doi:10.1017/S0043933909000452

# Problems associated with broiler breeder entry into lay: a review and hypothesis

**Y. EITAN* and M. SOLLER**

**Department of Genetics, The Hebrew University of Jerusalem, 91904 Jerusalem, Israel**
***Corresponding author: yoave@kv-yavne.co.il**

**Aggressive (*i.e.* over-) feeding of broiler breeder females in the period preceding onset of lay results in higher mortality and subsequent deleterious effects on egg and chick production (the 'over-feeding complex'). An intriguing aspect of the over-feeding complex is its close parallel, albeit at a lower level, to the well known 'Erratic Oviposition and Defective Egg Syndrome' (EODES) obtained when feeding female broiler breeders *ad libitum*. This is consistent with many studies showing that partial restriction (quasi-*ad libitum* feeding) results in partial expression of EODES (quasi-EODES). To explain the strong deleterious effects caused by rather minor over-feeding during this critical transition period, we propose that the very severe feed restriction of the growing pullet needed to prevent the onset of EODES, combined with the genetic increase in breast meat proportion achieved by intense selection over the past two decades, results in a situation where, during the critical weeks of maturation leading up to the first egg, the body lean mass must increase greatly at the same time that the ovary is maturing. During pullet maturation, empirically determined recommended feeding plans optimally balance the need to provide the rapid increase in muscle mass needed to achieve body lean mass threshold for entry into lay, with the need to maintain the ovary in a state of sufficient restriction to avoid appearance of quasi-EODES. With feed intake delicately balanced in this manner, even minor over-feeding tips the balance in the direction of quasi-EODES resulting in the appearance of the over-feeding complex. This may have been exacerbated in the past decade by a shift in the physiological control of EODES from body weight to feed intake.**

**Keywords:** broiler breeder; feed restriction; EODES; breast proportion; ovary; onset of lay threshold weight

## The OFC: sensitivity of the modern broiler breeder female to over-feeding during entry to lay

There is a general consensus, amply supported by reports from the field, that in the last decade, bringing the modern pullet into lay has become more complex and demanding



https://doi.org/10.1017/S0043933909000452 Published online by Cambridge University Press

(Robinson *et al.,* 1995; Hocking, 1996; Meijerhof, 2005). The problems appear to be centred on management of the breeder during the weeks from release of pullets from severe feed restriction at age 13-16 weeks to entry into lay at 24-28 weeks. Compared to the broiler breeder female of 15-20 years ago, the modern breeder is much more 'unforgiving' of even minor deviations from optimum feeding. In particular, even relatively minor over-feeding during this period (so-called 'aggressive' feeding) can result in high mortality at onset of lay (Cobb, 2008; Spradley *et al.*, 2008) due in large part to reproductive system problems such as internal lay, prolapse, inflammation of the oviduct and others (pers. comm. Dr H. Krishpin, DVM). This may be accompanied by lower peak lay and consequent reduction in egg and chick production (Katanbaf *et al.,*1989a, b; Robinson *et al.,* 1998a, b; Renema *et al.*, 2008). For convenience, we will use the term 'over-feeding complex' (OFC) for the set of effects resulting from over-feeding of broiler breeder females during the critical period leading to entry to lay.

## Erratic Oviposition and Defective Egg Syndrome (EODES)

Problems in broiler breeders on entry into lay are not new, and were encountered in the early 1970's as the well known 'Erratic Oviposition and Defective Egg Syndrome (EODES) (Jaap and Muir, 1968; Van Middelkoop, 1971, 1972). These problems were attributed to over- production of large yellow follicles (LYF), multiple hierarchies and consequent disturbances in oviposition. EODES has since been controlled with good success, initially by feed restriction during pullet growth, and later by continued feed restriction during lay. This continues to the present time with the severity of restriction relative to *ad libitum* feeding increasing yearly. The success of feed restriction in controlling EODES led naturally to the hypothesis that EODES was caused by *ad libitum* feeding. This has since been confirmed by numerous experiments showing that the symptoms of EODES are obtained by raising broiler breeders *ad libitum* (Hocking *et al.,* 1987; Katanbaf *et al.,* 1989b) by shifting restricted broiler pullets to *ad libitum* feeding during entry into lay (Yu *et al.,* 1992b), or even by forced feeding of White Leghorn layer hens (Walzem *et al.,* 1993).

