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Genetics and genomics of egg production traits in poultry species

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Abstract

Modern agriculture is under strong pressure to improve production efficiency to ensure sustainability. This is an imperative and an urgent matter, given the need for increased food production to feed the rapidly growing human population with dwindling natural resources and the need to minimize environmental degradation. One fascinating fact about the egg as a source of food is its uniqueness among all sources of animal-based proteins. On the one hand, the egg has evolved as a source of life for nonplacental animals – a chamber to protect and nourish the delicate avian embryo and ensure its adequate development and survival. At the same time, it represents a unique, accessible, and dense source of nutrient for human consumption, as it contains adequate amounts of all required nutrients, with the exception of vitamin C and fiber. This makes the egg a gold standard for human nutrition. On the other hand, eggs are unique as a source of food, as they are produced in their own package. This protects the internal components from microbial and physical damage, and preserves the organoleptic and chemical properties of these components. It is also ready to use without requiring further processing, manufacturing, or refrigeration. The mentioned factors, combined with the high productivity of the modern layer, have made the egg the cheapest and more widely available source of high-quality animal protein for human consumption.

Disciplines

Agriculture | Animal Sciences | Genetics and Genomics | Poultry or Avian Science

Comments

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Chapter 6

Genetics and genomics of egg production traits in poultry species

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1 Introduction

Modern agriculture is under strong pressure to improve production efficiency to ensure sustainability. This is an imperative and an urgent matter, given the need for increased food production to feed the rapidly growing human population with dwindling natural resources and the need to minimize environmental degradation. One fascinating fact about the egg as a source of food is its uniqueness among all sources of animal-based proteins. On the one hand, the egg has evolved as a source of life for nonplacental animals – a chamber to protect and nourish the delicate avian embryo and ensure its adequate development and survival. At the same time, it represents a unique, accessible, and dense source of nutrient for human consumption, as it contains adequate amounts of all required nutrients, with the exception of vitamin C

and fiber. This makes the egg a gold standard for human nutrition. On the other hand, eggs are unique as a source of food, as they are produced in their own package. This protects the internal components from microbial and physical damage, and preserves the organoleptic and chemical properties of these components. It is also ready to use without requiring further processing, manufacturing, or refrigeration. The mentioned factors, combined with the high productivity of the modern layer, have made the egg the cheapest and more widely available source of high-quality animal protein for human consumption.

Egg production has evolved as an industry with emphasis on resource utilization, making it biologically and economically efficient and sustainable. Relatively early in the genetic improvement of poultry, a conflict between fast growth and high egg production was recognized. Therefore, separate breeds and lines were developed for meat (broilers) and egg production (layers). From 1950 to 1990, the average egg production in Germany increased more than twofold, from 120 to 260 eggs per hen (Hartmann, 1992) and further increased to 298 by 2017 and to 317 in large facilities with enriched colony cages (Statistisches Bundesamt, 2018). In the United States, Anderson et al. (2013) summarized 53 years and 37 flocks of the North Carolina random sample test (1958–2011) and reported that production in the first production cycle had increased by 67 and 64 eggs in White Leghorn and brown-egg varieties; while mortality had decreased more than threefold (from 16.6% to 5.5%) for White Leghorn and almost twofold (10.9–6.4%) for brown-egg varieties in the same period. Although increased egg production is not the primary objective for broiler producers, it is still a very important trait for broiler breeder performance because of its importance in chick output. In this context, we shall focus this review on genetics and genomics of egg production traits in layer chickens and also briefly mention studies in broiler chickens and in other poultry species (turkeys, quails, ducks, and geese).

2 Measurements of egg production: partial and total egg production

Egg production is a longitudinal or trajectory trait, as the hen has a potential for an oviposition every single day of her life post sexual maturity. Within a population, egg production can be described in the form of a production curve (Fig. 1) based on rate of lay. The curve has different components: (a) an onset of lay defined by the age at sexual maturity; (b) an ascendant phase of increased rate of lay, which finalizes as the flock reaches peak; (c) peak production (maximum rate of lay) that can be maintained for some time before declining; and (d) the descendent phase, where rate of lay decreases with age. The slope of the decreasing rate sometimes is used as an indicator of persistency of egg

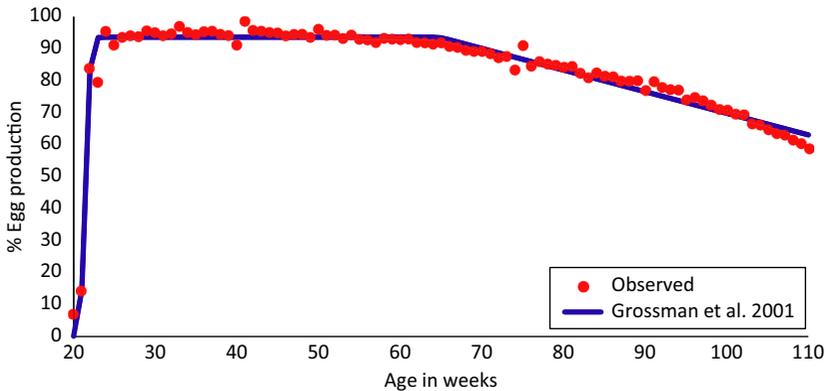


Figure 1 A typical single-cycle egg production curve in layers with fitted values from Grossman and Koops (2001) curve. Source: commercial flocks, unpublished.

production. The production curve is terminated when flocks are encouraged to molt, which induces a physiological rest during which the reproduction tract regenerates. After a molt, a second cycle of egg production can be obtained (Fig. 2). Pedigree or multiplication flocks (layer or broiler breeders) are not typically molted; but this practice is common in commercial production flocks. Due to its similarity with cow lactation curves, some models to analyze egg production use curves developed for dairy cows, such as the Wilmink curve and other types of curves (Wolc et al., 2004, 2011c, 2013).

