

Ovarian dysfunction in broiler breeder hens^{*)}

JOHN WILLIAMS

INRA PHASE Division, Tours Research Centre, 37380 Nouzilly, France

Williams J.

Ovarian dysfunction in broiler breeder hens

Summary

Commercial breeds of the domestic chicken include egg-layers (L) that produce table eggs, and meat strains. The former are lightweight hens that lay more than 250 eggs/bird at 60 weeks old. Meat strains are heavier birds bred for good carcass conformation and have a high rate of growth. Broiler breeders (BB), the parental and grand-parental strains, share these characteristics but the female lineage produces fewer eggs than egg-laying strains (175 eggs/bird at 60 weeks old).

The lower rate of lay is the result of several phenomena. The average sequence length is shorter in BB, possibly due to a lower frequency of follicular maturation. Secondly, they lay irregularly. Thirdly, there is a much higher incidence of double-yolked eggs, which may be linked to an irregular development of the follicular hierarchy of the ovary. Some observers suggest the presence of pairs of follicles of similar size in BB, but others point to atresia in the smaller follicles.

This irregular ovarian development is strongly dependent on the nutrition of the growing pullet. BB females normally receive a restricted ration equivalent to approximately 40% of the ad libitum feed intake to achieve the rates of lay cited above. If they are fed ad libitum, the rate of lay is less and there is a greater incidence of abnormalities in the ovary. Additionally, mortality and morbidities (the ascites syndrome, and leg problems) are higher in ad libitum fed hens. The pre-pubertal period from approximately 14 to 18 weeks of age seems to be particularly critical for feeding management. Attempts to simplify this management using fibre dilution of the diet have not been successful.

Behavioural studies on L and BB strains reveal that the latter do not display the full inventory of behaviours. Exploratory behaviours (preening, scratching and perching) are hardly expressed, and restricted feeding necessarily limits feeding behaviour to < 15 minutes per day in BB, whereas this is spread throughout the day in L and interspersed with other behaviours. BB peck at the emptied feeder indicating that the bird is not satiated and may experience undue hunger.

There is a clear ethical problem in the use of BB females in the meat production chain. Without feed rationing, mortality and morbidity are high, egg production is lower; the system is clearly unsustainable. Severe rationing is economically effective, but the acceptability of this technique is open to question if the animals experience chronic hunger. An alternative is a mid-weight strain (used in organic farming systems) but the end product costs more.

Keywords: hens, broiler breeders, ovary, dysfunction

Poultry production – a brief history

The domestic chicken (*Gallus domesticus*) has been bred for many centuries for various purposes ranging from a decorative animal with elaborate feathers to a farming commodity that produces eggs and meat for human consumption. In the second half of the twentieth century, the commercial breeding activity was progressively concentrated in the hands of a small number of companies that developed breeds for the domestic and export markets. Breeds were developed for specific purposes (fig. 1). The mixed breed, useful

for both egg and meat production, gave way in the 1950's to specialised egg and meat breeds. The former were further selected according to egg colour as some markets prefer white eggs and others prefer brown eggs. At the same time, an egg size of 60 to 65 g was a further selection goal. Selection for body weight first targeted the 'broiler' market in North America, where grilled or broiled meat cooked over a charcoal fire is popular. These breeds gradually took over the meat market worldwide, gaining popularity as supermarkets and cut joints became the prominent modes of distribution and consumption.

Modern breeds are hybrids that are the result of crosses made in the parental and grandparental lines (fig. 2). Selection for egg production has been very successful.

^{*)} The author gratefully acknowledges the co-financing of the European project 'Broiler Breeder paradox' (QLRT-2000-01732) by the EU's Fifth Framework Programme, and the work of all colleagues involved in it, whose results are an important source of the results cited herein.



Fig. 1. A broiler chicken of the Ross 308 strain (left) and a egg-laying hen of the hy-line strain (right). Note the differences in carcass conformation: width of the breast and thickness of the shank bone

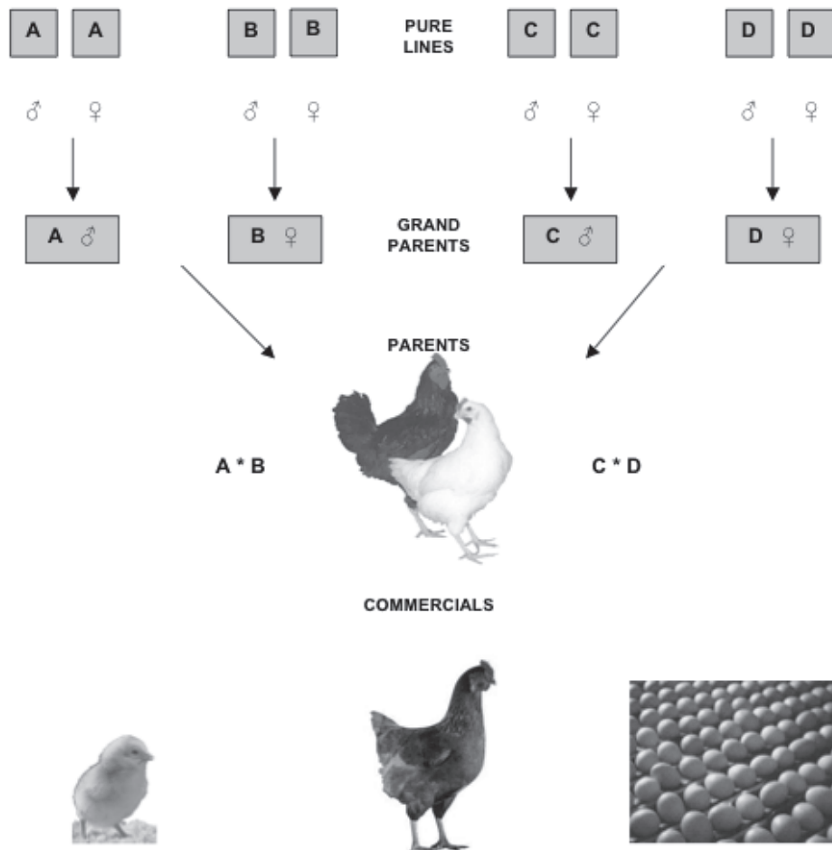


Fig. 2. A typical commercial breeding scheme involves four purebred lines, each producing a male of a female grandparental strain. The crosses of the grandparental strains give rise to a male and a female parental strain whose offspring are a commercial line, either and egg-layer or a meat-type strain

