# **Breeding Focus 2021 - Improving Reproduction**

Edited by

Susanne Hermesch

Animal Genetics and Breeding Unit, University of New England, Armidale, Australia

Sonja Dominik

CSIRO Agriculture and Food, Armidale, Australia

Published by

Animal Genetics and Breeding Unit

University of New England

Armidale, NSW, Australia

© Animal Genetics and Breeding Unit, 2021

All rights reserved except under the conditions described in the Australian Copyright Act 1968 and subsequent amendments, no part of this publication may be reproduced, stored in a retrieval system or be transmitted in any form, or by any means, electronic, mechanical, photocopying, recording, duplicating, or otherwise, without prior permission from the publisher:

Animal Genetics and Breeding Unit

University of New England

Armidale NSW 2351

Australia

http://agbu.une.edu.au

**ISBN**: 978-1-921597-86-2

eISBN: 978-1-921597-87-9

Cover design by Susan Joyal

Book design by Kathy Dobos

First published, 2021

# Contents

Preface	iii
Review: Cattle fertility and genetic improvement of fertility in developing countries Eva M. Strucken	5
Reproductive challenges in abalone breeding Natasha A. Botwright, Omar Mendoza-Porras, Roger Chong, Ya Zhang and Carmel McDougall	17
Opportunities from understanding health and welfare of sows Laura Vargovic, Jo Harper and Kim Bunter	37
Saltwater crocodile (Crocodylus porosus) embryo survival: risk factors Sally R. Isberg and Peter C. Thomson	49
New phenotypes for genetic improvement of fertility in dairy cows Irene van den Berg, Melissa Stephen, Phuong N. Ho, Mekonnen Haile-Mariam, Claire Phyn, Susanne Meier, Chris Burke, Nicole Steele and Jennie E. Pryce	59
The influence of bull fertility on beef herd productivity Laercio R Porto-Neto, John Bertram, Marina R S Fortes, Pamela Alexandre, Michael McGowan, Ben Hayes and Antonio Reverter	71
Improving reproductive performance in pigs Jo-Anne Harper, Kim Bunter and Laura Vargovic	85
Breeding for improved fertility of honey bees E.A. Frost, N.C. Chapman, R.G. Banks and S. Hermesch	97
Examining the relative importance of female reproduction in beef breeding herds when fully accounting for production costs Bradley J Walmsley	111
Improving reproduction in ewes Kim Bunter, Andrew Swan and Daniel Brown	127

Selection for reproductive efficiency in turkeys and broiler chickens: egg production, hatchability and fertility	143
Bayode O. Makanjuola, Emhimad A. Abdalla, Christine F. Baes and Benjamin J. Wood	
Genetic improvement of cow reproduction in northern Australia beef cattle breeds Kirsty L. Moore, Matt L. Wolcott and David J. Johnston	151
Climatic constraints facing sheep reproduction Gordon Refshauge and Simon de Graaf	163
Lamb survival, a challenge for the decades Sabine Schmoelzl, Lynden Smith, Amellia Redfearn and Rachelle Hergenhan	187

# Preface

"Breeding Focus 2021 – Improving reproduction" is the fourth workshop in the series. The Breeding Focus series was developed to provide an opportunity for exchange between industry and research across a number of agricultural industry sectors. With this goal in mind, workshops have included presentations across multiple agriculturally relevant animal species to take participants outside their area of expertise and encourage them to think outside the box. Reproduction is a main driver for profitability and genetic gain. We will discuss existing knowledge, identify gaps and explore genetic and management strategies to improve reproduction further in multiple species.

Successful reproduction is a complex characteristic comprising the formation of reproductive cells, successful mating and fertilisation, embryonic and fetal growth and eventually a successful birthing event. In livestock species, reproduction traits have mostly low heritabilities, which makes it challenging to improve reproduction as part of a multiple trait breeding objective. The complexity arises not just from the cascade of processes required to result in successful reproduction, but the relevant traits are different in males and females and they are influenced through health and fitness, nutrition, climate and other environmental and management factors.

Challenges to the improvement of reproduction can vary widely for different species. For less domesticated species such as abalone, the ability to produce and reproduce the animals in captivity presents a major challenge. In bees, reproduction has not been given great attention and little research has been undertaken to understand the underlying genetics of drone and queen reproduction. However, in all industries reproduction is recognised as the basis for genetic and economic gain. It directly influences the selection intensity that can be applied. It also determines how many animals are not required for replacement and can be sold. In all industries, irrespective of the challenge, cost-effective and easy to measure phenotypes of reasonable heritability are central. New technologies and approaches enable the development of novel phenotypes for genetic improvement which will be combined with a growing amount of genomic data in livestock species and together these developments provide new and exciting opportunities to improve reproduction further.