Egg production for individual hens is traditionally measured and included in selection programs, based on total egg number to a specific age of the hen (complete or partial production) or egg production rate at specific time points. Age at first egg is used as an indicator of age at sexual maturity at onset of lay. Alternative measures based on oviposition time and clutch pattern are also available. When basing egg production on a partial record, an optimal length of recording is critical because, as noted by Morris (1963), the use of only initial production records can lead to a decrease in persistency of lay.

Inclusion of a trait in a breeding program requires studying the genetic determination of the trait(s) of interest and their genetic correlations with other traits within the selection objective. Estimates of variance components allow for calculation of trait parameters, such as heritability, to determine the genetic merit of individual birds and predict the selection responses for the target trait, and genetic correlations (r_g) with the rest of the traits to be improved. This allows for prediction of correlated responses, to decide if selecting directly on the trait is more effective than selecting on the correlated traits. This may also allow maximizing the response to selection while minimizing the number of traits included in the breeding objective. Genetic correlations between traits and associated correlated responses to selection are due to linkage (physical

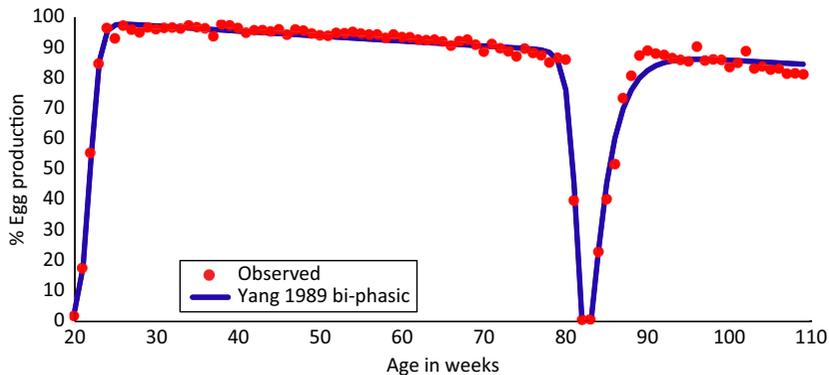


Figure 2 A typical two-cycle egg production curve, with molt, in layers with fitted values based on the Yang et al. (1989) curve extended to bi-phasic model by Wolc. Source: commercial flocks, unpublished.

proximity in the genome of the loci influencing multiple traits) and pleiotropy (a single locus influencing multiple traits). Estimates of heritability will be explored in subsequent sections. Table 1 summarizes estimates of genetic correlations among egg production, age at first egg, and two egg-quality traits (egg weight and shell quality).

Sexual maturity at an older age was associated with bigger egg weight in the majority of studies, and with loss in total egg production and poorer shell quality. Egg number had a negative genetic correlation with egg weight but an unclear genetic correlation with shell quality. Moreover, selection for increased egg number is expected to reduce egg weight and body weight. The latter is beneficial for layer chickens because feeding costs are the major cost for egg producers (Matthews and Sumner, 2015) and thus efforts are made to minimize feed costs by improving feed efficiency and reducing body weight (Zięba, 2005). It was shown that current commercial layer strains are lighter than their ancestors, despite a much higher number and mass of eggs produced (Jones et al., 2001).

Response to selection, expressed as the change in population average for target trait(s) per unit of time (i.e. year), is proportional to the accuracy of estimates of breeding values used for selection, intensity of selection (a function of the proportion of candidates selected), and the genetic standard deviation of the trait(s) under selection, and is inversely related to the generation interval. Phenotypes for total egg production are not available until the laying cycle is finished, which prolongs the generation interval. Therefore, intensive research has been carried out to define optimal age bracket for egg production recording for selection. In the 1990s, it was thought that egg production between 28 and 36 weeks of lay would be optimal for selection (Fairfull and Gowe, 1990). For a Polish population, Zięba (1990) showed that

Table 1 Genetic correlations^a between selected egg production and egg-quality traits in laying hens

Trait1 ^b	Trait2 ^c	Min correlation	Max correlation	Average correlation
AFE	EW	-0.06	0.52	0.20
AFE	EP	-0.99	0.06	-0.41
EP	EW	-0.63	0.05	-0.29
EP	Shell	-0.38	-0.10	-0.22

^a Data compiled from: Niknafs et al. (2012), Tongsir et al. (2015), Shad et al. (2007), Shadparvar and Enayati (2012), Savegnago et al. (2011), Wolc et al. (2010, 2011a, 2016), Yi et al. (2014), Francesch et al. (1997), Dunn et al. (2005), Sabri et al. (1999) and Nurgartiningasih et al. (2005).

^b AFE: age of first age; EP: egg production.

^c EW: egg weight; Shell: breaking strength.

a test of 7–9 weeks between 17 and 30 weeks of lay was most efficient for genetic improvement.

2.1 Estimates of genetic parameters

Research has focused not only on early production but also on changes of genetic parameters of egg production along the age trajectory, resulting in several papers reporting genetic parameters using monthly or bi-weekly records (Zięba, 1990; Preisinger and Savas, 1997; Savaş et al., 1998; Anang et al., 2000; Nurgartiningasih et al., 2002, 2005). Consecutive egg production records (monthly, bi-weekly, and so forth) on the same hen can be treated as repeated records of the same trait (repeatability model), as different traits (multi-trait model), or be modeled as a trajectory over time (random regression model (RRM); Wolc et al., 2011b, 2013).

Some studies have estimated a low (r_g around 0.2; Anang et al., 2000) or even negative (r_g between -0.28 and -0.11) genetic correlation between early and late egg production records (Preisinger and Savas, 1997; Nurgartiningasih et al., 2005; Wolc et al., 2007), concluding that early production is mostly a function of sexual maturity and should be considered separately from the rest of the laying cycle. For monthly egg production, Anang et al. (2000) reported heritability to be above 0.4 for the first 2 months (likely influenced by age at sexual maturity), around 0.2 for peak production, and around 0.3 for persistency. The drop in the estimates of heritability during the peak was even more dramatic in the studies of Nurgartiningasih et al. (2005) and Wolc et al. (2007), with heritability dropping from 0.4 to below 0.1 and not recovering until the end of the production cycle. In Thai Native chicken breed, the highest heritability was found in the early months of production, with estimates that ranged from 0.07 to 0.39 (Mookprom et al., 2017). Venturini et al. (2012) estimated relatively stable heritability (0.1–0.14) for tri-weekly periods 2–17, with a lower estimate for period one (0.04).