## Development of EODES is linearly related to degree of over-feeding

The problems engendered by over-feeding during the critical period leading to onset of lay in the modern commercial broiler breeder, mirror, albeit to a lesser degree, those presented by a full blown EODES. To some extent this is expected. Many studies since the 1980's (summarized in *Table 1*) have shown that levels of feeding intermediate between full restriction and full *ad libitum* generate partial manifestation of EODES (some illustrative examples are presented in *Table 2*). Thus, over feeding during the period before entry into lay would be expected to manifest as a quasi-EODES. What is unexpected is the very powerful effect generated by relatively minor over-feeding during this period on mortality and reproduction of the broiler breeder female during the critical period of onset of sexual maturity. The purpose of the present paper is to present a hypothesis concerning the genetic and management changes that have brought this about.



https://doi.org/10.1017/S0043933909000452 Published online by Cambridge University Press

**Table 1 Comparison of effects of *ad libitum* feeding of broiler breeder females and of moderate over-feeding relative to optimal restriction (Over-feeding).**

| Observed effect | Ad libitum | Over-feeding |
|---|---|---|
| Defective eggs | Hocking *et al.,* 1987, Katanbaf *et al.,* 1989b; Yu *et al.,* 1992b | Robinson *et al.,*1995 |
| Too many LYF | Hocking *et al.,* 1989; Katanbaf *et al.,* 1989c; Yu *et al.,*1992a | Robinson *et al.,* 1998a |
| Lower peak lay | O'Sullivan *et al.,* 1991 | Robinson *et al.,* 1998b |
| Multiple ovulation | Yu *et al.,* 1992b | Hocking, 1996 |
| Multiple hierarchies | Hocking *et al.,* 1987 | Hocking, 1996 |
| Double yolked eggs | Katanbaf *et al.,* 1989b; Yu *et al.,* 1992b | Meijerhof, 2005; Robinson *et al.,* 1995 |
| Shorter prime sequence | Robinson *et al.,* 1991 | Robinson *et al.,* 1995, 1998b |
| Longer intersequence | Robinson *et al.,* 1991 | Robinson *et al.,* 1995, 1998b |
| Fewer eggs | Yu *et al.,* 1992b; Robinson *et al.,* 1991 | Leeson, 2004; Robinson *et al.,* 1995, 1998b; Bruggeman *et al.,* 2005 |
| Fewer hatching eggs | Katanbaf *et al.,* 1989b | Robinson *et al.,* 1995, 1998b; Bruggeman *et al.,* 2005 |
| Higher Mortality | Katanbaf *et al.,* 1989a | Meijerhof, 2005; Cobb, 2005; |
| Internal Ovulation | Renema and Robinson, 2004 | Hocking, 1996 |
| Decline of Fertility | Katanbaf *et al.,* 1989b; *Yu et al.,* 1992b | Robinson *et al.,* 1995; Leeson 2004 |
| Decline in Hatchability | Yu *et al.,* 1992b | Robinson *et al.,* 1995, 1998b |

**Table 2 Illustrative examples comparing quantitative effects of optimal feed restriction (OR) *vs. ad libitum* (AL) feeding, to the effects of optimal restriction (OR) *vs.* moderate over-feeding (OF). Diff. are OR minus AL, or OR minus OF, as applicable. Cit., citation; U, units, see footnote for details.**