Data from German random sample tests on the Lohmann SSL breed (26) reveal a gain of 11,2% in total egg output from 1980 to 1995, and commercial breeds now produce more than 250 eggs at 60 weeks old, equivalent to a mean rate of lay of more than 90%. At the same time, production has become more efficient and the feed conversion ratio (FCR) has also been improved so that just over 2 g of feed are needed to produce 1 g of egg (ISA Brown Guide 2011). Similarly, the

growth of meat-line chicks has been greatly improved. In 1950, it took 98 days for a chicken to grow to 1.6 kg. By 1986, due to selective breeding, it only took 37 days, and by 2007 just 30 days to reach this target weight. Genetic selection has achieved a 327% increase in the growth rate of a chick in 60 years, and it has also resulted in improvements in feed efficiency. Efforts continue to be made in this direction, for example the

Aviagen company aims to further improve feed efficiency by 20 to 40% using genomic selection.

The genetic potential of modern breeds would probably not be fully exploited had it not been for the research effort dedicated to producing concentrated feed whose composition is not only carefully balanced according to the energy, fat, mineral and vitamin requirements of the growing or adult animal, but also its precise requirements in amino acids. The majority of compound diets rely heavily on two vegetable ingredients, maize corn and soybeans, to which methionine and cystine are added to balance the chicken's requirements for amino acids.

Physiologists will readily comprehend that the high growth rate of a broiler type chicken places high demands on the cardio-pulmonary system. The report published by the scientific committee on the health and welfare of chickens (SCAHAW) of the SANCO directorate of the European Commission concluded "Fast growth rates increase the risk of ascites and sudden death syndrome by increased oxygen demand of the broilers, which intensifies the activity of the cardio-pulmonary systems" (35). Mortality in broiler chickens during growth is seven times higher than that of a slow-growing strain, and the broiler additionally suffers

from lameness, breast blisters and dermatitis that do not affect slow growers to any significant extent.

The welfare of broiler breeder hens

As a consequence of the continuing genetic selection for faster growth and lower FCR in broiler progeny, it became necessary to impose progressively more severe food restriction on parent stock (broiler breeders) during rearing in order to limit their body weight at

sexual maturity (22-24 weeks of age). If breeding birds are fed *ad libitum* (like the progeny), their weights then are much higher (females > 5 kg), fat deposition is excessive, many birds are lame, and mortality associated with skeletal disease and heart disease is unacceptably high (10, 17, 31). High body weight is also associated with impaired immune function (7, 13, 24), abnormalities in ovarian development and structure, increased incidence of multiple ovulations causing reduced production of hatching eggs (9, 12, 15, 23), poor shell quality (28), and reduced fertility in males (11). Hence, the chronic food restriction applied routinely to breeding birds decreases fat deposition, heart disease, skeletal disease, lameness, mortality and food costs, and it increases fertility in both females and males (fig. 3).

All breeding birds are fed *ad libitum* to 1 week of age, and thereafter according to programmes of quantitative restriction recommended by the breeding companies. In the EU, rations are usually provided once a day and are eaten in less than 15 min (19). Females fed according to one such programme (Ross 1) to 21 weeks of age gained about a third as much weight and ate about a third as much food as did *ad libitum*-fed control birds (29). This level of food restriction is severe. It is at its most severe from 7 to 15 weeks of age, when a female's daily intake is only about a quarter of that of *ad libitum*-fed controls at the same age (30).

Behaviour of rationed breeding birds differs markedly from that of *ad libitum*-fed broiler progeny. The former are much more active than the latter, and they show increased pacing before expected feeding time and increased drinking and pecking at non-food objects afterwards (19). Expression of these activities is often stereotyped in form, and is characteristic of frustration of feeding motivation (4). It is correlated positively with the level of food restriction imposed (31). A comparison of *ad-lib* fed and restricted-fed broiler breeders showed that the latter spent a significant part of their time pecking at the empty feeder, and significantly more time packing at the litter than *ad-lib* fed birds (22). There is also evidence that blood indices of stress (heterophil/lymphocyte ratio, basophil and monocyte frequencies, plasma corticosterone concentration) are higher in restricted-fed breeding birds than in unrestricted birds (14, 18, 20, 21), and are correlated positively with the level of restriction imposed (13).