A general tendency for the genetic correlation between egg production periods to decrease as the distance between time periods increases was shown in the above mentioned studies using multi-trait models. Estimates of heritability from repeatability models were low at 0.06 (Anang et al., 2001) and even below 0.03 (Wolc et al., 2007), with only slightly higher estimates for repeatability.

2.2 Genomic analysis

Estimates of genomic heritability (proportion of phenotypic variance explained by genomic information) for egg number were similar in range (h^2 between 0.17 and 0.36) as were estimates from pedigree-based analyses (Yuan et al., 2015; Heidaritabar et al., 2016) and lower in other cases (genomic heritability of 0.16 and 0.19 for early and late production in Weng et al. (2016) vs estimates of 0.34 and 0.25, respectively, obtained using pedigree), suggesting the occurrence of 'missing heritability' (Manolio et al., 2009). The accuracy of genomic prediction of breeding values was higher (between 20% to almost double) than the accuracy of pedigree-based prediction for both early and late lay production, especially when phenotypes on contemporaries were not available (Wolc et al., 2011a,b,c; Heidaritabar et al., 2016).

Multiple genome-wide association studies for egg production or egg production rate have been performed (Atzmon et al., 2008; Wardecka et al., 2002; Goraga, et al., 2012; Goto et al., 2011; Hansen et al., 2005; Liu et al., 2011; Sasaki et al., 2004; Schreiweis et al., 2006; Tuiskula-Haavisto et al., 2002, 2004; Wolc et al., 2014; Yuan et al., 2015; Zhang et al., 2015). Significant associations were found on almost all chromosomes, suggesting the polygenic nature of these traits. Positional candidate genes include general transcription factor IIA (GTF2A1), claspin (CLSPN), phenylalanyl-tRNA synthetase (FARSB), KIAA1549, calmodulin 1 (CALM1) fibulin 5 (FBLN5) and as described by Yuan et al. (2015) and Zhang et al. (2015). Romé et al. (2015) suggested that some of the QTL for egg production may show significant interaction with the environment including diet.

2.3 Crossbred performance

Crossbred chickens were found to be hardy and easy to raise over 100 years ago (Cushman, 1892). Today, crossbreeding is still used to improve production and livability in chickens. Egg production was shown to have relatively high heterosis, up to or exceeding 20% (17–34% for egg production and reductions in age at first egg by 1–7 days; Hristakieva et al., 2014); 13% heterosis in the F1 for egg number in Omeje and Nwosu (1988); 18–23% heterosis for egg number and –2.8% for age at first egg in Iraqi et al. (2012); and 6.5–19.5% heterosis in egg production (Flock and Presinger, 1997). This led to the development

of a breeding scheme that was specifically aimed at improving crossbred performance, called Reciprocal Recurrent Selection (Flock and Presinger, 1997). It is a crossbreeding strategy in which selection of breeders of distinct purebred lines is based on performance of crossbred individuals resulting from the specific combination of the parental lines. Those schemes were later modified to combine information from both purebreds and crossbreds. Genetic correlations between purebred and crossbred performance for egg production and shell color tend to be in the moderate (r_g 0.56–0.73) (Wei and van der Werf, 1995) to high range ($r_g > 0.8$) (Besbes and Gibson, 1999; Mulder et al., 2016). Based on a comparison of different crosses, Fairfull et al. (1987) concluded that heterosis for egg production has a major epistatic component, whereas heterosis for sexual maturity is mostly explained by dominance. Estimates of the proportion of variance explained by dominance were 50–90% lower than variance explained by additive effects using both pedigree (Besbes and Gibson, 1999) and genomic data (Heidaritabar et al., 2016). With genomic data, heterosis can to some extent be predicted using squared differences in allele frequencies between the parental lines (Amuzu-Aweh et al., 2015), but the use of specific matings to maximize heterosis of a specific cross does not seem very practical since parental line accounted for 99% of the variance in heterosis between crosses, with very little within line variation (Amuzu-Aweh et al., 2015).

3 Measurements of egg production: oviposition time

Growth and maturation of follicles in the hen's ovary are controlled by luteinizing hormone. Its production, in turn, is influenced by light photoperiod, resulting in a 24–26 oviposition rhythm. Lillpers and Wilhelmson (1993) and Luc et al. (1996) published detailed analyses of both the biology and the cycle of egg formation. These developments stimulated research on the possibility of crossing the biological limit of one egg per 24–26 h. One of the newer traits that were a focus of research was oviposition time (Noddegaard, 1998; Lewis et al., 1995, 2004; Roy et al., 2014). Experiments were performed with extending or shortening hours with light (Biellier, 1985; Koelkebeck and Biellier, 1986). Currently, the lighting program has less impact on egg number than it did 30 years ago, but it has been shown that, in addition to affecting age at first egg (Arango et al., 2007), the lighting program can be used to reduce feed consumption (Morris, 2004).