We would like to thank everyone who has contributed to this event for their time and effort: the authors for their contributions to the book and presentations, the reviewers who all readily agreed to critique the manuscripts. We would like to express a special thanks to Kathy Dobos for her contributions into the organisation of this workshop and the publication. Thank you!

Susanne Hermesch and Sonja Dominik

Armidale, May 2021

# Selection for reproductive efficiency in turkeys and broiler

# chickens: egg production, hatchability and fertility

Bayode O. Makanjuola<sup>1</sup>, Emhimad A. Abdalla<sup>1</sup>, Christine F. Baes<sup>1,2</sup> and Benjamin J. Wood<sup>1,3</sup>

<sup>1</sup>Centre for Genetic Improvement of Livestock, University of Guelph, Guelph, Ontario, Canada

<sup>2</sup>Institute of Genetics, Vetsuisse Faculty, University of Bern, Bern, Switzerland

<sup>3</sup>School of Veterinary Science, University of Queensland, Gatton Campus, QLD, Australia

## Abstract

Improvements in meat poultry production have primarily been through breeding for faster growth and bodyweight, feed efficiency, yield and to a lesser extent the reproductive traits. Improved biosecurity and the targeted use of feed enzymes has also had an effect in improving performance. From a breeding perspective, the identification and selection of animals with higher genetic potential to achieve substantial and continuous improvement is critical. The identification of selection candidates for reproductive traits such as fertility and hatchability has traditionally been more difficult due to phenotyping and lower heritability. This is true for both broiler chickens and turkeys. The reproductive traits are important as they determine chick and poult cost at the start of a commercial production cycle before returns accrue after growth, slaughter and processing. The objective is to describe the different traits that affect reproductive performance in turkeys and broilers, as well as the different models used in genetic evaluation. Reproductive traits such as egg production, fertility and hatchability, clutch length and broodiness are described as are the benefits of genomic information. The heritability estimates for egg production ranged from 0.05 to 0.17, while those of fertility and hatchability ranged from 0.04 to 0.22. Estimated heritability for clutch length and broodiness was 0.21 and 0.15, respectively. Heritabilities and accuracy increased with the addition of genomic information. Furthermore, for longitudinal traits such as egg production, with information collected over a production curve, we show that a random regression approach appropriately captures all the factors affecting the traits. Using genomic data to evaluate reproduction performance using transmission ratio distortion revealed haplotypes and functional pathways that if managed, could increase hatchability and fertility in a turkey breeding program. Overall, the incorporation of genomic information resulted in better estimates of genetic parameters, thereby presenting the potential for better improvement of reproductive performance in turkeys.

## Background

Poultry meat production is one of the most important sources of animal protein and accounts for approximately 40% of meat production (FAO 2020). An increase of 16% in production by 2029 is projected (Executive Guide to World Poultry Trends 2020). Some of these increases will be attributable to the selection for faster growth rate, either reducing the time to reach market weight or by growing birds to heavier slaughter weights (Thiruvenkadan *et al.*, 2011; Havenstein *et al.*, 2007). Initially, selection in meat poultry had been for bodyweight improvement as it reduced production costs, increased carcass value and was relatively amenable to selection, which could be due to high heritability and ease of measurement. However, the antagonistic relationship between production and reproductive traits (Jambui *et al.*, 2017) has consequently changed the breeding program goals over time to a more balanced approach that takes into account production and reproductive traits without trading-off on animal health and welfare (Avendaño *et al.*, 2017). A number of individual traits including egg production, hatchability and fertility affect overall reproductive performance in turkeys. Consequently, appropriate genetic modeling of these traits is explored in the following.

## Egg production

Egg production is an economically important trait in both egg-type and meat-type poultry breeding. Phenotypic information is collected over the productive life of the animal and starts as early as 16 to 18 weeks for chickens and 30 weeks in turkeys. Traditionally, the modeling of this trait has been by using a single cumulative measurement or cumulative measurements of blocks of time such as start, middle and end. Each animal has only one or a couple of records representing the entire or some components of the production period. Using the estimated cumulative egg production over the lay period as a single performance measure would be analogous to the 305-d lactation model for milk yield traits commonly employed traditionally in dairy genetic evaluations. However, such approached does not account for the longitudinal nature of the trait including changes in the genetic and permanent environment effects overtime. As has been shown by Swalve (1995), this single performance measure type of model may yield an overestimated heritability and rank sires differently as demonstrated when the 305-d model and random regression test-day model were compared.

