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Eggshell strength in laying hens' breeding goals - a review

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This paper presents a review describing genetic and phenotypic attributes of eggshell quality traits that are considered worldwide in genetic selection of layers. Eggshell strength plays a key role in production of both table and hatching eggs; hence, breeding companies include quite a variety of traits associated with eggshell strength in their breeding criteria. While the level of eggshell resistance to mechanical damage, as the ultimate manifestation of eggshell strength, can be estimated based on recording of other indicative traits, the eggshell strength itself has got to be negotiated by hatching ease. It appears, however, that space for eggshell strength selection exists as genetic correlations between strength and hatchability are still close to null or even moderately positive. Unfavourable genetic correlations between breaking strength and other economically important traits such as albumen height, and, in particular, egg production and egg weight support the choice of braking strength as the breeding goal component. The most common indirect method of eggshell strength evaluation is specific gravity whereas from the breeder's point of view ultrasonic eggshell thickness measurement should be considered as a good choice selection criterion.

KEYWORDS: laying hens / eggshell strength / variance components / breeding goal

The eggshell is the outermost part of the egg protecting the developing embryo from mechanical damage and pathogen penetration. It also serves as storage of

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calcium indispensable for the formation of the embryo skeletal system and moderates gas exchange with the milieu. Eggshell has fundamental importance in the case of table eggs in the context of their resistance to potential damage that may occur during production and handling. It is estimated that 6-20% of all laid eggs undergo damage during production [Washburn 1982, Roland *et al*. 1988]. Economic losses associated with eggshell breakage amounted to ca. 247 million $ per year only in the United States [Singh *et al*. 2007]. For non-caging systems in Europe, this number is typically 2 to 6%, according to the Vencomatic company [van Mourik *et al*. 2017]. Eggs with detected fractures are worth approximately one euro cent less than intact eggs. This means an economic loss of €16 000 for a complete production round of 100 000 hens from 18^{th} to 90^{th} week of age, 400 eggs laid per hen, and an average fracture rate of 4% [van Mourik *et al*. 2017]. Eggs with the so-called eggshell cracks cannot be qualified as highest quality raw material and are therefore disqualified as potential hatching eggs. The presence of hairline cracks increases the risk of penetration by pathogenic bacteria, e.g. *Salmonella enterica*, to the egg interior. In 2004, over 9.5 thousand salmonellosis cases were observed in Belgium among patients who developed the disease after consumption of eggs and egg products [Messens *et al*. 2006]. The Centers for Disease Control and Prevention estimates that 1 million cases of nontyphoidal salmonellosis occur each year in the US. Worldwide, it is estimated that incidence of nontyphoid *Salmonella* ranges from 200 million to 1.3 billion, with estimated death toll of 3 million each year [Howard *et al*. 2012]. A cracked eggshell may promote leakage of the egg content and contamination of other eggs. This threatens food safety and increases food production costs. The eggshell can be damaged before the egg is laid, when it is being laid, and during egg collection, grading, packaging, and transport [Washburn 1982, Mertens *et al*. 2006]. The probability of egg breakage varies between the different stages of production. The number of egg breakages is strongly influenced by the layer housing system. The highest proportion of losses related to eggshell damage is recorded in the cage system, whereas alternative systems are associated with lower rates of egg breakage [Mertens *et al*. 2006].

The susceptibility of an egg to damage is strictly connected with the quality of the eggshell, which is often referred to as eggshell strength. It means resistance of the eggshell to cracking under the influence of external force [Hamilton 1982]. Factors determining eggshell strength include the genetic line of the layer (pure line/commercial hybrid), the age of the stock, moulting, nutrition, stress (e.g. thermal), diseases, production system, and nutritional additives. A review of these factors was presented in the papers by Roberts [2004] as well as by Ketta and Tumova [2016].

The mechanical eggshell strength is determined by eggshell structural and material attributes. The structural ones comprise eggshell thickness, size, shape, and curvature of the egg, while the material ones include proportion of organic and inorganic components. The organic components are represented by the sub-shell membranes, eggshell-forming proteins (protein matrix), and cuticle; in turn, the inorganic elements include the ultra- and microstructure of the eggshell. These both components interact with each other and the eggshell quality is a result thereof [Solomon 1991, Bain 2005].