3.1 Estimates of genetic parameters

The first indication of a genetic component affecting traits is the presence of between breed/line differences. This was shown for oviposition time by Lillpers

and Wilhelmson (1993), Garces and Casey (2003), Lewis et al. (2004), and Tůmová et al. (2007). Lillpers (1991) estimated the heritability of oviposition times to be 0.38, 0.68, and 0.78 in lines selected for egg number, egg mass, and egg mass with feed efficiency. Yoo et al. (1988) reported moderate estimates of heritability (0.57, 0.43, and 0.53 from ANOVA with sire and dam components, and from daughter-dam regression, respectively) for mean oviposition time in a White Leghorn population of commercial origin. In the same study, Yoo et al. (1988) reported a genetic correlation between mean oviposition time and rate of lay up to 65 weeks of age of -0.70 . The estimate of the genetic correlation between the oviposition interval and partial-record egg number was also negative (-0.45) in the study of McClung et al. (1976). All these early studies required laborious hand egg collection in hourly intervals to record the time when the eggs were laid. New technology such as the Weihestephan funnel nest box (Icken et al., 2013) allows accurate and automatic recording of oviposition time, as well as time spent in the nest. This technology, however, is expensive, thus reported sample sizes are relatively small. Estimates of heritability of oviposition time recorded in the Weihestephan funnel nest box ranged from 0.37 to 0.56, depending on the flock and laying period under study (Icken et al., 2013).

4 Measurements of egg production: clutch traits

The combination of the average oviposition time exceeding 24 h and the fact that chickens usually do not lay eggs in the dark results in a pattern of clutches (consecutive days with eggs followed by a brief pause) and length of the pause period that can be used to characterize egg production of individual hens. Intensive use of artificial incubation has allowed a reduction in or elimination of brooding behavior, as selection for high egg production favors hens with few and longer clutch lengths, with minimum pause days. Clutch-related traits have a more direct connection with oviposition time than a single number that captures egg production and also offers a physiological context. As a result, clutch traits have been considered as potential selection criteria (Bednarczyk et al., 2000; Noda et al., 2002; Chen and Tixier-Boichard, 2003a,b; Wolc et al., 2010, 2019). Clutch traits include the clutch number (periods of egg-laying with no pause), clutch size (average number of eggs laid during clutch), and pause length (average number of days between clutches).

4.1 Estimates of genetic parameters

Estimates of heritability of clutch traits were mostly in the moderate range. Luc et al. (1996) reported heritability estimates from a sire model of 0.43 and 0.68 for number of clutches and 0.49–0.50 for average clutch length in two White

Leghorn lines that were divergently selected for yolk to albumen ratio. Akbas et al. (2002), using sire and dam model, estimated a heritability of 0.37 for clutch number and 0.22 for clutch length in a commercial male line. Chen and Tixier-Boichard (2003b) estimated the heritability of clutch size and number to be around 0.4 in dwarf brown-egg layers. Icken et al. (2008) reported heritabilities for clutch number and average clutch size of 0.15 and 0.25 in a commercial White Leghorn layer line using a transponder funnel nest. In the study of Wolc et al. (2019), average clutch length and clutch number had heritability estimates that ranged from 0.31 to 0.42 and from 0.34 to 0.41 in brown and white egg layers, respectively. Chen and Tixier-Boichard (2003a) and Akbas et al. (2002) observed an increase in total egg number as a correlated response to selection for increased average clutch length. This confirms results of Wolc et al. (2019), who reported that egg production was genetically positively correlated with average (0.57 and 0.61) and maximum clutch size (0.61 and 0.45) and negatively correlated with clutch number (−0.55 and −0.28) and with age at first egg (−0.24 and −0.11) in Rhode Island Red and White Leghorn lines, respectively. The estimates of genetic correlations between egg number and clutch number obtained by Bednarczyk et al. (2000) for Rhode Island White hens were negative in generation 1995/96 (−0.43) but positive in generation 1996/97 (0.38). In a study with a transponder nest in a commercial White Leghorn layer line (Icken et al., 2008), estimates of the genetic correlation of clutch length with number of eggs and interval between clutches were 0.64 and −0.57, while clutch number had a negative genetic correlation with number of eggs (−0.53) but a positive correlation with clutch length (0.54). The phenotypic correlation between egg production and maximum clutch length of 0.11 in a Rhode Island Red line and 0.06 in a White Leghorn line reported by Wolc et al. (2019) were lower than the phenotypic correlations reported by Pavlidis et al. (2002) for early production in two White Leghorn lines selected for low and high body weight of between 0.56 and 0.71.

4.2 Genomic analysis

Wolc et al. (2019) investigated genomic control of clutch traits in two intensively selected commercial egg production breeds, Rhode Island Red and White Leghorn, utilizing the 50 000 SNP chip. The SNP explained 18%, 12%, and 30% and 37%, 21%, and 39% of phenotypic variance for average, maximum, and the number of clutches in both breeds. The same study identified four genomic regions (1 Mb) to be associated with average clutch size, two regions associated with maximum clutch size, and five regions associated with clutch number. These regions overlapped several potential candidate genes with annotated function related to reproduction or response to light stimuli: NPVF (regulation of follicle-stimulating hormone secretion); FOXO3 (oocyte

maturation, ovulation from ovarian follicle, and antral ovarian follicle growth); NR2E1 (steroid hormone receptor activity and visual perception); and ATP8A2 (detection of light stimulus).

5 Measurements of egg production: egg production curves

The existence of some level of regularity in the process of egg formation allows description of this process with mathematical models that are called egg production curves (Yang et al., 1989). Description of the egg production curve at the level of the flock or of the individual hen has several benefits, including higher accuracy of selection and prediction of future production (see review by Narinc et al., 2014b). Several linear and nonlinear models have been proposed to describe egg production curves at the flock level (Rymkiewicz-Schymczyk and Szwaczkowski, 2001). However, information on the production curve at a flock level is not always informative with respect to individual birds (Koops and Grossman, 1992) and, for breeding value estimation, an analysis of individual data is needed (Grossman and Koops, 2001). The average egg production curve can be included in the model for genetic evaluation as a fixed regression model and an individual deviation from the average curve can be fitted as random effects (RRM). RRM were originally implemented in breeding programs for dairy cattle (Schaeffer and Dekkers 1994; Schaeffer et al., 2000). Because of their advantages, including higher accuracy of estimated breeding values and utilization and modification of the pattern of the trait over time, the RRM were subsequently applied to other livestock species, including swine (Huisman et al., 2002) and poultry (Anang et al., 2002). Parameters of production curves can also be treated as traits, especially those that have a biological meaning, such as persistency, and can be directly used in selection programs (Wolc et al., 2011c).

