OVARIAN FORM AND FUNCTION IN BROILER BREEDERS:  
EFFECTS OF AGING AND OBESITY

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INTRODUCTION

Coincident with significant improvements in growth rate of broiler chickens has been a progressive reduction in reproductive fitness of broiler parent stocks (Opel, 1979; Siegel and Dunnington, 1985; Robinson, 1991). Broiler breeders, as well as turkey breeding stocks, are becoming dangerously unfit for reproducing due to the strong negative relationship between body weight and reproductive efficiency. Inefficiency is evidenced by decreased egg production, an increased incidence of hen mortality, infertility and embryonic loss.

Management protocols have been developed and are continually being refined to assist in the optimization of egg output, as well as the fertility and hatchability of eggs. In a sense, such management programs aim to overcome the above mentioned negative relationship by striving to program the broiler breeder hen to make her act and function like a Leghorn, while at the same time, producing offspring that grow quickly and efficiently. These hens must be the best of both worlds.

Egg production rate of all chickens is negatively affected by aging (Joyner et al., 1987; Bahr and Palmer, 1989). Hence, broiler breeders have two major factors, obesity and aging, contributing to poor reproductive efficiency. Other factors that can influence female reproduction are nutrition, environmental condition and disease status. These factors are poorly understood in terms of specific effects on the production of hatching eggs.

This review is a report of research conducted from 1987 to the present at the University of Alberta to further determine how ovarian form and function in broiler breeders are influenced by reproductive senescence and obesity.

A REVIEW OF THE OVULATORY CYCLE OF THE CHICKEN

Almost all of the research concerning the definition of the physiology of egg production in chickens has been undertaken using highly-efficient egg-type hens (for review see Etches, 1984; 1990). In indeterminate layers, (most domestic poultry), eggs are laid in sequences of one or more eggs, separated by a pause (non-laying) day, usually of a single day duration. The first egg of a sequence is laid shortly after "lights on", and successive ovipositions (laying of eggs) follow on successive days, slightly later each day. Hens that are laying at high rates lay long sequences (each egg separated by a period of time which is close to 24 hours). A sequence is terminated when the time of oviposition approaches approximately 6 to 8 hours after "lights on". A pause day follows, and a new sequence commences following the pause.

In egg-type chickens, the timing of oviposition is highly indicative of the timing of ovulation (release of a mature ovum from the ovary). The ovulatory cycle is regulated by two independent systems. The first

1Presentation made to the 1992 National Breeders Roundtable, May 7, 1992, St. Louis Mo.
is the development (maturation of hormone-producing systems) of the large ovarian follicles. The ovary of egg-type hens usually consists of an orderly hierarchy of five to seven large follicles (greater than 1 cm). The largest follicle (F1) is the nearest to ovulation. To ovulate a follicle must be sufficiently "mature" that its granulosa cells will synthesize progesterone in response to a preovulatory surge of luteinizing hormone (LH). The small ovarian follicles are a major source of estrogens and androgens, and this steroid output is highly LH responsive (Robinson and Etches, 1986). A schematic representation of ovarian steroidogenesis is presented in Figure 1.

The second factor regulating the ovulatory cycle is the poorly understood "circadian oscillator" which limits the release of LH to a period of about 8 hours (the "open period for LH release"). It is thought that the length of the open period is mirrored by the extremes of the egg-laying period.

In egg-type hens there is little evidence of ovarian dysfunction, while in meat-type hens, various reproductive disorders have been described. The incidence of arhythmic sequences was reported by Jaap and Muir (1968) to be higher in meat-type hens than in egg-type hens. The presence of two eggs in the oviduct at one time was reported by Jaap and Muir (1968) and by van Middelkoop (1972). Hocking et al. (1987) found that broiler breeder hens had a greater number of atretic yellow follicles than did egg-type hens. A condition known as "erratic oviposition and defective egg syndrome" (EODS) has become a common term to include several reproductive problems including, follicular atresia, internal ovulation, internal laying, the production of soft-shelled or membranous eggs, multiple-yolked eggs, multiple-egg days and ovipositions not occurring in sequences (Van Middlekoop, 1971; 1972; Siegel and Dunnington, 1985).