Taken together, these facts indicate that current commercial food restriction of breeding birds causes poor welfare. The breeding bird sector is thus presented with a welfare dilemma, because on the one hand stock may be suffering through chronic hunger, while on the other hand less severe restriction leads to defects in health and reproduction, or high mortality. In an experiment in which qualitative food restriction treatments (diet dilution with sugar-beet pulp, oat hulls or sawdust; appetite suppression with calcium propionate), with *ad libitum* access to food, were compared with quantitative restriction treatments (29), several conclusions were

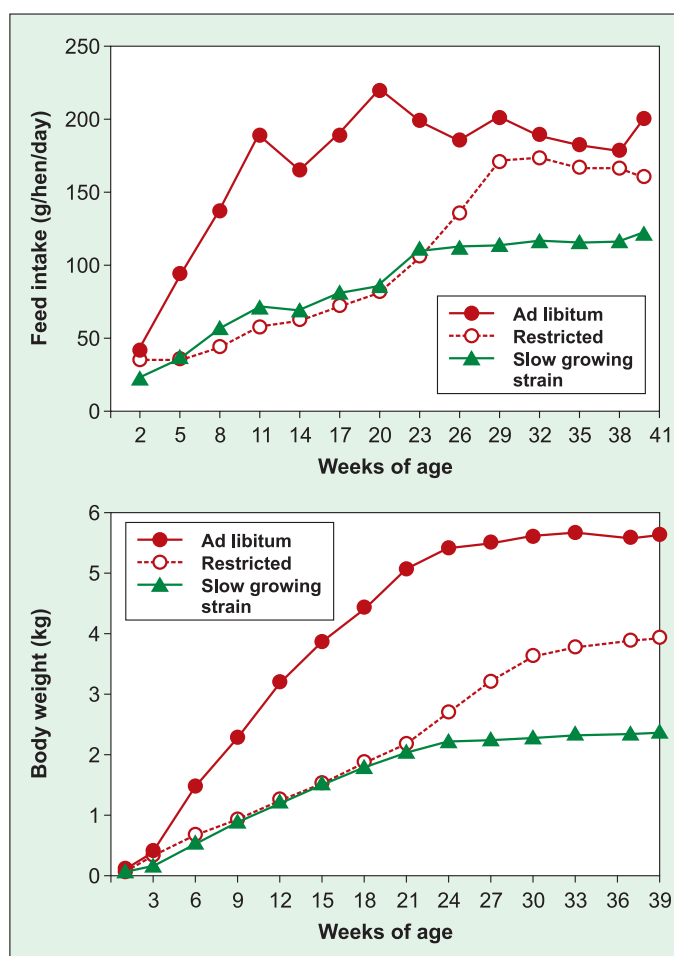


Fig. 3. Mean daily feed intake per hen (top panel) and body weight (bottom panel) in a broiler breeder fed *ad libitum* (continuous red line) or restricted (dashed red line) and a slow-growing strain (green line) used for organic or 'Label Rouge' production, from 0 to 40 weeks of age; (n = 12 pens of 14 hens per treatment). Adapted from the final report of European Project BBP, contract number QLRT-2000-01732

drawn. First, different methods of qualitative restriction can be used to control broiler breeder growth rate within desired limits. Problems with these include reduced uniformity in weight gain, increased excreta production and/or increased cost. Secondly, although they may suppress abnormal oral behaviours, they do not alter the increased general activity correlated with suppression of growth rate, which may more accurately reflect associated hunger. Furthermore, suppression of abnormal oral behaviours may only rarely correspond with reduction in blood indices of stress, and so cannot be taken to indicate improved welfare. In addition, some methods can add to physiological stress. There was insufficient evidence of improved welfare, based on behavioural and physiological criteria, to justify advocating the suitability of any of these methods for commercial use. In another experiment in which feeding motivational state was measured with different qualitative and quantitative restriction treatments (30), there was evidence that feeding motivation may be partially suppressed (in the short-term) with qualitative restriction due to a „gut-fill” effect.

Effects of feed on ovarian development in broiler breeders

In birds, only the left ovary develops at puberty and the right gonad remains vestigial. At 10 weeks of age, the organ has a granular appearance due to the presence of many small ovarian follicles (fig. 4). It grows rapidly from this age and when the hen starts to lay eggs, at 18-20 weeks of age, the striking feature is the presence of many large, yellow follicles and smaller yellow or white follicles. This appearance is due to yolk deposition in the cytoplasm of the oocyte. Removal and ranking of these large, yellow follicles reveals a hierarchy, which can be traced back by measurement with callipers or by weighing to beyond forty follicles. The largest follicle in a young laying hen has a mean diameter of approximately 27mm and it is 32-34 mm in hens at the end of their commercial productive period.

If broiler breeders are feed-restricted, the ovarian follicular hierarchy is very similar to that of a laying strain, but the average rate of lay is however lower in broiler breeders. If fed *ad libitum*, broiler breeders have more large yellow follicles in the hierarchy, and some are of identical size (fig. 5). This is coincident with the laying of double-yolked eggs (9% of total eggs in unre-

stricted fed birds; 2% in restricted fed birds) during the first two months of lay (1). In addition, ovarian abnormalities have been observed (3) in the form of ovarian involution and apoptosis-induced follicular atresia affecting the granulosa cells of the follicle. These abnormalities were often associated with signs of internal ovulations such as the presence of viscous and yolk-like fluid in the body cavity and signs of lipotoxicity.

The pattern of egg laying in broiler breeder hens

Gallinaceous birds lay eggs in sequences of varying lengths at more or less regular intervals. The term 'sequence', as used, refers to the total eggs laid on successive days; it is sometimes called a clutch. The first egg of a sequence is laid relatively early in the day, and successive eggs usually are laid an hour or two later each day. This time interval is known as the lag. When the cumulative lag exceeds 8 hours, the sequence ends and no egg is laid on the following day, referred to as the 'pause' day. Normally, sequences are separated by one pause day.