5.1 Estimates of genetic parameters

RRM can capture changes in variance components over time with fewer parameters than multi-trait models but their estimates are constrained by the complexity of functions used to model the production curve. In the studies of Anang et al. (2002) and Wolc and Szwaczkowski (2009), heritability estimates were moderate at the beginning of production (0.3–0.5), decreased to around 0.1 at peak production, and then gradually increased toward the end of the production period. When models that allowed for heterogeneous residual variance were used, estimates of heritability increased starting from period two (Wolc et al., 2011c). The proportion of variance explained by the permanent environment was population and model specific and was sometimes significantly smaller than that of the genetic effect (Wolc et al., 2013) and sometimes larger (Wolc et al., 2011c). Estimates of genetic correlations between egg production

in different periods decreased as the interval between those periods increased. Results with RRM confirmed previous estimates from multi-trait models, suggesting that early production is dominated by age at first egg, and that it is genetically different from later production performance.

5.2 Genomic analysis

RRM using genomic information improved predictive ability of monthly egg production records especially in late periods of production (persistence) relative to pedigree-based prediction (Wolc et al., 2016). Attention must be paid to a potential overestimation of variances at extreme time periods (both early and late). Also, higher computational resources are required than for pedigree-based analysis or analysis with a simpler model.

6 Biological traits related to egg production

6.1 Age at first egg

In nature, birds are seasonal and the photoperiod controls the physiological changes associated with reproduction cycles. In chickens, growing pullets are refractory to light stimulation up to about 9 weeks of age, becoming more sensitive to photo-stimulation as they get older and approach physical maturity. Grown pullets start laying eggs when the length of the day increases which, in the production industry, is supplemented with artificial light stimulation. However, there is also a strong genetic component for age at maturity, typically measured as age at first egg, with estimates of heritability reported to be moderate (0.36–0.55; Niknafs et al., 2012; Wolc et al., 2010, 2011a; Shad et al., 2013). Age at first egg has an optimum dependent upon breed and production system. On the one hand, earlier maturity can increase early egg production, although very early maturity (before the body frame is properly developed) can lead to prolapse, small egg size, and loss of persistency. On the other hand, late maturity tends to be associated with larger body and egg weights. Therefore, in markets in which the premium price for large eggs is significant, producers modify lighting programs to delay sexual maturity and maximize egg size (Arango et al., 2007).

Depending on the population, genomic relationships explained less (Weng et al., 2016) or similar (Wolc et al., 2014; Yuan et al., 2015; Heidaritabar et al., 2016) phenotypic variance in age at first egg than pedigree relationships, with very limited contribution of dominance variance (Heidaritabar et al., 2016). Across multiple generations, predictive ability was on average higher for genomic estimated breeding values than for pedigree-based estimated breeding values (Weng et al., 2016; Heidaritabar et al., 2016).

Several studies have reported QTL for age at first egg from genome-wide association studies (Sasaki et al., 2004; Abasht et al., 2009; Podisi et al., 2011; Liu

et al., 2011; Goto et al., 2011; Goraga et al., 2012; Tuiskula-Haavisto et al., 2004; Yuan et al., 2015). Significant associations were identified on chromosomes 1, 2, 3, 4, 5, 6, 7, 11, 13, 15, 16, 18, 20, 23, 24 and Z. Except for the region from 50 to 80 Mb on Gga1 and from 30 to 40 Mb on GgaZ, the associations were population/study specific. Numerous candidate genes have been identified that show significant association between variants and age at first egg: RALGAPA1 (Ral GTPase-activating protein, alpha subunit 1 (catalytic)) and GTPase-activating Rap/RanGAP domain-like 1 gene (Shen et al., 2012); GNRH1 (gonadotropin-releasing hormone 1 (luteinizing-releasing hormone)) DRD2 (dopamine receptor D2; Xu et al., 2011); ODC1 (ornithine decarboxylase 1; Parsanejad et al., 2004); nuclear receptor coactivator 1 gene (Huang et al., 2011); myostatin gene (Zhang et al., 2012); GDF9 (growth differentiation factor 9; Huang et al., 2015); and STAT5B (signal transducer and activator of transcription 5B; Ou et al., 2009). Most of these genes belong to the hypothalamic-pituitary-gonad axis pathway or influence growth and development.

6.2 Brooding

In nature, after laying a clutch of eggs, hens pause egg production to incubate them (see Section 4). This behavior, called brooding, has been significantly reduced in modern commercial strains. Successful selection against broodiness provides evidence of the genetic component in this behavior (Muir and Cheng, 2014). Studies utilizing designed crosses to study inheritance mode of broodiness give inconsistent results. Saeki and Inoue (1979) found evidence for sex-linked determination in a Red Jungle Fowl × Leghorn cross, while Romanov et al. (1999) suggested presence of at least two autosomal genes and no evidence for sex-linkage in a Bantham × Leghorn cross. Brooding was found to be regulated by the hormone prolactin (Wilkanowska et al., 2014), making the prolactin gene (PRL) and its receptor (PRLR) potential candidate genes for broodiness (Dunn et al., 1998). Polymorphisms in the promotor region of the prolactin gene were found to be associated with broodiness (Jiang et al., 2005) and egg production (Cui et al., 2006). Prolactin level in blood is regulated by dopamine. Some polymorphisms in the dopamine gene and in its receptor were found to be associated with broody behavior (Youngren et al., 2002; Xu et al., 2010).

6.3 Nesting behavior

In alternative production systems, the use of nests becomes a very important trait, as only eggs laid within nests are suitable for human consumption due to risk of bacterial contamination of floor-laid eggs. Cooper and Appleby (1996) showed that there are differences between individuals in the preference to using nests and that this behavior can be learned, as evidenced by a decline

in the incidence of floor eggs with age. Settar et al. (2006) observed this same trend in the incidence of floor eggs over time. Estimates of the heritability of the proportion of floor eggs were in the moderate range (0.39–0.44; Settar et al., 2006). The use of a transponder equipped funnel nest box allows precise recording of nesting traits, including time spent in a nest; but, due to its high costs, current estimates are based on limited numbers of observations, resulting in high variability of heritability estimates (between 0 and 0.56) between flocks and production periods (Icken et al., 2013).