EFFECTS OF AGING

The influence of aging on egg production rate has been the subject of much research, and a comprehensive review of the subject was prepared by Bahr and Palmer (1989). A typical egg production curve of commercial SCWL hens (Shaver) is presented in Figure 2. The data were collected from 160 individually-caged hens which survived to 68 weeks of age. Individual production rates were calculated for each 14-day period and the data were smoothed by transformation to a 5th order polynomial regression. In the industry, egg-type hens continue to lay at a rate of over 80% production for many months under optimal conditions.

An egg production curve based on individual hen data from 120 surviving feed-restricted broiler breeders (Indian River) is also shown in Figure 2. Data were collected and handled in an identical manner to that described above for egg-type hens. These hens were photo-stimulated 2 weeks later (20 weeks of age) than the egg-type hens were. Broiler breeders generally do not achieve high rates of egg production compared to egg type hens.

Robinson et al. (1990) reported a study concerning sequence length changes in hens throughout a production cycle. The data presented in Figure 3 represent average lengths of the laying sequences of the previously described 160 SCWL and 120 broiler breeders, the data being analyzed in the manner reported by Robinson et al. (1990). The shape of a sequence length curve resembles the shape of the egg production curves (Figure 2) in that the longest laying sequences are seen at the time of peak egg production.

All chickens exhibit a characteristically long laying sequence near the onset of production (Robinson et al. 1990), termed the "prime sequence". There is considerable variability in the length of the prime sequence between hens. We have monitored the relationship between the length of the prime sequence and total egg production in two feed-restricted broiler breeder flocks and one egg-type flock. The data presented in Table 1 indicate that there is a consistent correlation of approximately r = .385 between these two traits.
The relationship between aging and sequence length may have additional implications for reproductive efficiency other than reduced egg production alone. Two experiments have been conducted to test the hypothesis that the chick production potential of first-of-sequence eggs may be lower than that of "subsequent" eggs in a sequence. Since the frequency of first-of-sequence eggs increases with age, any impairment in the fertility of such eggs, or the viability of the embryos may partially explain why fertility and hatchability decline with age. Such a hypothesis had been suggested and tested on large and medium weight turkey hens by Bacon and Nestor, (1979).

In the first trial (Robinson et al., 1991a) eggs were collected from 103 individually caged hens for 45 days beginning at 45 weeks of age. Time of collection was recorded to facilitate the assignment of eggs to either first-of-sequence or "subsequent" sequence positions. Eggs were incubated for 7 days, broken open and fertility and embryo viability was determined. Least squares means for fertility did not differ significantly between first (87.02%) and subsequent eggs (89.56%). There was no significant difference in least squares means for embryo viability (number of viable embryos per 100 eggs set) between first (89.71%) and subsequent (92.75%) eggs. However, the number of viable embryos per 100 eggs set (fertility X viability) was significantly lower in first (78.74%) compared with subsequent eggs (83.17%).

Fasenko et al. (1992) re-examined the relationship between sequence position and chick production using 29 individually-caged hens throughout an entire production cycle. Eggs were assigned to sequence positions as described by Robinson et al. (1991a). Eggs laid on odd-numbered weeks were broken open for assessment of fertility and embryonic development (Eyal-Giladi and Kochav, 1976). Eggs laid on even-numbered weeks were incubated in a commercial hatchery to assess hatchability. Unhatched eggs were opened to determine fertility and the incidence of embryonic mortality. Fertility (n = 3,240 eggs) and hatchability (n = 1,653 eggs) were not influenced by egg sequence position, but both parameters did decline significantly with age. Embryo viability (n = 1,487 eggs) and preincubation embryonic development (n = 1,200) eggs were not influenced by hen age per se, however were significantly influenced by sequence position. Embryos from first-of-sequence eggs were more developed than embryos from subsequent eggs (first - 10.36; subsequent - 10.05). These data indicate that the increased incidence of first-of-sequence eggs seen as a consequence of aging may be caused by impaired ability of first-of-sequence eggs to develop properly following fertilisation.