Eggshell quality traits

Most eggshell quality traits represent quantitative characteristics determined by environmental and genetic factors. Selection in layer stocks should therefore aim at improvement of these traits. Before deciding on the selection criterion, it is necessary to define the breeding goal indicative traits and methods for their recording. Conditions that should be fulfilled by a given trait to be included in the selection criterion comprise easy and fast measurement thereof at possibly lowest recording cost, sufficient genetic variability, and high genetic correlation with the breeding goal traits that cannot be easily and inexpensively recorded.

Material properties of eggshell

Given its characteristic curvature and fragility, the measurement of the material traits of the eggshell with conventional methods is difficult. This is related to the fact that samples should have a uniform shape and size to facilitate the analysis of eggshell stresses. Analyses of the ultra- and microstructure of the eggshell are performed with optic microscopy, X-ray diffraction, small angle X-ray scattering (SAXS), microfocus-SAXS, and two-dimensional X-ray diffraction (2D-XRD) methods [Rodriguez-Navarro *et al*. 2002, Bain 2005]. Given their time inefficiency and the high cost of measurement devices, methods for evaluation of the eggshell material traits, at least currently, have a limited use in large-scale assessment of eggshell quality. Instead, they are used for basic research focused on exploration of the internal shell structure, characterization of its variability and a possible impact on eggshell strength. Implementation of these methods in the standard evaluation of egg quality would pose many problems.

Direct and indirect shell strength measurement methods

The methods for measurement of eggshell strength developed so-far can be divided into direct and indirect [Hamilton 1982]. The direct methods are based on the analysis of the force required to damage the shell. They comprise impact force tests, measurement of the puncture force, and measurements of eggshell breaking strength. Indirect methods include amongst others determination of egg specific gravity, non-destructive deformation, eggshell thickness, egg weight, and the proportion of the shell weight within the egg weight. The direct and indirect measurements of eggshell strength can be regarded as a reflection of its mechanical and physical properties, respectively [Hammerle 1969]. Indirect methods, both destructive and non-destructive, measure a parameter/trait associated with eggshell strength. They are based on an assumption that the outcomes of indirect measurements are highly correlated with the outcomes of direct measurements; however, majority of the breeding companies are still using breaking strength as the main selection criterion along with indirect methods.

Eggshell quality traits used in selection for eggshell strength

The most important and most common direct measurement of eggshell strength, the minimum force indispensable for breaking an egg, is the measurement of breaking force defined with the use of a quasi-static compression test [Hamilton 1982, Voisey and Hunt 1967]. In this test, the egg placed between two flat surfaces is compressed by a head moving at a constant rate until eggshell fracture. During the measurement, the force required for breaking of the eggshell is recorded [Tyler 1961]. The measurement of the breaking force is a destructive method; therefore, it is not possible to perform multiple measurements on the same egg, while the strength estimates obtained at different points of the shell may differ from each other as a result of differentiation of the eggshell thickness at various areas of an eggshell [Tyler and Geake 1964, De Ketelaere 2002, Sun *et al*. 2012, Yan *et al*. 2014, Kibala *et al*. 2015]. Factors that affect the quasi-static impact fracture force measurement include the velocity of the head, compression surface exerting pressure on the egg [Voisey and Hunt 1969, 1973] and the age of the layer, as the eggshell breaking strength declines with hen's age [De Ketelaere *et al*. 2002, Rodriguez-Navarro *et al*. 2002, Blanco *et al*. 2014]. An advantage of this method is its simplicity and speed, whereas its drawbacks include the destructive character of the measurement, and the high cost of the device for measurement of material strength (e.g. Instron, Robotmation, Stable MicroSystems). The measurement of breaking strength simulate the major types of damage affecting the eggshell during the production process [Hamilton *et al*. 1979]. Breaking strength is characterized by a moderate heritability ranging from 0.10 to 0.48 (Tab. 1). A significant impact on the magnitude of the heritability estimates is exerted by the statistical model employed for estimation of variance components and hen's breed/line (Table 1). Guo *et al*. [2015] showed that the highest heritability of breaking strength was found at the laying peak (32 weeks of age) and decreased gradually until the 66th week of age. It can be noted that the decrease of the heritability estimate with the age of hens is characteristic for most of the traits as the environmental effects accumulate.