6.4 Oviduct development

The length and weight of the oviduct were estimated to have moderate heritability (0.35 and 0.39), by Shen et al. (2017a), who also identified genomic regions associated with oviduct weight, which included GGA1: 167.79–174.29 Mb, GGA4: 73.16–75.70 Mb, and GGA8: 4.88–4.92 Mb. The suggested positional candidate genes were CKAP2 (Cytoskeleton Associated Protein 2), CCKAR Cholecystokinin A Receptor, NCAPG Non-SMC Condensin I Complex Subunit G, IGFBP3 Insulin-like growth factor-binding protein 3, and GORAB Golgin, RAB6 Interacting, which are involved in cell survival, appetite, and growth control (Shen et al., 2017a).

6.5 Follicle number

In a study on the genetic architecture and candidate genes for follicle number in chickens (Shen et al., 2017b), the frequency of small yellow follicles (SYF) had moderate heritability (0.28), while preovulatory follicles had lower heritability of 0.13, with an even lower estimate for the number of atresia follicles (0.05). The numbers of different stage follicles were genetically positively correlated. The highly significant SNPs that were associated with SYF were mainly located on GGA17 and GGA28, with suggested candidate genes being Anti-Mullerian hormone (AMH) and Regulator of G-protein signaling 3 (RGS3). Only four significant SNPs were identified for preovulatory follicles on GGA1, while no SNPs displayed significant genome-wide association with atresia follicles (Shen et al., 2017b).

7 Studies of genetics and genomics of egg production in broilers

There are much fewer published studies on egg production in broilers than in layers, most likely because it is not the primary trait of interest. However, estimates of heritability for egg production in broilers show similar tendencies to those in layer chickens. In the study of Koerhuis and McKay (1996), heritability of hen

housed production (HHP: 0.14) was similar to heritability of hen day production percent (0.1) but, as in layers, they reported a higher estimate of heritability for age at first egg (0.34). Farzin et al. (2011) analyzed monthly egg production records in a commercial female line and noted higher heritability in the first month (0.43) than in the second (0.15) and third month (0.09). Adjusting for age at first egg reduced heritability in the first month to 0.19. Danbaro et al. (1995) reported estimates of heritability and genetic correlations from a selection experiment in broiler breeders and found that genetic correlations for egg production were very high between consecutive months and decreased as the interval between observations increased, similar to layers. Estimates of heritability ranged from 0.18 to 0.51 for age at first egg in White Plymouth Rock and from 0.28 to 0.63 in White Cornish. Age at first egg estimated from the sire component of variance showed a low heritability (0.13) and was 0.19 when estimated from the dam component of variance (Danbaro et al., 1995). In a synthetic broiler line in India, Nayak et al. (2015) estimated heritability for egg numbers up to 40 weeks of lay to be 0.62 based on the dam component but negative based on the sire component; with respective estimates for age at first egg of 0.19 and 0.13.

7.1 Genomic analysis

Narrow sense heritability estimated using SNPs was 0.24 for HHP (Abdollahi-Arpanahi et al., 2016). When additive and dominance effects were fitted, 17% and 6% of variance were estimated to be due to additive and dominance effects, respectively (Abdollahi-Arpanahi et al., 2016). Momen et al. (2017) concluded that, in most cases, the largest accuracy and lowest mean squared error for prediction of HHP were achieved when using a linear combination of pedigree and genomic information. Predictive ability when using all segregating markers from 600k panel was close to the best prediction achieved by the regions showing the strongest association to the trait (Morota et al., 2014). In the study by Abdollahi-Arpanahi et al. (2016), genetic variance of egg production was found to be evenly distributed between different functional classes of SNPs (intronic vs. exonic vs. 5' UTR, etc.). In an earlier study, Abdollahi-Arpanahi et al. (2014) reported that SNPs with moderate minor allele frequencies (0.1-0.2) explained the largest part of the genetic variance in hen house production. The accuracy of prediction was 0.43 from pedigree and ranged from 0.70 to 0.79 for genomic methods with a very high accuracy of imputation with a panel as low as 377 SNPs (Wang et al., 2013).

8 Studies of egg production in quail

Quail refers to a large and diverse group of birds with breeds selected for eggs, meat, or dual-purpose production. Heritability of egg production in quail was

estimated to be low (0.04–0.05; Silva et al., 2013; Kaye et al., 2016) or low to moderate if analyzed within periods of lay (0.03–0.16 for the UFV1 strain, and 0.2–0.25 for the UFV2 strain in Ribeiro et al. (2017); 0.1–0.17 in Khadiga et al. (2017); 0.04–0.09 in Karami et al. (2017), and 0.11–0.14 in Lotfi et al. (2012)). A higher estimate of heritability (0.37) was reported by Narinc et al. (2014a). Two studies (Khadiga et al., 2017; Karami et al., 2017) noted a decreasing trend in estimates of heritability for egg production with increasing age. Estimates of heritability for age at first egg were slightly higher, at 0.23 (Kaye et al., 2016), 0.21 (Khadiga et al., 2016), and 0.31 (Daikwo et al., 2014). The highest genetic correlation between partial and total egg production was estimated for egg production from 77 to 112 days (in UFV1) and from 112 to 147 days (in UFV2) strains (Ribeiro et al., 2017). In models that considered both additive and dominance effects for egg number up to 200 days of age, the estimate of narrow sense heritability was 0.32 and 0.16 in two lines of quail, with the respective estimates of proportions of dominance variance of 0.07 and 0.12 (Mielenz et al., 2006). After 22 generations of selection for egg production, nine eggs were gained between 9 and 18 weeks of age (Fathi et al., 2016). Response to divergent selection for egg number was shown to be asymmetric, with –19 eggs in low line and +3 eggs in the high line after five generations (Nestor et al., 1983).