| Trait | OR *vs.* AL: *EODES* | | | | | OR vs OF: OFC | | | |
|---|---|---|---|---|---|---|---|---|---|
| | Cit. | U | OR | AL | Diff. | Cit. | U | OR | OF |
| Egg | 12 | No. | 169.8 | 128.7 | 41.1 | 11 | No. | 200.3 | 189.4 |
| Defective eggs | 2 | No. | 1.12 | 3.08 | -1.96 | 10 | % | 0.95 | 1.7 |
| | 6 | (%) | 1.3 | 13.2 | -11.9 | 1 | No. | 4.0 | 8.9 |
| | 12 | No. | 13.7 | 25.9 | -12.2 | | | | |
| Too many LYF | 3 | No. | 9.8 | 12.7 | -2.9 | 4 | No. | 6.9 | 7.6 |
| | 7 | No. | 7.15 | 13.1 | -6.05 | 11 | No. | 7.88 | 9.03 |
| | 12 | No. | 7.8 | 12.2 | -4.4 | | | | |
| Multiple ovulation | 12 | No. | 0.56 | 1.71 | -1.15 | 4 | No. | 0.19 | 0.34 |
| Double yolked eggs | 7 | % | 0.7 | 2.6 | -1.9 | 10 | % | 0.65 | 1.33 |
| | 12 | No. | 2.3 | 18.1 | -15.8 | | | | |
| Mortality[1] | 9 | d | 13.7 | 37.2 | -23.5 | | | | |
| Fertility decline | 6 | % | 98.4 | 83.6 | 14.8 | 10 | % | 83.4 | 81.4 |
| | 12 | % | 91.9 | 78 | 13.9 | 8 | % | 93.4 | 85.1 |
| Settable eggs | 12 | No. | 158.2 | 112.4 | 45.8 | 11 | No. | 180.4 | 169.2 |

[1]Meijerhof (2005) reports greater mortality in broiler females under over-feeding, but does not give actual values. Our own commercial experience (Y.E.) is that over-feeding can result in excess mortality in the range of +0.2% to +0.4% per week, for the first months of production.

(1) Bruggeman *et al.,* 2005; (2) Hocking *et al.,* 1987; (3) Hocking *et al.,* 1989; (4) Hocking, 1996; (5) Katanbaf *et al.,* 1989a; (6) Katanbaf *et al.,* 1989b; (7) Katanbaf *et al.,* 1989c; (8) Leeson, 2004; (9) Robinson *et al.,* 1991; (10) Robinson *et al.,* 1995; (11) Robinson *et al.,* 1998a; (12) Yu *et al.,* 1992b.



https://doi.org/10.1017/S0043933909000452 Published online by Cambridge University Press

## The model

The explanatory hypothesis contains two elements (and possibly a third) that are proposed to have combined 'synergistically' to generate the OFC.

ELEMENT 1: VERY SEVERE FEED RESTRICTION OF THE GROWING PULLET UNTIL THE START OF THE MATURATION PROCESS

It is remarkable that the commercial target body weight recommendations for broiler breeder pullets from hatch to the start of the maturation process at 14-16 weeks (Hocking *et al.* 1989; Eitan *et al.*, 1998) have remained almost the same as they were 20 years ago (Picard *et al.,* 2004; Cobb, 2008, 2005). Rearing pullets according to the current recommendations brings the actual daily feed restriction of the pullet to a much more severe level than in the past, *i.e.* from about 70% of *ad libitum* feeding 20 years ago, to about 33% of *ad libitum* feeding today (Picard *et al.,* 2004), and target body weight at entry into lay to 40% of *ad libitum* fed pullets (Hocking 1996; Renema and Robinson, 2004). Thus, it appears that increasingly severe feed restriction is required in order to maintain control of EODES (Hocking, 1996; Lewis, 2006) and 'The severity and duration of feed restriction to broiler breeder chicken have to be continuously adapted according to changing genotype and selection goals' (Bruggeman *et al.*, 2005). The direct implication is that partial feed restriction, if not sufficiently stringent, is interpreted by the ovary as quasi-*ad libitum* feeding and leads to a moderate manifestation of EODES, which would correspond to the OFC.