We have made an exhaustive analysis of sequence length in a strain of laying hen and a broiler breeder strain (36). The egg layers were fed *ad libitum* while

the broiler breeders were rationed. Several differences were observed. First, laying strains tended to lay longer sequences than the broiler breeder. This was particularly noticeable early in lay (months 2-3) where the range of sequence lengths observed in a layer was 1-64 eggs (modal length 3) against 1-21 (modal length 2) in the broiler breeder. By months 12-13, this range was 1-38 (modal length 2) in a layer compared to 1-8 (modal length 1) in the broiler breeder. This is part of the explanation



Fig. 4. Left panel: the ovary of an immature hen (10 weeks of age). Right panel: The ovary of a laying hen showing the large, yellow yolky follicles

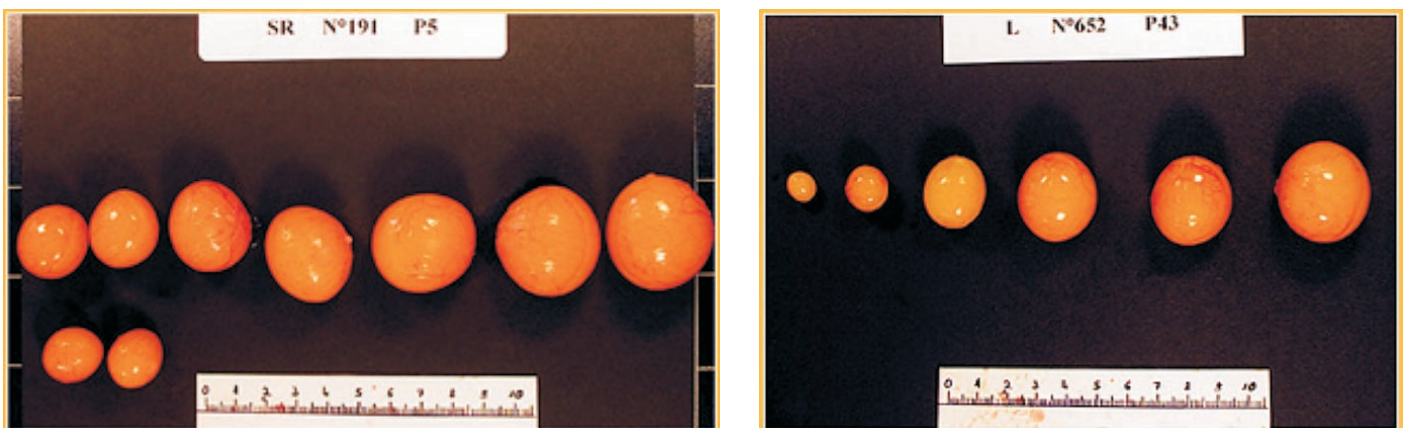


Fig. 5. Left panel: Dissection of the ovary of a restricted-fed broiler breeder hen (30 weeks old) showing the hierarchy of yellow yolky follicles. Right panel: Dissection of the ovary of a slow-growing strain of hen (30 weeks old). The examples shown are representative of the population. Data taken from European Project BBP, contract number QLRT-2000-01732

of the lower rate of egg production in a broiler breeder hen. Another important factor was the irregularity of the laying pattern in broiler breeders. In early lay, over 60% of the layer strain laid eggs in regular sequences separated by a single pause day, but only 27% of the broiler breeder hens were in this category. The majority of the broiler breeders (54.9%) showed irregularities characterized by 2 to 5 pause days between two consecutive sequences, while this occurred in only 21% of the layer breed. In the late stage of lay, these irregularities became more frequent in the layer strain, while in the broiler breeder strain, there was almost no regular laying and a high proportion of the hens had gone out of lay altogether for a mean duration of 33 days before resuming a new laying period. The irregularities that we and many others have observed are usually attributed to soft-shelled eggs (that are not always detected) or to internal ovulations. However, in view of the structural irregularity of the broiler ovary in ad libitum fed hens, the possibility of a gap in the follicular hierarchy cannot be excluded.

Physiological mechanisms

The asynchronous nature of the hen's ovulation cycle, whose length is slightly greater than 24 hours, has fascinated physiologists for many decades. Why are successive eggs in a sequence laid at a slightly later time on successive days? The hypothesis that best explains this was elaborated by Richard Fraps who proposed a relationship between a diurnal rhythm in thresholds of response in the neural apparatus and 'excitation hormone' concentration (6). The diurnal rhythm of the threshold of response is represented by the sine curve (fig. 6), and the sensitive region corresponds approximately to the dark period under a lighting schedule of 14 h light and 10 h darkness. 'Excitation hormone' concentration was associated with the maturing follicle and was tentatively associated with progesterone on the basis of experiments with injections of this hormone that advanced the time of ovulation.

It is interesting that two Canadian scientists developed a mathematical model of Frap's hypothesis that they jokingly named 'paper hens'. This model based on the neural rhythm and a rhythm of follicular maturation is able to predict the observed time of oviposition of eggs in sequences of 2 to 10 eggs with remarkable accuracy (5). One may draw the conclusion that it is unnecessary to introduce additional variables in this model and that work should concentrate on identifying the mechanisms that lie beneath these two interacting rhythms.

The advent of the radioimmunoassay, tissue culture and molecular

biology enabled many investigators, including those from my laboratory in Nouzilly, to piece together a few more pieces of the puzzle concerning the identity of 'excitation hormone' and the mechanism of follicular maturation. With the advent of the radioimmunoassay, investigators were able to measure progesterone in the blood of birds, and I have selected a few observations to support the hypothesis that progesterone is produced by the granulosa cells of large follicles of the ovary in increasing quantities as the follicle matures, and that it is currently the best candidate for the title of 'excitation hormone'. First, in the grouse (*Lagopus scoticus*), a decline in plasma progesterone is associated with the seasonal involution of the ovary. The presence of a developed ovary with yellow yolky follicles weighing more than 10 g is associated with progesterone plasma concentrations of more than 1 ng/ml, while these concentrations are always less than 0.6 ng/ml in the regressed ovary weighing less than 1 g (36). Also in growing pullets, plasma progesterone remains low while the ovary does not have any large follicles, and increases just before the onset of egg laying (37). Secondly, it is generally accepted that a peak of progesterone in the plasma occurs at 4 to 6 hours before the anticipated time of ovulation. Thirdly, this peak of progesterone in plasma is accompanied by a peak of LH. In the bird, ovulation can be induced by injecting ovine LH, and an injection of oLH causes plasma progesterone to increase. Finally, in multiple ovulating hens there is only one peak of LH of normal magnitude during the ovulatory cycle (34), and only one peak of progesterone but the plasma concentration is approximately twice as high as in single ovulating hens (36). However, this increase is more marked near the time of expected ovulation when a mature follicle is present in the ovary (36). In fact, a small dose of progesterone has been shown to exert a positive feedback ovulation acting through a stimulation of the secretion of LH, providing oestradiol is present in the circulation (38, 39).