8.1 Genomic analysis

Genome-wide association studies have been performed for egg-related traits in quail using microsatellite markers, and genome-wide significant or suggestive QTL were found for clutch length on chromosome CJA01 and for age at first egg and egg number on chromosome CJA06 (Minvielle et al., 2005). Minvielle et al. (2006) reported eight QTL on five autosomes associated with the shape of the egg production curve. Four genes from gonadotropin-releasing hormone pathway were found to be under positive selection in quail and associated with age at sexual maturity (Wu et al., 2018b).

9 Studies of egg production in turkeys

Estimates of heritability for egg production in turkeys were 0.17 (Arthur and Abplanalp, 1975), 0.22 (Willems et al., 2014), 0.32 (Case et al., 2010), and 0.24 and 0.43 (Wawro et al., 1996). Using RRM, estimates of heritability were shown to change with age, ranging for monthly records from 0.05 to 0.14 (Kranis et al., 2007) and from 0.03 to 0.18 (Luo et al., 2007). Estimates of heritability for cumulative monthly egg numbers were higher than for production rate, ranging from 0.16 to 0.54 for production from 1 to 40 weeks, with estimates in the moderate range for production in weeks 12 through 20 (Luo et al., 2007).

Estimates of realized heritability for egg production were higher in turkeys than heritability estimates reported for chickens or quail and ranged from 0.26 to 0.61 (McCartney et al., 1968; Nestor, 1971; Nestor et al., 1996). For age at first egg, estimates of heritability were 0.76 and 0.40 in two consecutive generations (Wawro et al., 1996).

Significant genotype by environment interactions for egg production in turkeys were found by Case et al. (2010), with genetic correlations between seasons of 0.76 in female and 0.86 in the male line. Long-term selection (37 generations) increased egg production to 250 days from 70 eggs in the random-bred control line to 199 eggs in a selected line (Emmerson et al., 2002) but no heterosis for egg production was observed in the reciprocal crosses between these two lines (Emmerson et al., 2002).

10 Studies of egg production in waterfowl

Genetic parameters, selection programs, and genetic gains of traits of economic interest in waterfowl (multiple duck and goose breeds) were summarized by Cheng et al. (2002, 2003); with egg production being included to some extent, even if the main goal in these species is to increase meat production, and/or other traits such as fatty liver, feather, and down. Duck breeds have been developed for either meat or egg production targets. Estimates of heritability in Muscovy ducks were 0.23 and 0.27 for egg production up to 40 and 52 weeks of age (Hu et al., 2004), which were similar to estimates in Dokki4 ducks (0.19–0.23; Younis et al., 2014). These estimates were higher than those obtained in the Brown Tsaiya ducks using the sire component of variance (0.02–0.14) by Tai et al. (1989), or using an animal model (0.12–0.16) by Cheng et al. (1995), or in the Philippine Mallard Ducks (0.09) by Roxas et al. (2005); but, they were lower than those estimated in the Shan Ma laying duck (0.38–0.43) by Lin et al. (2016) and in Tegal ducks (0.35) by Ismoyowati et al. (2009). In a selection experiment, realized heritability was found to range from 0.37 to 0.43 by Abrianto et al. (2017). For age at first egg, estimates of heritability ranged from 0.13 to 0.2 (Hu et al., 2004; Cheng et al., 1995; Lin et al., 2016). Egg production records at different ages were highly positively correlated with each other, not correlated with the body weight, and negatively correlated with age at first egg, egg weight, egg yolk weight at 40 weeks, and eggshell strength at 30 weeks (Cheng et al., 1995). A negative genetic correlation between egg number and age at first egg was also found by Hu et al. (2004) and by Younis et al. (2014).

In geese, meat production, fatty liver, feather, and down have been emphasized, but laying and gosling production traits are also important, and have been incorporated into multi-trait selection schemes (Cheng et al., 2002, 2003). The most important producer of geese is China, which accounts for up to 95% of the world market in recent years, with Poland second. Goose meat

prices are the highest among poultry species (170% greater than chicken in 2017) and the down and feathers are extremely valued (Utnik-Banaś and Žmija, 2018). Increased egg production was documented in an 8-year program (Shalev et al., 1991) in two goose lines (Grey-male, and White-female), realizing annual genetic gain of 2.7 eggs per generation, but with a decline after the initial 4 years of selection. The authors recommended the use of crossbred varieties for commercial production. Shrestha et al. (2004) summarized multi-trait parameters in Chinese and a synthetic line of geese selected for egg production over a 24-week laying period, with reduced body fat and simultaneous increase in body weight at 16 weeks. Egg production increased by 1.3 eggs per generation. Wolc et al. (2008) studied production and reproduction traits in a maternal and a paternal line of geese. Estimates of heritability for egg number up to 28 weeks of production were moderate (0.47 for the maternal line and 0.30 for the paternal line). In both lines, there was a strong negative genetic correlation between production and egg size (-0.63 and -0.84 , respectively). In the maternal line, moderate positive genetic correlations were observed for egg production with body weight and reproduction traits. In the paternal line, egg production was negatively correlated with the two reproduction traits. In general, Wolc et al. (2008) confirmed the unfavorable relationship between production and reproduction traits in geese. Lower estimates of heritability for egg production (0.21-0.40) were reported by Rosiński (2000) and by Shrestha et al. (2004) for Chinese and synthetic strains of geese. Rosinski et al. (2006) also studied the laying rhythm traits (number of 2 and 3+ egg clutches, length of 2+ egg clutches, and the length of the intervals between clutches) and their correlations with reproductive traits in the maternal line of Koluda white geese (W11). They used the sire, dam, and sire-dam variance components to estimate heritabilities. In general, the sire-based heritabilities were higher than the dam-based estimates, while the sire-dam-based estimates were intermediate. Estimates of sire-dam-based heritability for clutch traits ranged from 0.07 to 0.54. The authors concluded that several laying rhythm traits showed moderate heritability and could be used in selection programs. Rosinski et al. (2006) also reported high positive genetic correlations of the number of egg clutches with total egg number and laying rate. In more recent studies, Graczyk et al. (2017) studied partial and cumulative production of eggs as part of a conservation effort in native Zatorska geese, and reported heritabilities of 0.20 using single-trait analysis and of 0.12-0.24 when using a multiple trait approach.