Dairy lactation and egg production curves follow similar patterns, with an observable increase at the beginning of production to a peak after which there is a steady decline later in the production cycle. With the widespread implementation of test-day models (TDM) in dairy production, interest in modelling egg production as weekly or monthly records has grown. Anang *et al.* (2002) used monthly production of eggs as both the same trait measured in different months or different traits measured in different months. Additionally, Anang *et al.* (2001) first published the modelling of 6 cumulative monthly egg production records using a fixed regression model. In 2002, a random regression model was used to model monthly egg production (Anang *et al.* 2002). In turkeys, estimates of heritability for egg production have been found to range from 0.08 to 0.17 when a random regression model was applied (Kranis *et al.*, 2007; Emamgholi

Begli *et al.*, 2019, Table 1). These are being implemented into a production setting as a result of the advantages identified.

Month	Heritability
1	$0.11 \pm 0.02$
2	$0.13 \pm 0.01$
3	$0.15\pm0.01$
4	$0.17\pm0.02$
5	$0.17\pm0.02$
6	$0.08\pm0.01$

Table 1. Heritability estimates for egg production in turkeys using a random regression model

#### Fertility and hatchability

Fertility is influenced by both female and male effects and has direct effect on production as defined by the production of a live offspring. The intrinsic and extrinsic impact of the female and male factors on fertility has been discussed by Brillard (2003). From the female, the ability to store enough spermatozoa in their sperm storage tubules (SSTs) after mating or artificial insemination and the steady supply of stored sperm to fertilize eggs is crucial. The environment provided by the hen for the development of the fertilized egg and successful mating of the hen is also critical. For the male, in naturally mated flocks, the success of the male with the female, the frequency of mating, as well as the ability to produce a large quantity of good quality sperm cells are the physiological and behavioral factors that influence fertility (Brillard 2003). With turkeys, all mating is by artificial insemination at both the pedigree and commercial parent stock levels. Consequently, successful natural mating behavior is not a significant trait, but sperm production and quality are important. Phenotyping turkey spermatazoa for morphology and motility has been studied and shown that motility has a significant effect on fertilization capacity but these phenotypes have not been implemented commercially due to the difficulty of application in the field (Holsberger *et al*, 1998).

Studies have shown that all the above-mentioned factors are significantly affected by age of the animal (Gumułka and Kapkowska 2005; Beaumont *et al.*, 1997). Bramwell *et al.* (1996) found differences in the mean fertility between young (39 weeks of age) and old birds (69 weeks of age). The effect of age on fertility was more severe in females than males. Gumułka and Kapkowska (2005) indicated that the fertility is affected by the age of the hen and this was the result of changes in sperm storage and sperm penetration of the perivitelline layer. In addition, a higher frequency of mating was found to occur with young birds than with old birds (Hocking and Bernard 2000). The fertility of an egg itself can likewise be affected by the genotype of the embryo, which results from the genetic factors of both parents.

The estimation of genetic parameters of fertility in poultry has been performed predominantly fitting the genetic effect of the dam and omitting that of the sire (Szwaczkowski *et al.* 2000). Sapp *et al.* (2004) fitted the sire effect as a random non-genetic effect that does not account for the additive genetic effect of the sire. However, with the knowledge that both females and males affect fertility, Wolc *et al.* (2009) fitted both the additive genetic effect and permanent environment effects of both parents using a random regression model and accounted for the longitudinal nature of the fertility data. It was shown that the male and the female contribute to variation in fertility with estimates of heritability of weekly records were typically 7% for female and 10% for male. Ultimately, the goal of fertility is the ability for the fertilized eggs to hatch. Hence, hatchability is a trait of economic importance due to its effects on production output.

Hatchability as a reproductive trait is affected by age of the hen (Lapao *et al.*, 1999), egg size (Abiola *et al.*, 2008), nutrition of the dam that affects embryo development (Wilson 1997) and the storage length of the laid eggs which is the time it takes the eggs to be set in the incubator after laid (Heier and Jarp 2001). In practice, hatch of fertile is typically defined by candling of the egg approximately 7-10 days into incubation when a developing embryo can be identified. If the fertile and live developing embryo were to be identified earlier, it would be from that that date. Hatch of fertile is a trait predominantly determined by the dam because of the environment provided by the dam for the development of the embryo in the egg. Estimated heritability for fertility and hatchability ranges from 0.04 to 0.22 (Makanjuola *et al.*, 2021; Wolc *et al.*, 2019).