Genetic selection focused on increasing the value of breaking strength proved effective, as confirmed by the investigations of Combs *et al*. [1979], who carried out divergent selection of Leghorn hens for eggshell breaking strength measured with a quasi-static test. Highly significant differences between selected lines were observed as early as after two generations. Similar results were obtained by Boruszewska *et al*. [2009], who performed selection of highly productive Rhode Island Reds and a Polish native Green-legged Partridgenous hens for, amongst others, shell strength. The selection lasted for 4 generations and resulted in significant differentiation between groups selected divergently, in both breeds.

Table 1. Heritability estimates for eggshell traits in layer hens

Trait nature	Trait	Breed[1]	Week of life	h^2	Method/Model[2]	References
Destructive	breaking strength	RIW/RIR	33	0.16/0.24	REML/AM	Kibala *et al*. 2018
		WL	36-38	0.35-0.48	REML/AM	Gervais *et al*. 2016ab
		RIR/WPR/WL	26/65	0.14/0.14/0.14	5 different LM's	Arango *et al*. 2016
		RIR/WPR/WL	42/86	0.18/0.17/0.23	5 different LM's	Arango *et al*. 2016
		RIR	26/42/65/86	0.13	5 different LM's	Arango *et al*. 2016
		WL x DX	32-72	0.20-0.31	REML (h^2snp)	Sun *et al*. 2015
		BEL/WEL	32-36/67-70	0.34-0.35/0.23-0.33	REML	Blanco *et al*. 2014
		INF	30	0.21	REML/AM	Begli *et al*. 2010
		RIR/GLP	33	0.22/0.20	REML/AM	Boruszewska *et al*. 2009
		RIR	37-39	0.1		Icken *et al*. 2006
		BDL	40	0.24	REML	Zhang *et al*. 2005
		RIR	38-42	0.15/0.21/0.18/0.18	REML/S/D/SD/AM	Dunn *et al*. 2005a
		RIR	60	0.13/0.14/0.15/0.17	REML/S/D/SD/AM	Dunn *et al*. 2005a
		WL/RIR	40-46	0.38/0.43	REML/AM	Cavero *et al*. 2010
	shell thickness	RIW/RIR	33	0.16/0.30	REML/AM	Kibala *et al*. 2018
		WL	36-38	0.448	REML/AM	Gervais *et al*. 2016b
		WL	36-38	0.53	REML/AM	Gervais *et al*. 2016a
		RIW/RIR	55	0.19/0.23	REML	Kibala *et al*. 2015
		BEL/WEL	32-36/67-70	0.37-0.44/0.27-0.29	REML	Blanco *et al*. 2014
		INF	30	0.57	REML/AM	Begli *et al*. 2010
		RIR	37-39	0.19		Icken *et al*. 2006
		RIR	38-42	0.3	REML/AM	Dunn *et al*. 2005b
		BDL	40	0.34	REML	Zhang *et al*. 2005
Non-destructive	specific gravity	RIW/RIR	33	0.16/0.26	REML/AM	Kibala *et al*. 2018
		RIW/RIR	34	0.18/0.21	REML/AM	Rozempolska-Rucińska *et al*. 2011
		WL/CL/CR	34/50/64	0.30/0.23/0.11		Ledur *et al*. 2003
		WL	26-30/50-54	0.45/0.23/0.31		Sabri *et al*. 1999
		WL	30-35/40-45	0.13-0.83/0.31-0.75	REML/AM	Wei and Van Der Werf 1993
	non-destructive deformation	WL	36-38	0.37-0.49	REML/AM	Gervais *et al*. 2016ab, 2017
		WL	36-38	0.36-0.37/0.14-0.39	REML/AM/Realized heritability	Nirasawa *et al*. 1998
		WL	42-45/67-68	0.18-0.20/0.12-0.22	SV/DD	Grunder *et al*. 1989
	dynamic stiffness	RIR	26/42/65/86	0.31-0.43/0.41-0.44/0.31-0.37/0.25-0.31	6 models	Wolc *et al*. 2017
		WL	26/42/65/86	0.27-0.33/0.28-0.35/0.19-0.27/0.16-0.33	6 models	Wolc *et al*. 2017
		RIR/WPR/WL	26/42/65/86	0.33/0.33/0.36	5 different LM's	Arango *et al*. 2016
		RIR	26/42/65/86	0.38	5 different LM's	Arango *et al*. 2016
		BEL/WEL	32-36/67-70	0.65-0.70/0.35-0.43	REML	Blanco *et al*. 2014
		RIR	37-39	0.4		Icken *et al*. 2006
		RIR	38-42	0.33/0.46/0.53/0.58	(REML) S/SD/AM/D	Dunn *et al*. 2005a
	USG	RIW/RIR	33	0.22/0.37	REML/AM	Kibala *et al*. 2018
		RIW/RIR	55	0.09-0.17/0.12-0.21	REML/AM	Kibala *et al*. 2015
		WL x DX	32-72	0.21-0.31	REML (h^2snp)	Sun *et al*. 2015

