and with a framework of values and principles guiding our reflection.

Animal breeding has traditionally focused on cumulative short-term genetic changes because breeding goals were set in a purely economic framework. As a consequence, animal breeding may have and has led to unwanted side effects that are in conflict with sustainable animal husbandry (Olesen et al., 2000). To counteract some of the negative effects, selection goals should not be only expressed in terms of production efficiency, but also in characteristics which are linked to the health and welfare of the animals. Therefore, the concept of ‘robustness’ (Star et al., 2008) can be used. A broad definition was already given by Kitano (2004): “the maintenance of specific functionalities of the system against perturbations, and it often requires the system to change its mode of operation in a flexible way”. Knap (2005) mentions robust pigs as “pigs that combine high production potential with resilience to external stressors, allowing for unproblematic expression of high production potential in a wide variety of environmental conditions”. From this, one can conclude that the qualifying elements in the definition of ‘robustness’ are: production efficiency and functioning in a broad variability of environmental conditions. This functioning encompasses both physiological, behavioural and immunological characteristics. Robust animals will be less susceptible for disease stress and will recover faster, if needed (better health). From a welfare point of view, robustness as a selection goal should lead to animals with ameliorated ‘coping abilities’, leading to a better adaptation to the management system. If the animals dispose of this flexibility, their welfare is increased. Finally, also integrity is a precondition for robustness. Decreasing or harming the telos of an animal (Rollin, 1995) is not consistent with robustness. Lack of integrity is the case in broiler breeding and forms the heart of the broiler breeder paradox.

Sustainable breeding, besides profitability, also needs equilibrium between production level, efficiency, and the physiology (which encompasses welfare, behaviour, health, reproduction ... in other words the functioning of an animal). Therefore, more knowledge about basic biology of selection traits and their correlation is needed. A strong negative relationship is observed between body weight and reproductive efficiency in poultry, and the strength of this relationship is evidenced by the existence of two types of chickens of commercial significance which show extreme opposites in body weight and reproductive performance. Concomitant with improvements in growth rate of broiler chickens, the ability of meat-type parent stocks to reproduce has been severely reduced. Nevertheless, parents of meat-type poultry must not only have the genetic potential to exhibit fast and efficient meat growth, but also be capable of reproducing.

It is well known that broiler breeders require dedicated programs of feed restriction to maximize egg and chick production (Costa, 1981). The application of the restriction program in practice implicates at the same time the importance of carry-over effects of a specific feeding level during growth on the development of the reproduction axis. The emphasis for improving reproductive performance of broiler breeders has always been more on management than on genetic improvements. This is linked with the low percentage of energy cost for the breeder population in the total efficiency of feed energy for broiler meat production, including slaughter and breeder generation. Since feed restriction during rearing of broiler breeders is the most important management tool to avoid metabolic disturbances and mortality in broiler breeder rearing as well as to reach an acceptable level of egg laying afterwards, it follows that the “solution” for the problem namely the “fast growth versus reproduction-health”-paradox induces another: “acceptable reproduction – health versus hunger-stress – impaired welfare”. Any sustainable solution of the paradox as outlined here should be based on a better understanding of the impact of severeness and timing of feed restriction on performance parameters such as growth, feed efficiency, and reproductive performance, health and welfare. Therefore, the physiology of the nutrition-dependent reproductive ability of broiler breeders needs to be better understood and will be discussed in the third part. Finally, elements discussed above will be reconsidered in the broader framework and suggestions for solutions or further debate and analysis will be given.

The broader framework

Sustainable animal production

In the evolution of animal production systems since mankind has domesticated some animal species for his own use and benefit, four phases are
distinguished by Olesen et al., (2000), starting with “pioneering” (subsistence husbandry) followed by “production” (maximization of products), “productivity” (optimization of production) and “persistency” (the idea of sustainable production, starting around 1970). Two aspects of philosophy are important in our understanding of these different perspectives or phases: the ontology, our belief about what nature is and this can be approached in a reductionistic or holistic way. The other aspect is the epistemology, how we try to learn about nature or our ways to analyze things and this can be done in a rather subjective or objective way. The combination of these two perspectives with both approaches results in four categories of worldviews, including our views about agriculture and animal production: a cultural-social, an ecological, a personal-egocentric and a technical worldview (Olesen et al., 2000). Elements of sustainability as defined by Francis and Callaway (1993) include profitability, resource efficiency, productivity, environmental soundness and social viability.