ELEMENT 2: INTENSE SELECTION FOR INCREASED BREAST PROPORTION

In conjunction with increasingly severe feed restrictions, there has been a modification in breeding objectives which has placed much greater emphasis on increasing the proportion of lean breast meat in the carcass at point of sale (Melnychuk *et al.,* 2004). This may also have dictated an increase in the widely accepted physiological parameter of minimum body weight threshold for entering sexual maturation (Brody *et al.,* 1980; Soller *et al.*, 1984; De Beer and Coon, 2007). Recent results by Hocking (2004) showing independence of threshold weight at entry into lay from body fat composition also support the hypothesis that lean body mass, is critical for entry into lay.

An increase in threshold lean body mass for entry into lay is also implied by the increase in 24 week recommended target body weight of the female broiler breeder. For example, recommended 24-week body weight for out-of-season 'Cobb 500' female broiler breeders have increased from 2700 grams in 1987 to 3160 grams in 2005 (Cobb Management Guide, 2005). This period saw a major increase in the proportion of lean body mass of the commercial broiler chick at market weight. It is plausible that this change in body composition of the commercial broiler chick will be reflected in the proportion of lean mass of the female broiler at entry into lay.

THE NEGATIVE SYNERGISTIC EFFECT

As so often happens in broiler breeding and management, genetic changes create problems in bird functional aspects, which are compensated through management changes. The management changes in turn, interact with the birds genetic physiology, causing further functional problems (Eitan and Soller, 2002). In the present context, it is proposed that the severe feed restriction to 15 weeks that is implemented in order to prevent EODES, may have interacted with the emphasis on breast proportion, leading to the OFC. In detail, the hypothesis is as follows:

- During the first weeks post hatch, before initiation of severe feed restriction, the



https://doi.org/10.1017/S0043933909000452 Published online by Cambridge University Press

breast of the young chick accumulates muscle mass (Cobb 500 Management Guide, 2008)
- During the subsequent period of severe feed restriction, from 8 to 15 weeks (the latter part of early rearing), the accumulated breast muscle serves as an important source of protein for the growing pullet
- As a result, just before the start of the maturation process at 12 weeks the breast becomes 'V' shaped and breast muscle mass is small relative to its target final weight and proportion at onset of lay (Cobb 500 Management Guide, 2008; Meijerhof, 2005)
- Consequently, during the weeks from the start of the maturation process until first egg at 24-26 weeks, there is a need to rebuild the breast in order to achieve the minimal lean body mass (Element 2 above) needed for maturation (Soller *et al.,*1984; Renema *et al.,* 1999; Melnychuk *et al.*, 2004).

Thus, during this last period there is a very large protein requirement for building the body lean mass, caused by the need to compensate for the severe feed restriction until 14-16 weeks coupled with the intense selection for higher breast proportion over the past two decades.

Consequently, during the critical weeks of maturation from 21-24 weeks prior to entry into lay, the breast muscle must increase in mass to achieve minimum body lean mass for sexual maturity, while the ovary must reach its final mature state as well. But because of intense selection for a higher proportion of breast muscle on the one hand, and severe restriction until near the point of lay on the other, it can be postulated that lean body muscle mass is much further away from its final target state, than the ovary. Although very aggressive feeding levels would be justified from the point of view of bringing lean body mass up to the minimum threshold for onset of lay, these would be interpreted by the ovary as quasi-*ad libitum* feeding, leading to manifestation of the OFC. Therefore, feeding levels must balance the need to build lean body mass as rapidly as possible, so as to meet the minimum lean body weight requirement for entry into lay, against the need to maintain the animal in a state of physiological restriction to prevent onset of deleterious quasi-EODES by the ovary. Adjusting feed intake during this critical period is aimed at finding an empirical optimum level, which provides maximal rapid lean muscle growth needed for entry into lay, but which still maintains a state of sufficient restriction to avoid a shift to a state of quasi-EODES, with consequent development of the OFC. With the bird poised so delicately just below the point of quasi-EODES, any aggressive deviation from recommended feeding schedules will result in manifestation of the OFC.