[1]Breed: RIR – Rhode Island Red; RIW – Rhode Island White; WL – White Leghorn; BEL – Brown Egg Layer; WEL – White Egg Layer; WPR – White Plymouth Rock; CL – commercial line; INF – Iranian native fowl; BDL – Brown-egg Dwarf Layer; DX – Dongxiang chickens; PL – pure line; CR – crosses; GLP – Green-legged Partridgenous. [2]Method/Models: REML – Restricted Maximum Likelihood Method; AM – Animal Model; S – Sire model; D – Dam model; SD – Sire–Dam model; DD – Dam-Daughter regression; SV – Sire Variance; h2snp – SNP-based heritability; LM – linear model; MMLS – Mixed Model Least Squares/Maximum Likelihood; h^2 – heritability; USG – ultrasonic eggshell thickness measurement.

Table 2. Genetic (r_P) and phenotypic (r_G) correlations between breaking strength and other economically important traits

Trait		Breed[1]	Period (week of age)	r_P	r_G	Model[2]	References
Breaking strength	shell thickness	RIW/RIR	33		0.84/0.61	REML/AM	Kibala *et al*. 2018
		WL	36-38	0.68-0.73	0.75-0.82	REML/AM	Gervais *et al*. 2016b
		Fayoumi		0.77			Radwan *et al*. 2015
		RIR	40	0.319			Yan *et al*. 2014
		BEL/WEL	32-36/67-70	0.41-0.46/0.50	0.50-0.63/0.65-0.78	REML	Blanco *et al*. 2014
		INF	30	0.5	0.55	REML/AM	Begli *et al*. 2010
		RIR	37-39		0.39		Icken *et al*. 2006
		BDL	40	0.69	0.77	REML	Zhang *et al*. 2005
	USG[3]	RIW/RIR	33		0.83/0.73	REML/AM	Kibala *et al*. 2018
	non-destructive deformation	WL	36-38	-0.67 to -0.74	-0.77 to -0.84	REML/AM	Gervais *et al*. 2016ab
		WL	36-38		-0.82 to -0.78	REML/AM	Nirasawa *et al*. 1998
		WL	42-45/67-68	-0.64/-0.66	-0.82 to -0.80	DD	Grunder *et al*. 1989, 1991
	dynamic stiffness	BEL/WEL	32-36/67-70	0.30-0.33/0.47	0.40-0.55/0.55-0.61	REML	Blanco *et al*. 2014
		RIR	37-39		0.57		Icken *et al*. 2006
		RIR	37-43	0.21-0.38	0.43-0.53/0.40-0.63	S/D	Dunn *et al*. 2005a
		RIR	60	0.14	0.36/0.69	S/D	Dunn *et al*. 2005a
	specific gravity	RIW/RIR	33		0.89/0.67	REML/AM	Kibala *et al*. 2018
		WL	42-45/67-68	0.58/0.60	0.76/0.88	DD	Grunder *et al*. 1989
	dynamic stiffness	RIR/WPR/WL	26/42/65/86	0.78/0.45/0.53	0.28/0.23/0.27	LM	Arango *et al*. 2016
		RIR/WPR/WL	26/42/65/86	0.69/0.37/0.21	0.31/0.31/0.51	LM	Arango *et al*. 2016

[1]Breed abbreviations as in the Table 1; [2]Model: REML – Restricted Maximum Likelihood Method; AM – Animal Model; S – Sire model; DD – Dam-daughter regression model; LM – linear model; [3]USG – ultrasonic eggshell thickness measurement.