Because of the often conflicting elements, it is critical to weigh and give priorities to the different objectives in the term; moreover it is clear that such a definition of a sustainable animal production system is based on a holistic philosophy, but this can be approached methodologically in two ways as pointed out by Thompson and Nardone (1994) and Christiansen and Sandoe (2000): a resource sufficiency or a functional integrity approach:

- The former relies to a large extent on inputs and outputs and belongs to the evolutionary phase of productivity (the mainstream view of those involved in the animal husbandry sector until now); it is more informed by an objective epistemology and an ontology of reductionism.
- The latter is focused more on long-term “health” of a whole system and more informed by a subjective epistemology and an ontology of holism.

According to Sriskandarajah and Bawden (1994), functional integrity has philosophical priority over a resource sufficiency approach; the latter favours a status quo, even if quality of life is deteriorating, while analyzing livestock production in terms of functional integrity enhances discussion about priorities to give (e.g. productivity, resource efficiency, vs. animal welfare and integrity).

**Animal welfare and integrity**

Both animal welfare and integrity are hard to define as a concept and moreover are changing concepts; for example, it is too often assumed that animal welfare can be measured objectively and these measurements rely too much on physiological, immune or behavioural measures that are often not adequately validated (Rushen, 2003). This attitude however countered the defensive tactic of asserting that concerns about animal welfare were purely “emotional” or anthropomorphic (Fraser, 1995). Nevertheless, we will need more specific welfare indicators to assess each type of specific challenge, whether it is a housing, breeding, nutritional or stockmanship challenge; there is no such thing as a golden standard to measure objectively welfare in general.

Animal integrity goes beyond that of concern for health or welfare. One of the observed differences between both is that welfare can be affected not only by humans but by natural circumstances as well. In contrast, human action is required to affect integrity, and thus integrity demands human respect. It is defined as the intrinsic value of animals, e.g. a naturally evolved, unharmed wholeness of an individual, a species or a breed; therefore it is more a philosophical than an empirical issue (Christiansen and Sandoe, 2000).

In this context, broiler breeders are not naturally evolved or unharmed as a population (individuals) since, as a consequence of selection, they show abnormalities and a high mortality rate, even before attaining sexual maturity, when fed ad libitum. In other words, broiler breeders seem to be reduced to mere instruments for human interest: the production of eggs and chicks with a genetic high growth potential. In order to achieve this, their own growth must be extremely reduced by severe feed restriction, the severity of which having been ever increased over the last decades (Robinson et al., 2007). Therefore, this may be considered a violation of animal integrity.

As a conclusion, weighing concerns against each other implicates that all “parties” involved (being animals, farmers, consumers, industry, environment ...) should be considered for a particular breeding goal. Even though the policy that no harm to animals must be done unless necessary, and the harm must be outweighed by the benefits, balancing good against bad, is an utilitarian approach, it is recognizing that animals have intrinsic value and are not purely instrumental to man (Brom and Schroten, 1993).

The risks and implications of a certain breeding program must be assessed beforehand, based
on available scientific knowledge. However, the overall interpretation and the priority we attach to implications will be determined by our own ethical view, by what we understand as the meaning of animal welfare and/or integrity, by what we consider good reasons, by how we weigh the interests of animals against those of human beings (Sandøe and Holtuy, 1998).

**The genetic point of view**

**Occurrence of negative correlation between growth and reproduction**

In domestic poultry, a strong negative relationship is observed between body weight and reproductive effectiveness. The strength of this relationship is evidenced by the existence of two types of chickens of commercial significance that show extreme opposites in body weight and reproductive performance: broiler type and layer type chickens. Also empirical data further corroborate this negative relationship between selection for fast meat growth and reproduction, e.g. characterized as the ratio of percentage daily production of normal eggs over percentage of daily ovulation, DP/DO (Rauw et al., 1998). This ratio was 0.84 for a high weight line and 0.98 for a low weight line, and this was also reported for other weight divergent lines (Jaap and Muir, 1968; Antony et al., 1989; Liu et al., 1995). The percentage of chromosomal abnormalities was higher in a high body weight line (14.5%) versus a low body weight line (6.2%) (Reddy and Siegel, 1977) and consequently hatch of fertile eggs decreased.