## A POSSIBLE THIRD ELEMENT: A SHIFT OF EODES FROM DEPENDENCE ON BODY WEIGHT TO DEPENDENCE TO FEED INTAKE

Interestingly, while early studies (Hocking 1993, 1996) show a stronger interaction between EODES development and body weight than to feed intake, later studies (Hocking, 2004; Renema *et al.*, 2007; Robinson *et al.*, 2007) show a stronger relationship of EODES to feed intake than to body weight. Indeed, at the present time, management of the broiler breeder at entry into lay focuses more on control of rate of body weight gain, which is a matter of feed intake control, than on control of body weight *per se*. This may be relevant to our hypothesis, because minor increase in food intake over a short period would barely register at the body weight level, but would be noticeable at the food intake level. This may explain part of the greater sensitivity of the modern broiler breeder to even slight increase in feed intake.

It is important to emphasize that the proposed model does not conceive of the ovary and lean body mass as being in competition for the same nutrient stream. Rather, we



https://doi.org/10.1017/S0043933909000452 Published online by Cambridge University Press

conceive of the demands of rapidly increasing lean body mass as determining a nutrient stream that is more than adequate for the needs of the ovary, and which, from the standpoint of the ovary, can easily rise to levels that are interpreted as quasi-*ad libitum*. On this model, it is fortunate indeed that selection for increased breast proportion has been accompanied by selection for increased feed efficiency and decreased fat deposition. Otherwise, an even greater nutrient stream may have been required by the breast, with consequent increased likelihood of development of the OFC.

## The OFC and the Broiler Breeder Paradox

The Broiler Breeder Paradox (Decuypere, 2006) refers to the inability to achieve high reproductive status and high juvenile growth rate in broilers, without severely restricted feeding. However, broiler breeders present a number of other seemingly paradoxical aspects. These include the simultaneous presentation of both multiple ovulation and low egg production, and deleterious welfare effects of both *ad libitum* feeding and restricted feeding. Gous (2008) has recently added to this the paradox that fertility in broiler breeders is improved through the use of shorter, rather than longer day lengths. In this context, the OFC can be considered as yet another paradox. Namely, achievement of earlier sexual maturity of the female breeder through aggressive feeding, results in multiple problems in reproductive performance at entry into lay.

## Acknowledgement

We thank Professor Paul Siegel for general encouragement and critical reading of the manuscript. We extend special thanks to an anonymous referee who patiently led us to render explicit many of our underlying assumptions, and who provided valuable references supporting our model.

### References

**BRODY, T.B, EITAN, Y., SOLLER M., NIR I. and NITZAN Z.** (1980) Compensatory growth and sexual maturity in broiler females reared under severe food restriction from day of hatching. *Poultry Science* **21**: 437-446.

**BRUGGEMAN, V., ONAGBESAN, O., RAGOT, O., METAYER, S., CASS, Y.S., FAVREAU, F., JEGO, Y., TREVIDY, J.J., TONA, K., WILLIAMS, J., DECUYPERE, E. and PICARD, M.** (2005) Feed Allowance – Genotype interaction in broiler breeder hens. *Poultry Science* **84**:298-306.

**COBB, Cobb 500 breeder management guide** (2005, 2008). Cobb-Vantress, Inc. POB 1030 Siloam Springs, Arkansas 72761.

**DE BEER, M. and COON, C.N.** (2007) The effect of different feed restriction programs on reproductive performance, efficiency, frame size and uniformity in broiler breeder hens. *Poultry Science* **86**: 1927-1939.

**DECUYPERE, E., ONAGBESAN, O., SWENNEN, Q., BUYSE, J. and BRUGGEMAN, V.** (2006) Broiler breeder paradox :A project report. *World Poultry Science Journal* **62**: 443-453.

**EITAN, Y., SOLLER, M. and ROZENBOIM, I.** (1998) Comb size and estrogen levels toward the onset of lay in broiler and layer strain females under ad libitum and restricted feeding. *Poultry Science* **77**: 1593-1600.

**EITAN, Y. and SOLLER, M.** (2002) Associated effects of sixty years of commercial selection for juvenile growth rate in broiler chickens: Endo / Exo physiological or genetic? *7th World Congress for Genetic Applied to Livestock Production*, Montpellier, France.