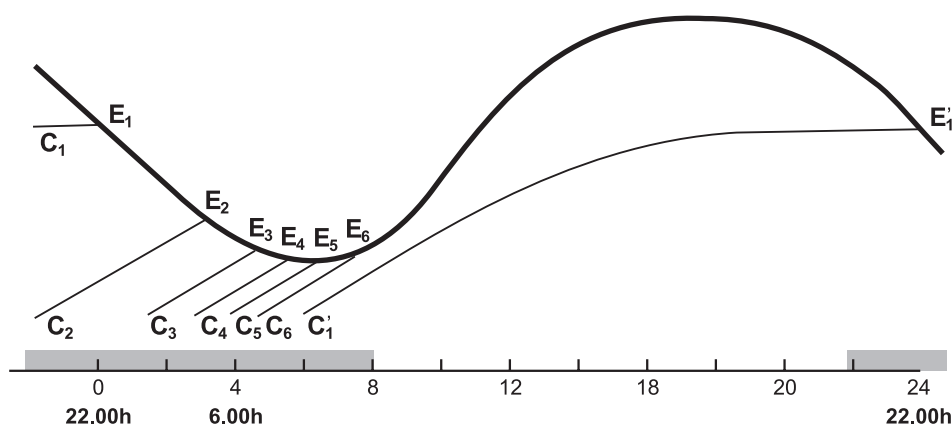


Fig. 6. Relationships between diurnal rhythm in thresholds of response (E_1 - E_6 , E_1' ...) in the neural apparatus and excitation hormone concentrations in a 6 egg sequence followed by one day with no excitation constituting a 7-day cycle. Ovarian follicles are designated by C_n . Adapted from (28)

Follicular maturation

Follicular maturation may be defined as the acquisition of the ability to secrete progesterone in sufficient quantity to trigger a response in the neural apparatus leading to ovulation of the ovum. This can be studied *in vitro* as it is possible to culture both the thecal and the granulosa cells of the avian ovarian follicle. We showed several years ago in a short-term incubation system using M199 that the granulosa cells produced considerable quantities of progesterone and that this was proportional to the position of the follicle in the hierarchy (36). That is, the first (F1) follicle produced most progesterone, followed by the second (F2) and the third (F3). This secretion response could be observed after 3 hr incubation and if the cells were stimulated by exposure to ovine LH, the response was greater and the hierarchy of the response was maintained. After 24 hr, the basal secretion had diminished. However, an oLH challenge produced a very large increase in progesterone secretion with the same hierarchy of response. There was an interesting feature of this response after 24 hr incubation. First, the F2 follicle produced a similar amount of progesterone to the F1 follicle after 3 hr incubation, and the F3 follicle similarly produced as much as the F2 after 3 hr incubation. In other words, there was evidence for follicular maturation.

Other authors have repeated these observations (25) and have also underlined some particular features of the avian ovary compared to mammals. First, the theca does not produce progesterone but it does produce androstenedione and secondly, although FSH can stimulate granulosa cell secretion of progesterone, it is not as effective as LH. Thirdly, the IGF system appears to play an important role in regulating the secretion of progesterone in the avian ovary as in mammals. It seems that follicular maturation in the hen can be viewed as the ability to secrete large amounts of progesterone, but the regulation of this process may depend as much on local paracrine or autocrine regulation as on systemic control by the hypothalamo-hypophyseal-ovarian axis.

Effects of restricted feeding on the endocrine ovary of the broiler breeder

There is no doubt that laying broiler breeder hens fed *ad libitum* during early life show an over-development of the ovary as mentioned previously. However, experiments on hormone production by granulosa and thecal cells are conflicting. The IGF-I induced production of progesterone by granulosa cells was higher in rationed than in *ad libitum* fed hens in one experimental strain selected for growth, but the opposite result was observed in a second strain selected for feed conversion efficiency. The F1 > F2 > F2 relationship held true, however, in all cases (25). The IGF system in the ovaries of broiler breeder hens during the juvenile growth phase was evaluated to measure the effect of feed restriction (8). The transcripts of IGF-I, IGF-II, IGF receptor

(IGF-R), two IGF Binding Proteins (IGF-BP2 and IGF-BP5), GH receptor (GH-R) and insulin receptor (I-R) were measured at 4, 8, 12 and 16 weeks of age in the ovaries of *ad libitum* fed and feed restricted hens. The transcripts of all genes screened were detected in all feed regime groups and at all ages sampled. However, no significant overall effects of feed restriction on these transcripts were found despite the marked difference in body growth (200% at 16 weeks of age). Similarly there were no significant age effects except for the expression of GH-R that showed a decrease after 8 weeks of age ($p < 0.01$). Feed restriction seems to have a relatively limited effect on the expression of these components of the ovarian IGF system in juveniles, but possible changes nearer to sexual maturity (beyond 16 weeks of age) remain to be investigated. It does not seem that components of the IGF system, GH or insulin are involved in the mechanisms that alter ovarian development and are affected by restricted feeding during growth.