More recently, the availability of genomic information has permitted the simultaneous combination of pedigree and genomic relationships in a single-step genomic evaluation method (ssGBLUP). With this method, an increase of about 23% in heritability estimates was observed for fertility and hatchability using a random regression model (Figure 1, Makanjuola *et al.*, submitted). In addition, the prediction accuracy from the ssGBLUP method was higher than those from the traditional pedigree method (Makanjuola *et al.*, submitted). This is in accordance with studies in turkeys (Abdalla *et al.*, 2019) and dairy cattle (Oliveira *et al.*, 2019).

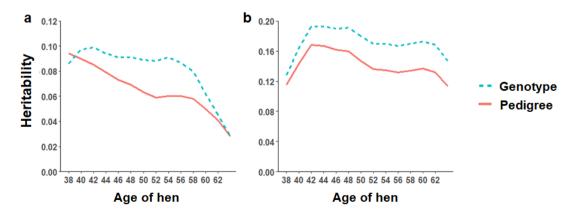


Figure 1. Heritability estimates for different ages in turkeys. a) fertility and b) hatchability

# Clutch length, broodiness and their unfavorable genetic correlations with production

In poultry, two more reproduction traits, namely clutch length and broodiness, are quite important. While clutch length refers to the number of eggs laid in a single brood by a bird, broodiness is the behavioral tendency to sit on a clutch of eggs to incubate them (Ohkubo, 2017). Emampholi Begli *et al.*, (2019) estimated heritability for clutch length and broodiness in turkeys at 0.21 and 0.15, respectively. Broodiness was negatively correlated with egg number (-0.85) and clutch length was negatively correlated with body weight of females. Such undesirable genetic correlations between production and fertility traits have been observed in poultry (Jambui *et al.*, 2017) and in many other livestock species e.g., swine (Holm *et al.*, 2004), dairy (Pryce *et al.*, 2004), and sheep (Safari *et al.*, 2007). As there is a need to maintain a balance in the selection programs to allow gain across all traits, turkey breeders use the so-called cross breeding system where sire lines are selected mainly for meat production traits (e.g., body weight, meat quality and feed efficiency), whereas dams are primarily selected for egg production traits.

An alternative is to perform a multi-trait selection for production and fertility traits of interest to investigate the causal effects among traits. This allows for knowledge about cause-and-effect mechanisms that underlie interrelationships between various phenotypes. Recently, Abdalla *et al.*, (2021) inferred the phenotypic causal networks among five production traits in a turkey population and assessed the effect of the use of such causal structures on the accuracy of prediction of breeding values, as well as the ranking of selection candidates. When causality was included, it was found that there were changes in the estimates of genetic and residual variances. Applying structural equation models led to an approximate 20% gain in accuracy of breeding values prediction in addition to changes in the ranking of animals. The authors were also able to quantify the effect of traits on each other. For instance, the effect of body weight on walking ability suggested that a 1-unit genetic improvement in body weight is expected to result in a 0.27-unit decline in walking ability but not the reverse effect. The use of structural equation models in turkey breeding programs seems promising and is expected to help in designing breeding programs that aim at improving both production and fertility traits.

#### Assessment of turkey fertility using transmission ratio distortion

Improvement of reproductive traits using genetic selection could be difficult given their complex genetic background (Fleming *et al.*, 2018). Beyond enhancing fertility through genomic selection, the availability of genomic markers has facilitated methods to investigate the decline in reproductive performance as well as the ability of parents to contribute equally to subsequent generations. This phenomenon is called transmission ratio distortion (TRD) and has been used to identify many autosomal recessive lethal loci in livestock species such as in cattle (Guarini *et al.*, 2019). Potential TRD effect on fertility in turkeys has been recently evaluated by Abdalla *et al.*, (2020). The data consisted of 23,243 birds that were genotyped based on a 61,705 SNP chip. To evaluate its different patterns, the authors used two different approaches to study TRD. The first, allelic parametrization, assessed the probability of allele transmission from he-

#### **Breeding Focus 2021 – Improving Reproduction**

terozygous parents to offspring and second genotypic parameterization, this parameterization captures the interaction between alleles of offspring genotypes.