**EFFECTS OF OBESITY**

The consequences of over-feeding female broiler breeders have been examined in terms of *ad libitum* feeding as well as moderate excesses in feed intake. In one experiment, 60 Indian River broiler breeder pullets were raised to 22 weeks of age following the body weight targets suggested by the breeder. At 22 weeks of age, the birds were housed individually in cages with 30 hens being feed restricted and 30 hens being allowed *ad libitum* access to feed. The experiment continued until 62 weeks of age. The details of the experiment have been published elsewhere (Robinson et al., 1991b). Body weight of the 30 *ad libitum*-fed hens was approximately 700 g heavier than that of the 30 feed restricted hens throughout most of the laying period. At 62 weeks of age, the body weight differential was 542.3 g, of which the weights of fat, water, protein and ash were 369.4 g, 113.1 g, 49.9 g and 9.9 g respectively. At this time, the carcasses of the restricted hens contained on average 901 g of fat while the carcasses of the *ad libitum*-fed hens contained 1270 g of fat. Hence, the larger birds were also fatter birds. Mean egg output was lower in the *ad libitum*-fed hens (136.2 eggs) compared to the restricted hens (176.6 eggs). A similar number of laying sequences was observed between the two groups of hens (approx 45 sequences), however, the length of the prime sequence was significantly longer in restricted hens (24.2 days) than in full-fed hens (14.9 days). *Ad libitum*-fed hens exhibited a higher incidence of pauses of greater than 11 days duration compared to restricted hens. In this study fertility, embryo viability (day 7) and embryo production (fertility X embryo viability) were not significantly influenced by level of feeding. In summary, *ad libitum* feeding reduced reproductive performance by reducing the length of the prime sequence and by increasing the number of long intersequence pauses.
In a second larger-scale study we examined the consequences of *ad libitum* feeding during two periods in the life of a broiler breeder hen, from 4 weeks to 20 weeks of age and from 20 to 68 weeks of age (Yu, 1992). A 2 X 2 factorial design (two periods X two levels of feeding) was used and the treatment groups were denoted as follows: RR (restricted during rearing and laying), RF (restricted during rearing and full-fed during laying), FR (full-fed during rearing and restricted during lay) and FF (full-fed during rearing and lay). A total of 200 hens (50 per treatment group) were studied. Feed restriction during the rearing period reduced body weight at 18 weeks of age from 4.2 kg (full-fed birds) to 1.9 kg. While there was a major difference in the percentage of carcass fat (full-fed = 27.4%; restricted = 7.3%), at 18 weeks of age, the level of protein in the carcasses was not different (full-fed = 13.9%; restricted = 13.4%). At 62 weeks of age the weights of the abdominal fat pads for FF, FR, RF and RR were 304.1 g, 189.4 g, 353.7 g and 197.7 g respectively.

Reproductive performance was significantly poorer the longer the duration of *ad libitum* feeding. The total egg production (and settable egg production) were as follows: FF - 122.2 (102.6), FR - 162.9 (143.9), RF 132.5 (118.1) and RR 176.6 (172.4). Fertility, hatchability and hatch of fertile eggs were all reduced with full-feeding. The effects of full-feeding were more severe when it occurred during the breeding period than the rearing period. The FF hens exhibited severe reproductive problems (32.6% soft-shelled and membranous eggs, 18.1% multiple-yolked eggs and 7.5% multiple-egg days) compared to RR hens (4.5% soft-shelled and membranous eggs, 2.3% multiple-yolked eggs and 1.2% multiple-egg days). The incidence of erratic laying (defined as ovipositions that occurred outside of the prime laying period (700-1500 h) was recorded from 19 to 29 weeks of age. Erratic laying accounted for 40.8%, 28.7%, 24.5% and 13.3% of the eggs laid during this time duration for FF, FR, RF, and RR hens respectively. Erratic laying was significantly correlated to the laying of soft-shelled and membranous eggs (r=.692), multiple-yolked eggs (r=.292), multiple-egg days (r=.507) and the number of settable eggs laid during this period (r=-.687). Selection pressure applied to erratic ovipositions may identify a groups of hens which may be more capable of controlling their ovarian function. One of the most obvious signs of ovarian hypertrophy was seen in the dramatic increase in the number of large follicles in birds in response to *ad libitum* feeding. In general, at sexual maturity, as well as at 33 and 62 weeks of age, birds that were full-fed had approximately 2 additional large yellow yolky follicles. In most full-fed hens, there was evidence of the existence of partial or complete double or in some cases triple hierarchies.