Recent work has demonstrated that the leptin receptor could be involved in the regulation of the follicular hierarchy as differences were noted in its expression in the ovary. Whereas expression of the leptin receptor mRNA did not change in the theca, it clearly decreased with follicular differentiation in the granulosa of slow growing layer hens. In fast growing broiler breeder hens fed *ad libitum* and presenting significant reproductive dysfunction, the decrease was disrupted and dramatic up-regulation of granulosa cell expression of the leptin receptor was observed (2). On the other hand, feed restriction decreased the overall level of expression of the leptin receptor mRNA and restored the decrease with follicular growth. The level of expression of the leptin receptor probably modulates the action of leptin on follicular differentiation. Since blood leptin and other metabolic factors were not affected by the genotype or by nutritional state, the factors involved in the regulation of leptin receptor gene expression remain to be determined, but these results demonstrate the involvement of leptin in the nutritional control of reproduction in birds. Acting via action the ovary, leptin possibly controls follicular hierarchy through the regulation of steroidogenesis.

Alternative feeding, behaviour and welfare of broiler breeders

Several attempts have been made to improve the welfare of broiler breeders by altering the diet composition. Reducing energy concentration of the rations by increasing the fibre content of mash diets fed *ad libitum* to broiler breeders limited body weight gain but increased variability and physiological indices of welfare compared with conventionally restricted birds (29). However, in a small-scale experiment Zuidhof et al. (40) fed a restricted amount of feed containing fibre and observed an apparent improvement in bird welfare based on changes in behaviour and heterophil – lymphocyte ratios. This was repeated on a larger scale (16)

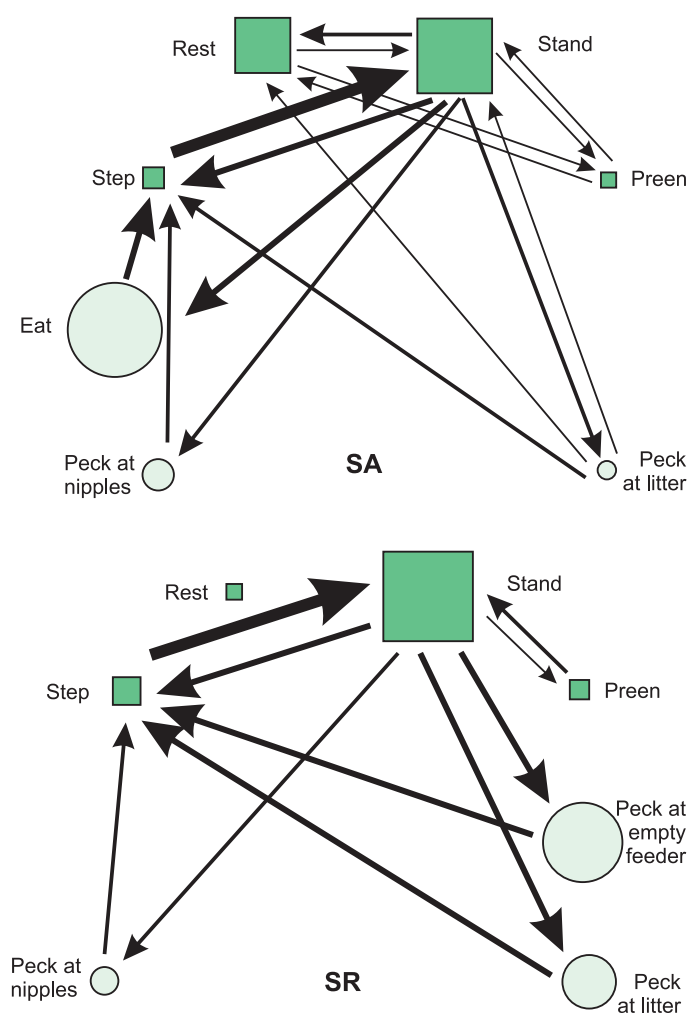


Fig. 7. Transition analysis comparing the behaviour of standard broiler breeders fed *ad libitum* (SA) or fed restricted (SR) 4-5 h after feed distribution. The size of squares is proportional to the time spent in corresponding states; that of circles is proportional to the number of pecks (events); and the size of the arrows is proportional to the frequency of transitions. While the SA hens spend time feeding the SR birds instead peck either at the empty feeder or the litter. Data originally reported to the EC under contract QLRT-2000-1732

which confirmed that hens decreased spot pecking when rationed and fed on a diet containing 200 g fibre per Kg.

Within the framework of an EC funded cooperative research project involving three member states and a breeding company, the time-budgets of broiler breeders were measured at 3, 9, 15, 21, 27 and 33 weeks of age, by scan sampling (12 scans per h) during 3 periods of 1 h (1 = prior to, 2 = immediately after, 3 = 5 h after feed distribution) in an attempt to find a behavioural indicator that could be used in selection for individual adaptability (27). This proved to be unsuccessful, but the authors observed a clear difference in the behaviours of restricted and *ad libitum* fed broiler breeders. The restricted birds spent far more time pecking at the empty feeder or the litter when *ad libitum* fed birds were resting or preening, indicating that restricted birds were not satiated. Furthermore, both *ad libitum* fed broilers and layers were studied in this experiment and the data

show that these chickens spread their feeding over time whereas restricted fed animals typically consumed their feed in less than 15 minutes. A more detailed observation and analysis of the behaviour of restricted or *ad libitum* fed broiler breeders revealed significant differences (22). This analysis, based on quantifying the properties of behavioural states and the transitions from one behavioural state to another, showed that restricted birds spent twice as much time standing, twice as much time stepping, thirteen times less time resting and 30% more time preening than *ad libitum* fed birds. In addition, there was a significant increase ($\times 2.3$) in the number of transitions from stepping to standing in restricted compared to *ad libitum* fed birds (fig. 7).