The prevalence of TRD was widely distributed across the turkey genome where 12 and 14 haplotype candidates were significantly associated with allelic and genotypic TRD, respectively (Abdalla *et al.*, 2020). The functional analysis for these genomic regions revealed quite interesting findings that support the theory that the identified haplotypes are involved in reproduction decline in turkeys. Several gene ontology functional terms, Reactome pathways and Medical Subject Headings showed significant enrichment of genes associated with TRD. Many of these terms (e.g. mitotic spindle assembly checkpoint, DRM complex and Aneuploidy), Reactome pathways (e.g. Mismatch repair) and Medical Subject Headings (e.g. Adenosine monophosphate) are known to be related to fertility and embryo development. Knowledge about these novel candidate lethal haplotypes, functional terms and pathways may enhance reproduction rate and as a result, breeding programs in turkeys.

# Conclusion

The opportunity of increasing poultry production output through the improvement of reproductive traits holds great promise with the use of more appropriate models like random regression, especially for longitudinal traits. Additionally, the incorporation of genomic information in this model has been found to increase genetic parameters, thereby allowing for the potential to select animals with better genetic merits.

## References

Abdalla, EA., Wood, BJ, and Baes, CF (2021) Accuracy of breeding values for production traits in turkeys (Meleagris gallopavo) using recursive models with or without genomics. *Genetics. Selection. Evolution.* **53**, 1–10.

Abdalla, EA, Id-Lahoucine, S, Cánovas, A, Casellas, J, Schenkel, FS, Wood, BJ, Baes, CF (2020) Discovering lethal alleles across the turkey genome using a transmission ratio distortion approach. *Animal Genetics*. **51**, 876-889

Abiola, SS, Meshioye, OO, Oyerinde, BO, Bamgbose, MA (2008) Effect of egg size on hatchability of broiler chicks. *Archivos de Zootecnia* **57**, 83–86.

Anang, A, Mielenz, N, Schuler, L (2001) Monthly model for genetic evaluation of laying hens. 1. Fixed regression. *British Poultry Science* **42**, 191–196.

Anang, A, Mielenz, N, Schuler, L, Preisinger, DR (2002) The use of monthly egg production records for genetic evaluation of laying hens. *Jurnal Ilmu Ternak dan Veteriner* **6**, 230-234.

Avendaño, S, Neeteson, AM, Fancher, B (2017) Broiler Breeding for Sustainability and Welfare – are there Trade Offs? In 'Proceedings of 6<sup>th</sup> International Broiler Nutritionists Conference. Queenstown New Zealand' June, 2008. pp. 17.

Beaumont, C, Millet, N, Le Bihan-Duval, E, Kipi, A. Dupuy, V (1997) Genetic parameters of survival to the different stages of embryonic death in laying hens. *Poultry Science*. **76**, 1193–1196.

Bramwell, RK, McDaniel, CD, Wilson, JL, Howarth, B (1996) Age effect of male and female broiler breeders on sperm penetration of periveitelline layer overlying the germinal disc. *Poultry Science* **75**, 755-762.

Brillard JP (2003) Practical aspects of fertility in poultry. *World's Poultry Science Journal*, 59, 441-446.

Emamgholi Begli, H, Wood, BJ, Abdalla, EA, Balzani, A, Willems, OW, Schenkel, F, Harlander-Matauschek, A, Baes, CF (2019) Genetic parameters for clutch and broodiness traits in turkeys (*Meleagris gallopavo*) and their relationship with body weight and egg production. *Poultry Science* **98**, 6263-6269.

Food and Agriculture Organisation (FAO) (2020) Food Outlook – Biannual Report on Global Food Markets: November 2020. Rome. Available at: doi.org/10.4060/cb1993en (verified 3 May, 2021)

Food and Agriculture Organisation (FAO) (2021). FAOSTAT [online] Available at <u>http://www.fao.org/faostat/en/#data/QL/visualize</u>. (verified 3 February, 2021)

Fleming, A, Abdalla, EA, Maltecca, C, Baes, CF (2018) Invited review: Reproductive and genomic technologies to optimize breeding strategies for genetic progress in dairy cattle, *Archives Animal Breeding*, **61**, 43-57

Guarini, AR., Sargolzaei, M, Brito, LF, Kroezen, V, Lourenco, DAL, Baes, CF, Miglior, F, Cole, JB, Schenkel, FS. (2019) Estimating the effect of the deleterious recessive haplotypes AH1 and AH2 on reproduction performance of Ayrshire cattle, *Journal of Dairy Science* **102**, 5315-5322.