**GOUS, R.M.** (2008) The Broiler Breeder Paradox. *International Hatchery Practice* **22 (6)**: 11-13.

**HOCKING, P.M., GILBERT, A.B., WALKER, M. and WADDINGTON, D.** (1987) Ovarian follicular structure of white leghorn fed ad libitum and dwarf and normal broiler breeder fed ad libitum or restricted to point of lay. *British Poultry Science* **28**: 493-506.



https://doi.org/10.1017/S0043933909000452 Published online by Cambridge University Press

**HOCKING, P.M., WADDINGTON, D., WALKER, M.A. and GILBERT, A.B.** (1989) Control of the development of the ovarian follicular hierarchy in broiler breeder pullets by food restriction during rearing. *British Poultry Science* **30**: 167-174.

**HOCKING, P.M.** (1993) Effects of body weight at sexual maturity and the degree and age of restriction during rearing on the ovarian follicular hierarchy of broiler breeder females. *British Poultry Science* **34**: 793-801.

**HOCKING, P.M.** (1996) Role of body weight and food intake after photostimulation on ovarian function at first egg in broiler breeder females. *British Poultry Science* **37**: 841-851.

**HOCKING, P.M.** (2004) Roles of body weight and feed intake in ovarian follicular dynamics in broiler breeders at the onset of lay and after a forced molt. *Poultry Science* **83**: 2044-2050.

**JAAP, R.G. and MUIR, F.V.** (1968) Erratic oviposition and egg defects in broiler type pullets. *Poultry Science* **47**: 417-423.

**KATANBAF, M.N., DUNNINGTON, E.A. and SIEGEL, P.B.** (1989a) Restricted feeding in early and late feathering chickens. 1. Growth and physiological response. *Poultry Science* **68**: 344-351.

**KATANBAF, M.N., DUNNINGTON, E.A. and SIEGEL, P.B.** (1989b) Restricted feeding in early and late feathering chickens. 2. Reproductive response. *Poultry Science* **68**: 352-358.

**KATANBAF, M.N., DUNNINGTON, E.A. and SIEGEL, P.B.** (1989c) Restricted feeding in early and late feathering chickens. 3. Organ size and carcass composition. *Poultry Science* **68**: 359-368.

**LEESON, S.** (2004) How does feed allocation affect the performances of breeders and their progeny. *Poultry International* **May**: 10-14.

**LEWIS, P.D.** (2006) Constant and changing photoperiods in the laying period for broiler breeders allows normal or accelerated growth during the rearing period. *Poultry Science* **85**: 321-325.

**MEIJERHOF, R.** (2005) The impact genetics has on breeder management. *World Poultry* **21(5)**:18-21.

**MELNYCHUK, V.L., KIRBY, J.D., KIRBY, Y.K., EMMERSON, D.A. and ANTHONY, N.B.** (2004) Effect of strain, feed allocation program and age at photostimulation on reproductive development and carcass characteristics of broiler breeder hens. *Poultry Science* **83**: 1861-1867.

**O'SULLIVAN, N.P., DUNNINGTON, E.A., SMITH, E.J., GROSS, W.B. and SIEGEL, P.B.** (1991) Performance of early and late feathering broiler breeder females with different feeding regimens. *Poultry Science* **32**: 981-995.

**PICARD, M., BRUGGEMAN, V., JEGO, Y., ONAGBESAN, O. and HOCKING, P.** (2004) Growth and laying performances of two broiler breeder genotypes fed diluted diets ad libitum or restricted. from a CD of European Research Project on Broiler Breeder Paradox (QLK5-ct-2001-01732).

**RENEMA, R.A., ROBINSON, F.E., NEWCOMBE, M. and McKAY, R.I.** (1999) Effect of Body Weight and Feed Allocation During Sexual Maturation in Broiler Breeding Hens 1. growth and carcass characteristics. *Poultry Science* **78**: 619-628.

**RENEMA, R.A. and ROBINSON, F.R.** (2004) Defining normal: comparison of feed restriction and full feeding of female broiler breeder. *World's Poultry Science Journal* **60**: 508-521.