Conclusion

The continued selection of broiler strains of the domestic chicken for body weight and breast muscle conformation over past decades has resulted in a series of undesirable correlated responses. These have negatively affected the hen's ability to reproduce. Compared to a strain selected for egg production, the broiler breeder lays less eggs which are of poorer quality and fertility (9), and the ovarian follicular hierarchy shows irregular growth, leading to more double-yolked eggs, and there is also increased ovarian atresia. Overall reproductive efficiency can be improved if the birds are reared and then maintained on a restricted diet, and this also has the advantage of reducing mortality from 31% to 6% (9). However, the available evidence suggests that birds on a restricted diet are not satiated and may experience chronic hunger, a view echoed in a report from the European Commission's Health and Consumer Directorate (35) that noted 'the current commercial food restriction of breeding birds causes poor welfare'. More than thirty years' research has not resulted in any innovative solution and further experimentation on feed restriction is very difficult to justify ethically since the essential control treatment (*ad libitum* feeding) leads to very high mortality and probable suffering of the animals.

It is time for the legislator and the consumer to make an informed choice on the system of producing chicken meat in the EU. This choice must also take into account the welfare problems of the growing broiler chicken which is fed *ad libitum* to obtain the maximum growth rate. The European Food Safety Agency's (EFSA's) recent reports (32, 33) on broiler poultry production and on welfare aspects of the management and housing of the grand-parent and parent stocks make clear statements. First in relation to the growing broiler chick: 'The major welfare concerns that have a genetic basis and that may interact with management factors to lead to poor welfare include skeletal disorders, contact dermatitis, ascites and sudden death syndrome. Most of these are linked with fast growth rates.' Secondly, there is a recommendation that 'birds that require less feed restriction should be selected as future breeders.

This may involve reduced selection pressure on high growth rates'. Interestingly, slower growing strains of chicken that do not have these welfare problems are available, and their parental and grand-parental lines do not require feed restriction to reproduce efficiently. These slow-growing strains are produced by major breeding companies and used in Europe for various quality labelled systems, including organic poultry, and free-range production. As they grow more slowly than broilers, they consume more feed and the production cost is increased, but the organoleptic quality is better.

Since 1997, the legally binding Protocol annexed to the Treaty of Amsterdam recognizes that animals are „sentient beings”, and requires the EU and its Member States to „pay full regard to the welfare requirements of animals”. Slower growing poultry are more compliant with this requirement than broiler production and it may only be a matter of time before the European Commission fully takes note of the EFSA reports and phases out the production of broiler chickens in Europe.