Reproductive effectiveness can be characterized by a combination of phenotypes including egg production, libido, sperm and oocyte quality, sperm storage by the hen, gamete-gamete interactions, genetic compatibility and hatchability, not to mention the potential interactions among the phenotypes (Decuypere et al., 2003). Regardless of mechanism, the ability of meat-type parent stocks to reproduce has been severely reduced. It may however be mentioned here that inconsistent results as for effects of selection for body weight on male sperm characteristics have been obtained (Siegel, 1963; Marini and Goodman, 1969; Edens et al., 1973; Nestor, 1977).

**Biological explanation for the occurrence of this negative genetic correlation**

This question has been addressed for more than half a century and Lerner (1954) puts forward the theory of genetic homeostasis. Heterozygosity, stabilizing selection and negative genetic correlations will all result in intermediate optima in order to maintain homeostasis, in other words maintain additive variance which acts as a buffering effect to a wide range of environments at a population level. The competition for resources by two characters may result in negative genetic correlations (Rendel, 1963) and this led to the “Resource Allocation Theory” (Goddard and Beilharz, 1977). If the responses are limited, fitness will decrease with an increased allocation of resources to a particular trait of fitness; in order to maximize fitness (health, reproductive longevity ...) an optimal partitioning of resources is accomplished by allocating intermediate proportions to the different traits contributing to fitness. As experienced in broiler breeders, undesirable side effects may and will increasingly appear with ongoing selection for growth and feed efficiency of broilers. Therefore, broiler and broiler breeder selection may be considered as a forerunner for similar problems in other species. With selection, the “optimal” situation is shifted towards high (growth, meat) production and fewer resources are left to respond adequately to other demands (Rauw et al., 1998). Therefore, the breeding goal has to be redefined into a broader perspective or alternatively the resource situation has to be increased, if possible.

**Why these rather unidirectional selection goals in broiler production?**

Poultry breeding is a competitive business and success in poultry breeding business not only depends on efficient pedigree programmes in order to maximize annual genetic gains or efficient multiplication of the commercial products, but also on defining the correct or right breeding goal. Its definition is an essential starting point for any successful breeding programme (Emmerson, 2003). For long, the ultimate measure of performance for poultry meat output was the meat output per chick, but since the early 1990’s, it has become clear that meat output per breeder animal has become a dominant indicator of success (e.g. Pollock, 1999), an indication that both growth and reproduction are important. The meat output per breeder is composed of at least three parameters: 1) growth of the broiler, 2) feed conversion of the broiler and 3) breeder effectiveness.

Any assessment of the efficiency of feed energy utilisation for growth in meat animals must consider not only the feed conversion in the slaughter generation, but also the cost of maintaining an effective breeder population. In prolific species such as poultry, the majority of feed is consumed by the slaughter generation (approximately 95% vs. 5% for the breeder generation). Therefore, selection
goals will be directed predominantly towards traits that favour growth, feed conversion efficiency and carcass quality in the slaughter generation, with much less emphasis on reproductive traits of the breeder (Decuypere et al., 2003). In slow-reproducing species such as cows, the metabolizable energy (ME) intake is distributed approximately equally between breeder and slaughter generations and therefore it is theoretically as profitable to manipulate traits relating to the efficiency of the breeding cow as it is to manipulate growth in the slaughter animals (Webster, 1989). The rather low impact of breeding for broiler breeder reproductive efficiency, linked with the low percentage of energy cost for the breeder population in total efficiency of feed energy for broiler meat production (including slaughter and breeder generation) was also calculated in terms of profitability by Emmerson (2003).

Indeed, in an integrated broiler breeder-broiler business, the percentage of improvement in profit resulting from a 1% improvement in the following trait performances was:

- For egg production of the breeders: 0.23
- For hatchability in the hatchery: 0.46
- For broiler weight: 0.32
- For broiler mortality: 0.42
- For feed conversion: 1.31
- For breast meat percentage: 3.10

Of course these figures are market and price dependant and they will also change with market weight of the broiler: as this increases, the relative contribution of day-old chick cost, and hence of egg production by the breeder and hatchability will decrease. In the content Emmerson (2003) describes, the broiler day-old chick cost is about 20% of a broiler at slaughter age at a body weight of 1.8 kg and 12.5% of a broiler at body weight of 3 kg. From foregoing it is clear that breeding goals in the broiler industry have focussed and will continue to focus on growth, carcass quality and feed efficiency and much less, if at all, on reproductive efficiency.