It was estimated that the increase of eggshell strength by 1 Newton would result in a 0.5% decrease in the number of eggs damaged during the production cycle [Tuiskula-Haavisto *et al*. 2011]. Breaking strength showed low to moderate positive genetic correlation with reproduction traits like fertility rate (0.06-0.10), hatching rate from eggs set (0.19-0.27) and hatching rate from fertile eggs (0.22-0.29; Tab. 3). Grunder *et al*. [1989] observed high positive genetic correlation of 0.60 to 0.92 between this trait and percentage of intact eggs (Tab. 3) – percentage of eggs remaining intact from oviposition to placement in fibre trays after grading. Breaking strength was also negatively correlated (-0.23 to -0.60) with the presence of microcracks in eggshell.

Table 3. Genetic and phenotypic correlations between eggshell traits and other economically important traits

Trait[1]		Age	Breed[2]	r_P	r_G	Model[3]	References
% intact eggs	BS	42-45/67-68		0.28/0.33	0.28/0.33		
	NDD	42-45/67-68	WL	-0.26/-0.35	-0.26/-0.35	D	Grunder *et al*. 1989
	SG	42-45/67-68		0.36/0.46	0.36/0.46		
Age at sexual maturity	BS	42-45/67-68	WL	0.08/0.04	0.08/0.04	S	Grunder *et al*., 1991
	BS		INF			REML/AM	Salehinasab *et al*. 2014
	EST		INF			REML/AM	Salehinasab *et al*. 2014
	NDD	25-38	WL (strong line/weak line)	-0.05/-0.07	-0.05/-0.07	REML	Gervais *et al*. 2017
	SG	42-45/67-68	WL	0.06/0.05	0.06/0.05	S	Grunder *et al*. 1991
	SG		INF			REML/AM	Salehinasab *et al*. 2014
Albumen height	BS	30	INF	-0.009	-0.009	REML/AM	Begli *et al*. 2010
	BS	32-36	BEL (male/female line)	-0.19/-0.10	-0.19/-0.10	REML	Blanco *et al*. 2014
	BS	40	BDL	-0.02	-0.02	REML	Zhang *et al*. 2005
	BS	67-70	WEL (male/female line)	0.02/0.04	0.02/0.04	REML	Blanco *et al*. 2014
	EST	32-36	BEL (male/female line)	-0.13/-0.07	-0.13/-0.07	REML	Blanco *et al*. 2014
	EST	40	BDL	-0.06	-0.06	REML	Zhang *et al*. 2005
	EST	67-70	WEL (male/female line)	0.05/0.14	0.05/0.14	REML	Blanco *et al*. 2014
	Kdyn	32-36	BEL (male/female line)	-0.03/-0.03	-0.03/-0.03	REML	Blanco *et al*. 2014
	Kdyn	67-70	WEL (male/female line)	0.06/0.09	0.06/0.09	REML	Blanco *et al*. 2014
	SG	35/54	WL	0.04	0.04	S+D	Poggenpoel 1986
Egg production	BS	42-45/67-68	WL			S	Grunder *et al*. 1991
	BS	36-38	WL (strong line/weak line)	-0.08/-0.11	-0.08/-0.11	REML/AM	Nirasawa *et al*. 1998
	BS		INF			REML/AM	Salehinasab *et al*. 2014
	EST	35/54	WL	-0.12	-0.12	S+D	Poggenpoel 1986
	EST	35/54	WL	-0.09	-0.09	S+D	Poggenpoel 1986
	EST		INF			REML/AM	Salehinasab *et al*. 2014
	NDD	25-38	WL (strong line/weak line)	0.04/0.04	0.04/0.04	REML	Gervais *et al*. 2017
	NDD	42-45/67-68	WL	-0.04/0.06	-0.04/0.06	S	Grunder *et al*. 1991
	SG	42-45/67-68	WL	0.00/-0.05	0.00/-0.05	S	Grunder *et al*. 1991
	Kdyn	26-50	RIR	0.07	0.07	S/D	Dunn *et al*. 2005a
	Kdyn	58-74	RIR	-0.01	-0.01	S/D	Dunn *et al*. 2005a
Egg weight	BS	32-36/67-70	BEL/WEL	-0.19/-0.08	-0.19/-0.08	REML	Blanco *et al*. 2014
	BS	37-39	RIR				Icken *et al*. 2006
	EST	30	INF	0.24	0.24	REML/AM	Begli *et al*. 2010
	EST	32-36	BEL (male/female line)	-0.02 to 0.12	-0.02 to 0.12	REML	Blanco *et al*. 2014