Molecular genetic studies in ducks have focused on estimation of effects of candidate genes. In the Gaoyou ducks, a polymorphism in the prolactin (*PRL*) gene (intron 1) was not significantly associated with either age at first egg, egg number, or clutch length (Hui-Fang et al., 2009). Variation in the prolactin gene was significantly associated with egg production and egg weight in native Chinese ducks (Wang et al., 2011) and with egg number to 300 days in Khaki

Campbell ducks (Chuekwon and Boonlum, 2017). A polymorphism in the growth hormone gene (*GH*) was significantly associated with egg number in Muscovy ducks (Wu et al., 2014a). A polymorphism in the ovoinhibitor gene (*OIH*), which is the main proteinase inhibitor in the egg white, was associated with age at first egg, weight at first egg, and egg number at 72 weeks of age (Wu et al., 2018a). Polymorphisms within the genes insulin-like growth factor 2 (*IGF2*) and dopamine receptor 2 (*DRD2*) genes were associated with egg production traits, and both genes are highly expressed in the ovary of Muscovy ducks (Ye et al., 2017). Blood protein polymorphisms (transferrin, albumin, and hemoglobin) were associated with egg production in Tegal ducks (Ismoyowati, 2008).

In a genome-wide gene expression analysis, a total of 843 differentially expressed genes were identified between high and low egg production ovaries in ducks (Tao et al., 2017). Some genes, such as melanocortin 5 receptor (*MC5R*), apolipoprotein D (*APOD*), oral calcium release-activated calcium modulator 1 (*ORAI1*), and dual-specificity tyrosine (Y) phosphorylation regulated kinase (*DYRK4*), were more active in high-producing ovaries and, thus, may play role in regulation of egg production (Tao et al., 2017).

In geese, Yu et al. (2015) developed a sequence strategy to detect SNPs that differed in allele frequency between geese with high and low estimated breeding values for egg production. Of 139K SNPs evaluated, 55 SNPs showed distinct allele frequency differences. Ten of these SNPs were genotyped in 492 geese to verify their association with egg production, of which eight were significant. They also cloned five novel candidate genes that harbored SNPs with impacts on egg-laying: membrane-associated guanylate kinase (*MAGI-1*), *KIAA1462*, Rho GTPase-activating protein 21 (*ARHGAP21*), acyl-CoA synthetase family member 2 (*ACSF2*), and astrotactin 2 (*ASTN2*). The authors concluded that these eight SNP and five genes were promising candidate markers for selection for egg number in geese (Yu et al., 2015). Xu et al. (2016) studied the role of DBH (Dopamine β -hydroxylase) in modulating reproduction in two Chinese goose breeds. Expression of DBH was explored in multiple tissues, including oviduct, pituitary, hypothalamus, and the stroma of the ovary. They reported that the reproductive and endocrine tissues of Yangzhou geese with higher egg production had greater gDBH expression than Zhedong geese. Five non-synonymous SNPs were identified in the coding region of DBH gene between Zhedong and Yangzhou geese. The authors concluded that DBH may regulate reproductive activity by the hypothalamus-pituitary-gonadal (HPGA) axis.

11 Conclusion

Egg production is a biologically complex process that is expressed over a long period of time, during which both genetic (gene expression) and environmental

conditions can vary. Heritability estimates tend to be low to moderate, especially when adjusted for age at first egg. Genome-wide association studies identified mostly small effects dispersed across the genome, suggesting a polygenic determination. Significant progress has been obtained in egg production using traditional selection, and genomic selection is a promising tool to further enhance genetic gain.

12 Future trends

Traditional selection has resulted in the improvements in multiple egg production traits, as discussed in this chapter. Recent application of numerous genome-selection-based tools has the potential to accelerate improvements in the near future by increasing the accuracy with which individuals with genetics for superior performance can be identified, and then used for reproduction of superior progeny. Understanding the specific genes involved with the various egg production traits and subsequent identification of genetic variation in these genes will further advance overall improvements. The recent development of novel gene-editing tools will allow specific improvements of the genome to be made and further improve overall efficiency of egg production to feed the growing global population. The gene-editing tool CRISPR is very promising for allowing rapid genetic change in poultry species. Application of this tool within a practical breeding program will require answers to multiple questions, including which specific variants should be edited, are there negative correlations to other traits, can similar gains be made through less expensive, more traditional selection technologies, and will there be consumer acceptance of products that are improved through direct gene-editing (Fulton, 2018).

13 Where to look for further information

Genetic improvement of egg production is relevant globally. There are multiple scientific meetings that provide forums in which genetic improvements in animal production, including egg production, are discussed. The World's Congress on Genetics Applied to Animal Production (WCGALP) is perhaps the best-known international forum. An electronic archive of the proceedings from previous meetings is available at: <http://www.wcgalp.org/proceedings>. Results of published associations between SNPs and various phenotypes are available at: www.animalgenome.org. Novel research on poultry genetics is published in journals focused on poultry, for example: *Poultry Science* <https://academic.oup.com/ps/>; *British Poultry Science* <https://www.tandfonline.com/loi/cbps20>; *World's Poultry Science Journal* <https://www.cambridge.org/core/journals/world-s-poultry-science-journal>; and journals focused on genetics, for example: *Genetics Selection Evolution* <https://gsejournal.biomedcentral.com/>;

Journal of Animal Breeding and Genetics <https://onlinelibrary.wiley.com/journal/14390388>; *PLoS ONE* <https://journals.plos.org/plosone/>; *Animal Genetics* <https://onlinelibrary.wiley.com/journal/13652052>; and others.

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