Gumułka, M, Kapkowska E (2005) Age effect of broiler breeders on fertility and sperm penetration of the perivitelline layer of the ovum. *Animal Reproduction Science* **90**, 135-148.

Havenstein, GB, Ferket, PR, Grimes, JL, Qureshi, MA, Nestor, KE (2007) Comparison of the performance of 1966-versus 2003-type turkeys when fed representative 1966 and 2003 turkey diets: Growth rate, livability, and feed conversion. *Poultry Science* **86**, 232-240.

Heier, BT, Jarp, J (2001) An epidemiological study of the hatchability in broiler breeder flocks. *Poultry Science* **80**, 1132–1138.

Hocking, PM, Bernard, R (2000) Effects of the age of male and female broiler breeders on sexual behaviour, fertility and hatchability of eggs. *British Poultry Science*, 41, 370-377.

Holm, B, Bakken, M, Klemetsdal, G, Vangen, O (2004) Genetic correlations between reproduction and production traits in swine. *Journal of Animal Science* **82**, 3458–3464.

Holsberger DR, Donoghue AM, Froman DP, Ottinger MA (1998) Assessment of ejaculate quality and sperm characteristics in turkeys: sperm mobility phenotype is independent of time. *Poultry Science* **77**, 1711-1717.

Jambui, M, Honaker, CF, Siegel, PB (2017) Correlated responses to long-term divergent selection for 8-week body weight in female White Plymouth Rock chickens: sexual maturity. *Poultry. Science*. **96**, 3844-3851.

Kranis, A, Su, G., Sorensen, D, Woolliams, JA (2007) The application of random regression models in the genetic analysis of monthly egg production in turkeys and a comparison with alternative longitudinal models. *Poultry Science* **86**, 470-475

Lapao, C, Gama, LT, Soares, MC (1999) Effects of broiler breeder age and length of egg storage on albumen characteristics and hatchability. *Poultry Science* **78**, 640–645.

Makanjuola, BO, Olori, VE and Mrode, RA (2021) Modeling genetic components of hatch of fertile in broiler breeders. *Poultry. Science* (in print) https://doi.org/10.1016/j.psj.2021.101062

Ohkubo, T (2017) Neuroendocrine control of broodiness. *Advances in Experimental Medicine and Biology* **1001**, 151-171

Oliveira, HR, Lourenco, DAL, Masuda, Y, Misztal, I, Tsuruta, S, Jamrozik, J, Brito, LF, Silva, FF, Schenkel, FS (2019) Application of single-step genomic evaluation using multiple-trait random regression test-day models in dairy cattle. *Journal of Dairy Science* **102**, 2365–2377.

Pryce, JE, Royal, MD, Garnsworthy, PC, Mao, IL (2004) Fertility in the high-producing dairy cow. *Livestock. Production Science* **86**, 125–135.

Safari, E, Fogarty, NM, Gilmour, AR, Atkins, KD, Mortimer, SI, Swan, AA, Brien, FD, Greeff, JC, van der Werf, JHJ (2007) Genetic correlations among and between wool, growth and reproduction traits in Merino sheep. *Journal Animal Breeding and Genetics* **124**, 65–72.

Sapp, RL, Rekaya, R, Misztal, I, Wing, T (2004) Male and female fertility and hatchability in chickens: a longitudinal mixed model approach. *Poultry Science* **83**, 1253-1259.

Szwaczkowski, T, Wezyk, S, Piotrowski, P, Cywa-Benko, K (2000) Direct and maternal genetic and environmental effects for fertility and hatchability in laying hens. *Archiv fuer Gefluegelkunde*, **64**, 115-120.

Swalve, HH (1995) The effect of test day model on the estimation of genetic parameters and breeding values for dairy yield traits. *Journal of Dairy Science* **78**, 929–938.

Thiruvenkadan, AK, Prabakaran, R. and Panneerselvam, S. (2011) Broiler breeding strategies over the decades: an overview. *World's Poultry Science Journal*, **67**, 309-336.

Wilson, HR (1997) Effects of maternal nutrition on hatchability. Poultry Science 76, 134-143.

Wolc, A, White, IMS., Olori, VE, Hill, WG (2009) Inheritance of fertility in broiler chickens. *Genetics Selection Evolution* **41**: 47.