	EST	40	WL	-0.23/0.58	-0.23/0.58	MMLS	Sreenivas *et al*. 2013
	EST	67-70	WEL (male/female line)	0.18 to 0.26	0.18 to 0.26	REML	Blanco *et al*. 2014
	Kdyn	32-36	BEL (male/female line)	0.01/0.06	0.01/0.06	REML	Blanco *et al*. 2014
	Kdyn	67-70	WEL (male/female line)	0.21/0.12	0.21/0.12	REML	Blanco *et al*. 2014
	Kdyn	38-42	RIR	-0.02	-0.02	SD	Dunn *et al*. 2005a
	NDD	25-38	WL (strong line/weak line)	0.06/-0.06	0.06/-0.06	REML	Gervais *et al*. 2017
	NDD	42-45/67-68	WL	0.01/-0.02	0.01/-0.02	D	Grunder *et al*. 1989
	SG	42-45/67-68	WL	-0.04/-0.10	-0.04/-0.10	D	Grunder *et al*. 1989
	SG	34	RIW/RIR			REML/AM	Rozempolska-Rucińska *et al*. 2011
Fertility rate	BS	45-46	Line C/Line D (WL)			REML/AM	Cavero *et al*. 2011
	BS	42-45/67-68	WL	-0.05/0.03	-0.05/0.03	S	Grunder *et al*. 1991
	Kdyn	45-46	WL			REML/AM	Cavero *et al*. 2011
	NDD	42-45/67-68	WL	-0.01/-0.02	-0.01/-0.02	S	Grunder *et al*. 1991
	SG	42-45/67-68	WL	0.03/0.08	0.03/0.08	S	Grunder *et al*. 1991
Hatching rate of eggs set	BS	45-46	Line C/Line D (WL)				Cavero *et al*. 2011
	Kdyn	45-46	WL			REML/AM	Cavero *et al*. 2011
	SG	34	RIW/RIR				Rozempolska-Rucińska *et al*. 2011
Hatching rate of fertile eggs	BS	45-46	Line C/Line D (WL)			REML/AM	Cavero *et al*. 2011
	Kdyn	45-46	WL			REML/AM	Cavero *et al*. 2011
	NDD	42-45/67-68	WL	0.02/0.01	0.02/0.01	S	Grunder *et al*. 1991
	SG	42-45/67-68	WL	-0.02/0.01	-0.02/0.01	S	Grunder *et al*. 1991
Micro-cracks	BS		RIR	-0.18	-0.18		
	BS	26/42/65/86	RIR/WPR/WL	-0.29/-0.28/-0.68	-0.29/-0.28/-0.68	LM	Arango *et al*. 2016
	BS		RIR/WPR/WL	0.07/-0.19/-0.51	0.07/-0.19/-0.51		
	Kdyn		RIR/WPR/WL	-0.29/-0.87	-0.29/-0.87		

[1]% intact eggs – percentage of eggs remaining intact from oviposition to placement in fibre trays after grading; BS – breaking strength; NDD – non-destructive deformation; SG – specific gravity; EST – eggshell thickness; Kdyn – dynamic stiffness.
[2]Breed abbreviations as in the Table 1. [3]Method/Models as in the Table 2.

Most of the studies reported unfavourable genetic correlations between breaking strength and other economically important traits such as age at sexual maturity (0.08 to 0.20), albumen height (-0.17 to -0.38), egg production (-0.09 to -0.43) and egg weight (-0.04 to -0.57). Favourable genetic correlations between breaking strength and albumen height as well as egg production were observed only in Iranian native fowl [Begli *et al*. 2010, Salehinasab *et al*. 2014]. The result, however, was of a large standard error. The egg quality was assessed on small amount of eggs, as well. The result suggests however, that in native fowl stocks, where breeders do not put high selection pressure on egg production, it is possible to preserve no or only small negative genetic correlation between eggshell strength traits and other economically important traits. Moderate positive genetic correlation between breaking strength and albumen height was also observed in selected Leghorn female line [Blanco *et al*. 2014]. This line had lower mean egg weight, breaking strength, and shell thickness compared to the male line.