Therefore, improvement of reproductive performance of broiler breeders has been focussed more on management than on genetic improvement and empirically it is well known that broiler breeders require dedicated programmes of feed restriction to maximize egg and chick production. This of course is at the heart of the broiler breeder paradox: the apparent impossibility of reconciling production requirements (good reproductive performance, good health and low mortality of the female broiler breeder; satisfactory growth and performance of the offspring) without recourse to severe feed restriction (Decuypere et al., 2006; Renema et al., 2007; Zuidhof et al., 2007). The idea that both ad libitum and heavily restricted broiler breeders have impaired welfare, but for different reasons, constitutes the welfare/welfare paradox.

**Importance of defining breeding goals for broiler breeders**

Defining breeding goals is an essential starting point for any successful breeding programme (Emmerson, 2003). Moreover, breeding goals become increasingly a blend of economics, consumer preferences and social concerns (including ethical concerns) and therefore these goals become diversified and increase in number. One consequence of this evolution is that correlations between traits associated with breeding goals must be considered; if genetic correlations between traits are positive and high, economic considerations will not compete markedly with selection for traits relevant for welfare or ethics, at most it will slow down a bit the speed of genetic improvement for single production related traits. However, traits will compete with each other if genetic correlation is low or even negative and this will slow down significantly the overall achieved genetic gain (Mills and Beilharz, 1997). Although it is difficult to assign an economic value to considerations such as welfare and integrity, breeders will be expected (or forced?) to define them in terms of production if it has to be taken into account in breeding plans.

A second consequence is the diversity of this broader economic, socio-cultural and ethical framework and the differences between regions or continents. In view of the internationalisation of poultry breeding companies (and also for other production animal species) and their worldwide trade, differentiation in breeding goals is the logical consequence and at the same time diversity is a goal on itself for maintenance of genetic variability. The possible genotype x environment interactions worldwide, as well as the uncertainty and associated risks about future circumstances, are incentives to differentiate between breeding goals and to maintain different breeding stocks (Olesen et al., 2000). Moreover, establishment of breeding goals is a process that must be regularly reviewed and re-evaluated which creates on its turn opportunities to include also some of the more “ethical oriented” aspects in these goals (Emmerson, 2003).

However, coming back to the heart of the broiler breeder paradox, in broiler selection for increased growth and feed efficiency, the welfare of broiler breeders has been questioned in light
of the severity of food restriction increasing every year, with a proportional increase in growth performances of the progeny obtained by genetic selection (Karunajeewa, 1987). Physiological stress is associated with restricted feeding on the one hand and the excessive body weight for ad libitum-fed broiler breeders on the other hand. Both are questionable according to several welfare parameters (Hocking et al., 1993). Unrestricted animals are overweight and display several pathologies, leading to unnecessary suffering and/or death. Although severe feed restriction prevents these syndromes, thereby improving welfare, it has been said that feed restriction is cruel because animals cannot eat to satisfy their hunger. The dilemma facing the broiler breeder industry is thus a production/welfare and welfare/welfare paradox. There is a need to balance those problems inherent to excess intake against those that accompany severe feed restriction.

Before changing selection goals or finding new strategies in management for an altered balance as mentioned above, the fundamental question is if there is any causal or functional link between fast growth and extreme lean tissue growth potential on the one hand versus reproductive effectiveness of the broiler breeder on the other hand. So, from a genetic perspective, this question can be phrased in the context of the genetic and phenotypic correlations among the phenotypes. Therefore, a next paragraph will discuss this dilemma from a functional or physiological point of view.

**The physiological point of view**

The control of growth rate in broiler breeders is one of the most important management tools, together and interacting with light simulation, to ensure the best reproductive performance (Decuypere et al., 2003; Bruggeman et al., 2010). In females, three key points are essential. First, the rate of growth must be predetermined so that the desired body weight is attained a few weeks before onset of lay. The desired body weight is established by giving the birds a certain amount of feed, which is at some ages up to 70% restriction compared to their unrestricted counterparts.