References

1. *Bruggeman V., Onagbesan O., Ragot O., Metayer S., Cassy S., Favreau F., Jégo Y., Trevidy J. J., Tona K., Williams J., Decuyper E., Picard M.*: Feed allowance-genotype interactions in broiler breeder hens. *Poult. Sci.* 2005, 84, 298-306.
2. *Cassy S., Metayer S., Crochet S., Rideau N., Collin A., Tesseraud S.*: Leptin receptor in the chicken ovary: potential involvement in ovarian dysfunction of ad libitum-fed broiler breeder hens. *Reprod. Biol. Endocrinol.* 2004, 8, 72.
3. *Chen S. E., McMurtry J. P., Walzem R. L.*: Overfeeding-induced ovarian dysfunction in broiler breeder hens is associated with lipotoxicity. *Poult. Sci.* 2006, 85, 70-81.
4. *Duncan I. J. H., Wood-Gush D. G. M.*: Thwarting of feeding behaviour in the domestic fowl. *Anim. Behav.* 1972, 20.
5. *Etches R. J., Schoch J. P.*: A mathematical representation of the ovulatory cycle of the domestic hen. *Br. Poult. Sci.* 1984, 25, 65-76.
6. *Fraps R. M.*: Neural basis of diurnal periodicity in release of ovulation-inducing hormone in fowl. *Proc. Natl. Acad. Sci. USA* 1954, 40, 348-356.
7. *Han P. F. S., Smyth J. R.*: The influence of restricted feed intake on the response of chickens to Marek's disease. *Poult. Sci.* 1972, 51, 986-990.
8. *Heck A., Metayer S., Onagbesan O. M., Williams J.*: mRNA expression of components of the IGF system and of GH and insulin receptors in ovaries of broiler breeder hens fed ad libitum or restricted from 4 to 16 weeks of age. *Domest. Anim. Endocrinol.* 2003, 25, 287-294.
9. *Heck A., Onagbesan O., Tona K., Metayer S., Putterflam J., Jégo Y., Trevidy J. J., Decuyper E., Williams J., Picard M., Bruggeman V.*: Effects of ad libitum feeding on performance of different strains of broiler breeders. *Br. Poult. Sci.* 2004, 45, 695-703.
10. *Hocking P.*: Welfare of broiler breeders. *Proc. WPSA Spring Meeting, Scarborough, UK* 1999, pp. 18-23.
11. *Hocking P. M., Duff S. R. I.*: Musculo-skeletal lesions in adult male broiler breeder fowls and their relationships with body weight and fertility at 60 weeks of age. *Br. Poult. Sci.* 1989, 30, 777-784.
12. *Hocking P. M., Gilbert A. B., Walker M., Waddington D.*: Ovarian follicular structure of White Leghorns fed ad libitum and dwarf and normal broiler breeders fed ad libitum or restricted until point of lay. *Br. Poult. Sci.* 1987, 28, 493-506.
13. *Hocking P. M., Maxwell M. H., Mitchell M. A.*: Relationships between the degree of food restriction and welfare indices in broiler breeder females. *Br. Poult. Sci.* 1996, 37, 263-278.
14. *Hocking P. M., Maxwell M. H., Mitchell M. A.*: Welfare assessment of broiler breeder and layer females subjected to food restriction and limited access to water during rearing. *Br. Poult. Sci.* 1993, 34, 443-458.
15. *Hocking P. M., Waddington D., Walker M. A., Gilbert A. B.*: Control of the development of the ovarian follicular hierarchy in broiler breeder pullets by food restriction during rearing. *Br. Poult. Sci.* 1989, 30, 161-173.
16. *Hocking P. M., Zaczek V., Jones E. K. M., Macleod M. G.*: Different concentrations and sources of dietary fibre may improve the welfare of female broiler breeders. *Br. Poult. Sci.* 2004, 45, 9-19.
17. *Katanbaf M. N., Dunnington E. A., Siegel P. B.*: Restricted feeding in early and late-feathering chickens. 1. Growth and physiological responses. *Poult. Sci.* 1989, 68, 344-351.
18. *Katanbaf M. N., Jones D. E., Dunnington E. A., Gross W. B., Siegel P. B.*: Anatomical and physiological responses of early and late feathering broiler chickens to various feeding regimes. *Arch. Geflügelk.* 1988, 52, 119-126.
19. *Kostal L., Savory C. J., Hughes B.*: Diurnal and individual variation in behaviour of restricted-fed broiler breeder. *Appl. Anim. Behav. Sci.* 1992, 32, 361-374.
20. *Maxwell M. H., Hocking P. M., Robertson G. W.*: Differential leucocyte responses to various degrees of food restriction in broilers, turkeys and ducks. *Br. Poult. Sci.* 1992, 33, 177-187.
21. *Maxwell M. H., Robertson G. W., Spence S., McCorquodale C. C.*: Comparison of haematological values in restricted- and ad libitum-fed domestic fowls: white blood cells and thrombocytes. *Br. Poult. Sci.* 1990, 31, 399-405.
22. *Merlet F., Putterflam J., Faure J. M., Hocking P. M., Magnusson M. S., Picard M.*: Detection and comparison of time patterns of behaviours of two broiler breeder genotypes fed ad libitum and two levels of feed restriction. *Appl. Anim. Behav. Sci.* 2005, 94, 255-271.
23. *Nestor K. E., Bacon W. L., Renner P. A.*: The influence of genetic changes in total egg production, clutch length, broodiness and body weight on ovarian follicular development in turkeys. *Poult. Sci.* 1980, 59, 1694-1699.
24. *O'Sullivan N. P., Dunnington E. J., Smith E. J., Gross W. B., Siegel P. B.*: Performance of early and late feathering broiler breeder females with different feeding regimens. *Br. Poult. Sci.* 1999, 32, 981-995.
25. *Onagbesan O. M., Vleugels B., Buys N., Bruggeman V., Safi M., Decuyper E.*: Insulin-like growth factors in the regulation of avian ovarian functions. *Domest. Anim. Endocrinol.* 1999, 17, 299-313.
26. *Presinger R., Flock D. K.*: Genetic changes in layer breeding. *Proc. 49th Ann. Meeting Europ. Ass. Anim. Production.* 1998, 38, 20-28.
27. *Putterflam J., Merlet F., Faure J., Hocking P., Picard M.*: Effects of genotype and feed restriction on the time-budgets of broiler breeders at different ages. *Appl. Anim. Behav. Sci.* 2006, 98, 100-113.
28. *Robinson F. E., Wilson J. L., Yu M. W., Fassenko G. M., Hardin R. T.*: The relationship between body weight and reproductive efficiency in meat-type chickens. *Poult. Sci.* 1993, 72, 912-922.
29. *Savory C. J., Hocking P. M., Mann J. S., Maxwell M. H.*: Is broiler breeder welfare improved by using qualitative rather than quantitative food restriction to limit growth rate? *Anim. Welfare* 1996, 5, 105-127.
30. *Savory C. J., Larivière J.-M.*: Effects of qualitative and quantitative food restriction treatments on feeding motivational state and general activity level of growing broiler breeders. *Appl. Anim. Behav. Sci.* 2000, 69, 135-147.
31. *Savory C. J., Maros K.*: Influence of degree of food restriction, age and time of day on behaviour of broiler breeder chickens. *Behav. Processes* 1993, 29, 179-189.
32. Scientific Opinion on the influence of genetic parameters on the welfare and the resistance to stress of commercial broilers. EFSA.
33. Scientific Opinion on welfare aspects of the management and housing of the grand-parent and parent stocks raised and kept for breeding purposes. EFSA 2010.
34. *Sharp P. J., Beuving G., Middelkoop J. H. van*: Plasma luteinizing hormone and ovarian structure in multiple ovulating hens. 1976, 1259-1267.
35. Welfare of Chickens Kept for Meat Production (Broilers). *Europ. Comm. Health&Consumer Protection Directorate-General Directorate B – Scientific Health Opinions Unit B3 – Management of scientific committees II*; 2000.
36. *Williams J. B.*: The endocrine control of egg production in poultry. University of Edinburgh 1978.
37. *Williams J. B., Sharp P. J.*: A comparison of plasma progesterone and luteinizing hormone in growing hens from eight weeks of age to sexual maturity. *J. Endocrinol.* 1977, 75, 447-448.
38. *Wilson S. C., Sharp P. J.*: Induction of luteinizing hormone release by gonadal steroids in the ovariectomized domestic hen. *J. Endocrinol.* 1976, 71, 87-98.
39. *Wilson S. C., Sharp P. J.*: The effects of progesterone on oviposition and ovulation in the domestic fowl (*Gallus domesticus*). *Br. Poult. Sci.* 1976, 17, 163-173.
40. *Zuidhof M. J., Robinson F. E., Feddes J. J., Hardin R. T., Wilson J. L., McKay R. I., Newcombe M.*: The effects of nutrient dilution on the well-being and performance of female broiler breeders. *Poult. Sci.* 1995, 74, 441-456.

Corresponding author: Prof. John Williams, INRA PHASE Division, Tours Research Centre, 37380 Nouzilly, France