A loss of control of the ovarian hierarchy in full-fed hens was also apparent when the steroidogenic capability of large follicles was determined *in vitro*. The F2 follicles appeared to be functionally similar to normal F1 follicles, in that they produced progesterone, and were not involved in androstenedione production to the extent that F2 follicles normally are. Furthermore, the small follicles of full-fed hens produced significantly more androstenedione than did small follicles of restricted hens. The physiological significance of the latter observation is not yet known but is presently the subject of further study.

The above experiments clearly demonstrated that full-fed hens lose the capability to regulate the recruitment of follicles into the hierarchy. A third experiment was conducted to determine the time-course of these changes in ovarian morphology brought about as a result of full-feeding (Robinson *et al.*, 1991c). Fifty individually-caged Indian River broiler breeder hens that had previously been feed restricted were assigned to one of five treatment groups (n=10) at 40 weeks of age. Tmt 1 hens were killed at 44 weeks of age. Some hens were restricted for an additional 7 days (Tmt 2; 45 weeks) or 14 days (Tmt 3; 46 weeks). Tmt 4 and Tmt 5 hens were allowed to eat *ad libitum* from 44 to 45 and 44 to 46 weeks of age respectively. Fat-soluble red and black dyes were fed on alternate days to facilitate daily yolk deposition patterns in the eggs and ovarian follicles. Hens were feed restricted to a level of 128 g of feed per day. Feed consumption for Tmt 4 and 5 hens averaged 284 g, 186 g, 197 g, and 236 g for the first four days of *ad libitum* feeding and remained at approximately 230 g per day thereafter. *Ad libitum* feeding increased body weight by 0.5 kg and 0.69 kg after 7 and 14 days of full feeding, respectively. The number of large follicles was

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*The data (three papers) have been submitted for publication in Poultry Science.*
significantly greater after 14 days of full-feeding (restricted - 5.3 follicles; ad libitum-fed - 7.0 follicles). The weight of the ovarian stroma, which represents the pool of small non-hierarchical follicles was increased by 1.3 g and 3.9 g after 7 or 14 days of ad libitum feeding respectively. It was interesting to note that 50% and 40% of the hens exhibited some evidence of simultaneous development of follicles after 7 days or 14 days of full-feeding respectively, compared to only 3.3% of the feed restricted hens. It is obvious that the loss of regulation of the ovarian hierarchy associated with full-feeding occurs during the first few days of over consumption.

Robinson et al. (1990) sorted 44 hens on the basis of total egg production into the upper and lower 50% of the flock, as well as the upper and lower 25% of the flock. It was observed that the superior hens in the flock laid significantly longer sequences. Briefly, the egg production for the +25%, +50%, 100%, -50% and -25% groups to 62 weeks of age were 159.1, 167.9, 184.0, 200.2 and 205.4 eggs respectively. When the body weights of these hens were plotted (Figure 4) it can be seen that the superior hens were significantly lighter in weight than were the poorer hens. The upper and lower production groups can be seen to segregate very soon after the onset of lay in terms of body weight. From these data it can be reaffirmed that there is indeed a negative relationship between egg production and body weight gain. The question could be asked, are the best hens efficient egg layers because they are small? Alternatively, are the small hens efficient because they are laying?