**RENEMA, R.A., ROBINSON, F.E. and ZUIDHOF, M.J.** (2007) Reproductive efficiency and metabolism of female broiler breeders as affected by genotype, feed allocation and age at photostimulation. 2. Sexual maturation. *Poultry Science* **86**: 2267-2277.

**RENEMA, R.A., ROBINSON, F.E. and ZUIDHOF, M.J.** (2008) Management and feeding of broiler breeders. *XXIII World's Poultry Congress*, Brisbane, Australia session #3, OR101.

**ROBINSON, F.E., ROBINSON, N.A. and SCOTT, T.A.** (1991) Reproductive performance, growth rate and body composition of full fed versus feed restricted broiler breeder hens. *Canadian Journal of Animal Science* **71**: 549-556.

**ROBINSON, F.E., RENEMA, N.A., HARDIN, R.T. and WILSON, J.L.** (1995) The effect of 20 week body weight and feed allocation during early lay on female broiler breeders. *Journal of Applied Poultry Research* **4**: 203-210.

**ROBINSON, F.E., RENEMA, N.A., BOUVIER L., FEDDES, J.J.R., WILSON, J.L., NEWCOMBE, M. and McKAY, R.I.** (1998a) Effect of photostimulatory lighting and feed allocation in female broiler breeders 1. Reproductive development. *Canadian Journal of Animal Science* **78**: 603-613.

**ROBINSON, F.E., RENEMA, N.A., BOUVIER, L., FEDDES, J.J.R., WILSON, J.L., NEWCOMBE, M. and McKAY, R.I.** (1998b) Effect of photostimulatory lighting and feed allocation in female broiler breeders 2. Egg and chick production characteristics. *Canadian Journal of Animal Science* **78**: 615-623.

**ROBINSON, F.E., ZUIDHOF, M.J. and RENEMA, R.A.** (2007) Reproductive efficiency and metabolism of female broiler breeders as affected by genotype, feed allocation and age at photostimulation. 3. Reproductive efficiency. *Poultry Science* **86**: 2278-2286.

**SOLLER, M., EITAN, Y. and BRODY, T.** (1984) Effect of diet and early quantitative feed restriction on the minimum weight requirements for onset of sexual maturity in white rock broiler breeders. *Poultry Science* **63**: 1255-1261.

**SPRADLEY, J.M., FREEMAN, M.E., WILSON, J.L. and DAVIS, A.J.** (2008) The influence of twice-a-day feeding regimen after photostimulation on the reproductive performance of broiler breeder hens. *Poultry Science* **87**: 561-568.



https://doi.org/10.1017/S0043933909000452 Published online by Cambridge University Press

**VAN MIDDELKOOP, J.H.** (1971) Shell abnormalities due to the presence of two eggs in the shell gland. *Archiv für Geflügelkunde* **35**: 122-127.

**VAN MIDDELKOOP, J.H.** (1972) The relationship between ovulation interval of White Plymouth Rock and the laying of abnormal eggs. *Archiv für Geflügelkunde* **36**: 223-230.

**WALZEM, R.L., SIMON, C., MORISHITA, T., LOWENSTINE, L. and HANSEN, R.J.** (1993) Fatty liver hemorrhagic syndrome in hens overfed a purified diet. Selected enzyme activities and liver histology in relation to liver hemorrhage and reproductive performance. *Poultry Science* **72**: 1479-1491.

**YU, M.W., ROBINSON, F.E., CHARLES, R.G. and WEINGARDT, R.** (1992a) Effect of feed allowance during rearing and breeding on female broiler breeders 1. Growth and carcass characteristics. *Poultry Science* **71**: 1739-1749.

**YU, M.W., ROBINSON, F.E., CHARLES, R.G. and WEINGARDT, R.** (1992b) Effect of feed allowance during rearing and breeding on female broiler breeders 2. Ovarian morphology and production. *Poultry Science* **71**: 1750-1761.



https://doi.org/10.1017/S0043933909000452 Published online by Cambridge University Press