Second, it is important to synchronize growth and sexual maturity. Reaching sexual maturity is not accomplished just by gaining weight, but also body fat (Bornstein et al., 1984), body fat-free mass or lean body mass (Soller et al., 1984), photoperiod (Costa, 1981) and age (Brody et al., 1984) are important factors. Katanbaf et al., (1989) observed that full-fed broiler breeders are dependent upon reaching a critical age to start laying, while feed-restricted hens are dependent upon attaining a critical body weight and carcass fat stores. Yu et al., (1992 a, b) suggested that feed intake and changes in body composition (minimum fat level) during the pre-breeding period are the most important factors in the determination of the age of sexual maturity in broiler breeders. A further reduction in fat content as expected by a further selection for FCR (feed conversion ratio) may therefore result in later maturity of breeder hens, because the required body composition for sexual maturity is not reached at an acceptable age. This may even be aggravated because of the need for a more severe feed restriction in breeders selected for fast growth, so that both selection for leanness and more stringent feed restriction act together to delay the minimal fat stores needed to reach sexual maturity.

The third essential key point in females, an accurate feeding based on production rate, is necessary at the start of and throughout the laying period. Not only the level, but also the timing and duration of severe feed restriction during rearing could be important in controlling reproductive performance in later life of the broiler breeders. Results from Bruggeman et al., (1999) have shown the existence of critical periods during rearing in which feeding levels have repercussions on different reproductive parameters (e.g. restriction from week 2 – 15 for delaying age at first egg, from week 7 – 15 for increasing total and servable egg production, from week 2 – 6 for decreasing egg weight, from week 16 – 24 for decreasing multiple follicles sets at age of first egg).

Male broiler breeders that have a very high growth potential also have to follow prescribed growth curves, taking into account the size and maturity of the females at the age of sexual maturity in order to optimize mating and to reduce aggressive behaviour towards the females. A lower crude protein (12% vs. 17%) during rearing of males from 2 – 26 weeks (which occurs separately from the females) improved their fertility in reproductive life (Romero-Sanchez et al., 2007a), and a slow male feed program from 16 – 26 weeks of age not only made them more efficient but also improved their fertility in later life. Moreover it allowed an increasing male feed allocation during the production period which further improved fertility (Romero-Sanchez et al., 2007b) and this was paralleled with an improved broiler progeny performance. This suggests that the
males with the greatest genetic potential were not adequately mating when feed allocation during the production is not adequate and too low (Romero-Sanchez et al., 2008).

**Physiological effects of feed restriction on reproduction in female breeders**

Reproductive processes in females are the result of controlled interaction between the hypothalamus-pituitary and the ovary, and are influenced by environmental, selection or nutritional effects (Decuypere et al., 1999). A well-described effect of feed restriction in broiler breeder females is the reduction of ovary weight, the number of yellow follicles during lay, and the incidence of erratic ovipositions, defective eggs and multiple ovulations (Hocking et al., 1989; Hocking, 1993; Yu et al., 1992). Unrestricted access to feed leads to a low egg production rate and fewer suitable eggs for incubation. This is evidence that the observed disturbances in follicular growth, differentiation, and ovulations in animals fed ad libitum could be attributed to changes in the steroid-producing capacity and in the sensitivity of the follicles to locally produced growth factors in interaction with each other and with gonadotrophins (Decuypere et al., 1999; Onagbesan et al., 2006). There is now overwhelming evidence that the avian ovary is a site of production and action of several growth factors that have also been implicated in the functioning of the mammalian ovary. Several members of the Insulin-like growth factor family (IGF), the Epidermal growth factor family (EGF), the bone morphogenetic protein system (BMP-BMPR), the Transforming growth factor-α family (TGF-α), Fibroblast growth factors (FGF), the Tumour necrosis factor-α (TNF-α) and others have been identified either in the granulosa and/or their compartments of ovarian follicles and in the embryonic and juvenile ovary (reviewed by Onagbesan et al., 2009). From our results (Decuypere et al., 2006; Onagbesan et al., 1999, 2003, 2006) it became clear that for both BMP’s and IGF’s, feed restriction enhances the interaction between growth factors and gonadotrophins for the production of ovarian steroids as well as the proliferation of granulate cells. The interaction may explain the differential yellow follicle number and (partly) egg production rate between restricted and ad libitum fed broiler breeders. Granulosa cells from feed-satiated broiler breeder hens appear susceptible to apoptosis and follicles undergo follicular atresia and prolonged retention of follicles within the hierarchy. Hyperphagia, enhanced adiposity and increased hepatic lipogenesis, lipogenic dysregulation and changed endocrine signals may result in the accumulation of excess triglycerides and fatty acids in non-adipocytes, hence in hypotoxicity and ovarian dysfunction and cell death (Chen et al., 2006).