Favourable genetic correlations were observed between breaking strength and egg quality traits i.e. eggshell thickness, ultrasonic-determined shell thickness, non-destructive deformation, dynamic stiffness, and specific gravity (Tab. 2), making those traits useful in selection.

Despite limitations, most of breeding companies have used breaking strength as a selection criterion for over 50 years [Bain 2005]. The evaluation of breaking strength is, however a destructive method; therefore, the evaluated eggs cannot be intended for hatching or sale [Hamilton 1982], which further increases the cost of the analyses. Additionally, it is impossible to carry out multiple measurements of the same egg. For this reasons, new and non-destructive methods of shell strength evaluation have been introduced in laying hens

The measurement of egg specific gravity developed by Olsson [1934] is the most frequently used indirect method for assessment of eggshell strength. It can be measured by immersion of eggs in a series of sodium chloride solutions with increasing concentrations and determining that in which the egg sinks. Another option is the use of a specially constructed balance facilitating measurements of the weight of a dry egg and a water-immersed egg. Egg specific gravity is next calculated with the use of the Archimedes' principle [Pym 1969]. The method is rapid, practical, and cost efficient [Hamilton 1982]. Yet, the reliability of the measurement depends on the temperature of water or saline solutions, which therefore should be constantly monitored [Voisey and Hamilton 1976]. Another factor influencing the value of egg specific gravity is the egg storage time. The longer the time, the lower the specific egg gravity; therefore, the measurement should be carried out within the possible shortest time after the egg is laid or the time which has elapsed from laying an egg till the measurement should be accounted for when defining the specific gravity [Hamilton and Thompson 1981]. Another option is measurements performed for all eggs at the same time that has elapsed since they were laid or after the time required for stabilisation of the air space [Voisey and Hunt 1974]. The presence of hairline cracks does not affect the value of egg specific gravity, provided that the egg is immersed for a short time [Voisey and Hamilton 1977a]. In turn, cracked eggs should not be examined [Voisey and Hunt 1974]. Therefore, many authors challenge the credibility of this method [Wells 1967, Voisey and Hamilton 1977a, Sloan *et al*. 2000]. Olsson [1934] showed that egg specific gravity was strongly correlated with the eggshell percentage in the egg; therefore, an increase in its value is accompanied by increasing eggshell thickness and strength. Genetic correlation between breaking strength and specific gravity was high and ranged from 0.67 to 0.89 and (Table 2). The eggshell quality is regarded to be low if the value of egg specific gravity is lower than 1.08 g/cm^3. Furthermore, hatching eggs with specific gravity below 1.08 g/cm^3 from meat-type hens exhibited a lower rate of fertilisation by 1-5% and hatchability by 3-9% as well as higher embryo mortality rates, compared with eggs of higher specific gravity [McDaniel *et al*. 1981, Bennett 1992]. As suggested by McDaniel *et al*. [1981] and Bennett [1992], the method had an inconsiderable effect on fertilisation and embryo mortality rates; nevertheless, the eggs are not advisable to be intended for hatching due to the possibility of contamination with pathogenic microorganisms. Specific gravity showed moderate to high heritability estimates ranging from 0.16 to 0.83, depending on statistical model employed for estimation of the heritability coefficient, hen breed/line and age as well as the genetic structure of the stocks examined (Tab. 1). Nonetheless, selection to increase egg specific gravity would be effective. McPhee *et al*. [1982] selected 5 generations of Australorp hens to obtain high egg specific gravity. The realised heritability amounted to 0.23. Simultaneously, a 3.4% decrease in the number of eggs with a thin shell and a decline in the weight and albumen content as well as average body weight and feed intake accompanied that selection. This points to a necessity of choosing the selection criterion traits after prior analysis of their genetic correlations with the breeding goal traits. Specific gravity was positively correlated with percentage of intact eggs (0.72-0.93), fertility rate (0.11), hatching rate of fertile eggs (0.06-0.43), hatching rate of eggs set (0.47-0.66). Most studies showed that specific gravity was positively correlated with age at sexual maturity (0.03-0.53). Egg weight and egg number are the most important traits in layer production. Moderate negative genetic correlation was observed between specific gravity and egg number (-0.10 to -0.40) as well as egg weight (-0.09 to -0.36). Results indicating positive genetic correlation between specific gravity and egg weight and ranging from 0.02 to 0.18 were, however, also reported [Grunder *et al*. 1989].