A solution to this question may be apparent from the data in Figure 5. In this study 120 feed-restricted hens were sorted into groups: +50% (earliest), 100% (all hens), and -50% (latest) on the basis of when they started to lay eggs. Age (and body weight) at first eggs were as follows: early hens - 24.1 weeks (2.78 kg); all hens - 25.1 weeks (2.93 kg) and late hens (26.1 weeks (3.08 kg). It would appear that once hens began to lay, they diverted less nutrients into carcass growth. The variability in age at sexual maturity may be attributed in part to minor differences in feed allocation between individual hens and also to inherent flock variability. The relationship between age at photostimulation and body weight curves is the subject of ongoing research.

SUMMARY

Broiler breeder chickens require dedicated programs of feed restriction to maximize egg output. From the above studies conducted at the University of Alberta, it is apparent that modern breeder hens have the genetic capability to produce at least 180 eggs by 62 weeks of age. The effects of over-feeding would appear to be very deleterious in achieving high rates of lay in such birds. Undoubtedly, poor flock uniformity is an ultimate cause of poor reproductive efficiency, as not all of the flock is at the desired target weight. Considerable research effort needs to be expended to fine tune the relationship between nutrient partitioning in the hens body, particularly at the time when egg production starts to decline.

ACKNOWLEDGEMENTS

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REFERENCES


Table 1. Laying sequence data and the correlation between prime sequence length and total egg production in two broiler breeder flocks and a SCWL flock.

<table>
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<th>Broiler Breeders Flock 1&lt;sup&gt;3&lt;/sup&gt;</th>
<th>Broiler Breeders Flock 2&lt;sup&gt;4&lt;/sup&gt;</th>
<th>Egg-Type Flock&lt;sup&gt;5&lt;/sup&gt;</th>
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<td>0.0001</td>
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<sup>3</sup>Details of the flock have been reported previously (Robinson et al. 1990).

<sup>4</sup>A flock of feed-restricted broiler breeders described in legend of Figure 2.

<sup>5</sup>A flock of ad libitum-fed commercial SCWL described in the legend of Figure 2.
Figure 1. A schematic representation of ovarian steroidogenesis in the domestic fowl (from Robinson, 1991).
Figure 2. Profiles of percent egg production for 160 Shaver SCWL hens and 120 Indian River broiler breeder hens which survived to 68 weeks and 58 weeks of age respectively. The SCWL hens were photo-stimulated at 18 weeks of age and the broiler breeders were photostimulated at 20 weeks of age. The SCWL were fed ad libitum and the broiler breeders were feed restricted with some minor differences in feed allocation during the rearing or breeding periods. Data were smoothed by transformation to 5th order polynomial regression equations.
Figure 3. Profiles of sequence length for the two groups of birds described in the legend to Figure 2. Data were smoothed by transformation to 5th order polynomial regression equations.
Figure 4. Mean values for body weight (data presented as 5th order polynomial regression lines) for all 44 hens (100%), the upper and lower 50% and the upper and lower 25% of the flock. For equivalent egg production, sequence length and inter-sequence pause length data see Robinson et al. (1990).
Figure 5. Body weight of 120 broiler breeder hens (all hens) and that of the 50% of the flock which started to lay first (early hens) and the 50% of the flock that started to lay the latest (late hens). Those hens which start to lay early (24.1 weeks) do not gain as much weight as hens that start laying later (26.1 weeks).
Question: Dan Zelenka

Do you have any method for determining if birds which exhibited two-day pauses in their lay cycle were ovulating internally?

Response: F. E. Robinson

At the present time we rely on end-of-season carcass dissection to verify the incidence of internal laying. This is not too accurate due to dissolution of follicles in the body cavity. Ideally, the application of ultra-sound imaging techniques may help examine the incidence of internal laying. Upon autopsy, we find a very low incidence of internal laying in both SCWL and broiler breeders.

Question: Milton Boyle

Did you see any difference in growth rate during the rearing period between your best and worst hens?

Response: F. E. Robinson

We are presently examining the relationship between pullet growth rate and reproductive performance. We will be presenting some of this material at the Poultry Science meeting in Arkansas this August.