Besides these changes at the ovarian level, changes in the concentrations and/or pulsatility of luteinizing hormone (LH) and follicle-stimulating hormone (FSH) may be important factors explaining the alterations in follicular development and ovulation between broiler breeders fed different amounts of feed. Plasma LH/FSH ratio was increased by restricted feeding (Bruggeman, 1998; Onagbesan et al., 2006). Moreover, the sensitivity of the pituitary to luteinising hormone releasing hormone (LHRH) as well as to ovarian feedback factors (Hicroids) is influenced by the nutritional level. After sexual maturation and establishment of lay, the long-term feed-restricted animals showed the highest responsiveness to both LHRH-A and ovarian factors, compared to animals fed ad libitum (Decuypere et al., 1999). It is possible that this increased sensitivity at the hypothalamic-pituitary level in feed-restricted animals may as well contribute to the difference in laying performance between ad libitum-fed and restricted broiler breeder females (Bruggeman et al., 1998). However, the growth factors such as IGF and BMP’s e.g. regulating the responsiveness of the ovary to the effect of LH and FSH, are likely more important in controlling rate of ovulation and laying rate of the hen (Onagbesan et al., 2006; Wang and Johnson, 1993).

**Effect of broiler selection on the physiology of reproduction in female breeders**

It was found in many experimental selection models that obesity in hens was associated with poor egg production (Leclercq et al., 1985; Cahaner et al., 1986) and hatchability of eggs produced by lean broiler breeders is higher than that of fat birds (Cahaner et al., 1986). Although comparisons of reproductive performances between fat and lean adult breeder hens are reported in several papers, a straightforward comparison between selection strategies or even between different lines for similar selection procedures is not easy in view of the different feeding programmes used (Buyse et al., 1999). Since lean and fat lines are characterized by a different appetite, even as adult hens, comparisons of reproductive traits under ad libitum feeding conditions can be quite different from restricted
conditions, and restriction conditions will be differential for lean and fat lines if the restriction is not imposed as a percentage of the ad libitum uptake for both lines what is often not realised.

In a study of Onagbesan et al., (1999a), a growth selected line (GL or fat line) and a feed conversion selected line (FC or lean line) were reared under ad libitum and restricted conditions (75% of the ad libitum condition). The average number of yellow follicles/ovary decreased, egg production increased and atresia of yellow follicles decreased under restricted feeding. The effects of restrictions were more pronounced for the FC than for the GL-line. Moreover, in vitro P4 (progesterone) production of granulosa cells as a response to different doses of LH showed no differences for F1 and F2 follicles for ad libitum fed GL hens, while feed restriction made them respond like the FC-line. The latter is similar to laying hens where P4-production by F1-granulosa cells is greater than that of F2-granulosa cells. Similar observations were made for the effects of several growth factors on granulosa cells from both lines and feeding regimens. Taken together, these data indicate that correlated responses in reproductive abilities with selection for rapidly growing and hence fat birds cannot simply be explained in energetic or mechanistic terms. This selection affects endocrine/paracrine mechanisms that, at least partly, are involved in the selection goals (N-retention and growth, protein and lipid metabolism) but because of the multiple effects of hormones and the interrelationship of these hormonal parameters with other endocrine systems, this may be the basis of a number of correlated responses (Decuypere et al., 2003).

**Concluding remarks and suggestions for solutions**

The foregoing discussion, firstly, leads to the main concrete question: can the growth requirement of broiler breeder hens be allied with good reproductive performance, good health, and welfare, either by a feed restriction programme which does not cause undue hunger, or by innovative genetic selection?

Therefore, further breeding should consider not only how to increase production and production efficiency, but also how to alleviate correlated side effects by extending or changing selection goals for obvious economic reasons as well as for the unacceptability of some correlated responses to an increasing number of people. Whether the selection goals have to be extended by additional criteria or changed to settle for lower productivity levels will depend on the answer to the questions asked as to what extent the dilemmas discussed here are merely hazards from a selection policy as applied until now or are causally linked and hence inevitable consequences of the applied selection goals. More and more data in literature illustrate that fast and efficient growth of the broilers and efficient reproduction of the broiler breeder are mutually exclusive selection goals, suggesting that there is a causal negative biological relation. Indeed, changes in growth related hormones or factors, as a consequence of selection for fast and efficient growth seem to be linked to changes of the same growth factors in the ovary of broiler breeders, resulting in gonadal dysfunction. If that is true, then one has to make choices in future broiler breeder management and/or breeding goals.

1. **Intense selection of broilers can be continued with the known consequences of the need for severe feed restriction of the breeders. This becomes difficult to defend when taking into account the animal welfare policy in some societies. New feeding regimens/diets more adapted to the animals’ needs, by diminishing the duration or the intensity of feed restriction or by introducing diets with energy dilution are suggested and have been studied. However, a search for the optimal balance welfare/growth and reproduction goals still needs further investigations and it is questionable if it can be reached at all just by management tools.**

2. **Changing selection goals in the broiler industry, thereby diminishing the need for severe feed restriction in breeders by selection, but without deterioration of the quality demands of the broiler. Introduction of the dwarf broiler breeder hens, which seem to maintain a relatively good reproductive fitness even with ad libitum feed allowances during growth (Hocking et al., 1987; Triyuwanta et al., 1992) could be such an alternative. The presence of the sex-linked dwarf gene (dw) may reduce the need for feed reduction in the breeder while allowing the production of fast-growing offspring because of its sex-linkage and recessiveness. However, one has to bear in mind that this divergent selection leads to an unnatural biological situation in which natural mating can become very difficult because of the extreme size differences between male and female. The production of broilers depends on artificial insemination in such cases, as in the turkey industry. From an ethical point of view, and in the light of foregoing discussion about integrity, such development can and will be questioned.**
3. In view of the possible unavoidable mechanistic link between selection for fast and efficient growth of the broilers and reproductive and welfare problems of broiler breeders, an increasing pressure to settle for lower bird productivity levels (in broilers) in order to reach acceptable productivity that can be combined with acceptable management systems in broiler breeders will be the consequence. Introduction of new genetic lines of broiler breeder females that would tolerate ad libitum feeding could be such a possibility. The production of slower-growing label chickens (France), for example, has led to a practice of mating a heavy broiler cockerel with a slow-growing label breeder hen. The resulting broiler reaches market weight 10 – 12 days later than a standard broiler.

Although breeding is a competitive business and breeding decisions are economically driven, it is also a society sensitive sector because it involves changes in the appearance, behaviour and sometimes welfare of the animals (Fabre technology platform, 2005). It means that a balance of food safety, quality, biodiversity, efficiency, animal health and welfare should be reached and this in an economic viable way. The breeder breeder and broiler sector could be a forerunner for similar problems in other species, but the primary breeders will have to develop novel approaches to help provide sustainable solutions to the problems as mentioned, and of course those problems have first to be defined and then agreed upon. Establishment of breeding goals is indeed an ongoing process that must be regularly reviewed and re-evaluated; this creates on its turn opportunities to include also some of the more “ethical oriented” aspects of these goals. Therefore, future research, even in the broad field of animal sciences, must become even more pluridisciplinary and focus on developing an integrative understanding of the lifetime functioning of whole animals and their interrelationships with the environment, and regular evaluation of these steps with breeding reality (Sefabar, 2005).

Because some of the issues, raised by this new perception on breeding, are fundamentally ethical in nature, both scientists (who are mostly oriented towards very narrow questions) and ethicists (who are oriented to very broad, fundamental and theoretical questions) must direct research at levels of analysis appropriate to the issues (Fraser, 2001). Polarisation of the debate has to be avoided because this could prevent a real ethical analysis of important issues and consensus building, and assigning economic value to considerations such as welfare/integrity should be realized as much as possible. In both aspects also political leaders have their responsibility as consensus builders and value keepers in our society, what at least they are expected to be.

References


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