Non-destructive deformation (NDD; static stiffness – Kstat**)** is measured with a quasi-static compression test; this method is non-destructive and assesses only eggshell deformation caused by predetermined maximum force of 0.5; 1.0, or 1.5 kg [Voisey and Hamilton 1977b]. As reported by Hamilton [1982], the value of the optimal force in measurement of non-destructive deformation at the equatorial part of the egg is 9.8N. Non-destructive deformation characterises the structural traits of the eggshell [Hamilton *et al*. 1979]. It can be used for estimation of the eggshell breaking strength [Voisey and Hamilton 1976] as a correlated trait. The measurement of Kstat is dependent on the speed of the head of the device measuring strength of the material, egg temperature [Voisey *et al*. 1979], eggshell thickness and curvature, and egg diameter [Amer 1998, Bain 1990]. The efficiency of the method is ca. 400 eggs per hour [Voisey and Mac Donald 1978]. The value of Kstat declines with the layers' age [De Ketelaere *et al*. 2002]. Nirasawa *et al*. [1998] showed that an increase in eggshell breaking strength was accompanied by a decline of the value of non-destructive deformation. Genetic correlation between these traits ranged from -0.77 to -0.82 (Tab. 2). A drawback of the method is its time inefficiency and the high cost of the recording equipment.

Divergent selection toward the non-destructive deformation carried out over 10 generations of Leghorn hens resulted in an increase of the trait estimates from 64.7 to 100.6 in a line of a high NDD (line of a weaker eggshell) and a decline from 59.9 to 51.9 µm/kg in a line selected for a low NDD (line of a stronger eggshell – Nirasawa *et al.* 1998). Gervais *et al*. [2017] found that after 17 generations of divergent selection for non-destructive deformation this trait was moderately correlated with egg production (0.222 in the strong line and 0.204 in the weak line). The genetic correlations between non-destructive deformation and egg weight were very small: 0.066 in the strong line and -0.108 in the weak line [Gervais *et al*. 2017].

Heritability of non-destructive deformation ranged from 0.12 to 0.49 (Tab. 1) depending on statistical method used for calculation of the heritability coefficient and hens' breed and age. High negative genetic correlation ranging from -0.65 to -0.88 (Tab. 3) was observed between this trait and percentage of eggs remaining intact during production process. Slight to moderate negative genetic correlation was also noticed between non-destructive deformation and fertility rate (-0.08), hatching rate of fertile eggs (-0.17 to -0.42) and sexual maturity (-0.06 to -0.19). Genetic correlation coefficients between non-destructive deformation and egg weight had small positive (0.07-0.08) or negative (-0.11) estimates, thus pointing to the lack of mutual relation. Like for most of the eggshell quality traits unfavourable genetic correlation between non-destructive deformation and egg production was recorded (0.10-0.36).

One of the most important indirect methods for assessment of eggshell strength is the measurement of its thickness. The importance of this parameter is related to the fact that there is a high correlation between its magnitude and the percentage of cracked eggs [Tyler and Geake 1963]. The thickness measurement is usually performed using a micrometric screw at 3 points of the equatorial part of the egg. According to Tyler [1961], the eggshell thickness at this point is the most uniform. The value of this trait declines with the age of layer hens [De Ketelaere *et al*. 2002].

Eggshell thickness exhibits high variability, depending on the measurement point. It is substantially greater in the longitudinal (from the pointed to the blunt end of the egg) than in the latitudinal plane of the egg [Tyler and Geake 1964]. Therefore, Sun *et al*. [2012] proposed a new parameter, which is a measure of the total eggshell thickness, i.e. uniformity of eggshell thickness (UET). UET is the inverse of the coefficient of eggshell thickness variability measured in a destructive manner using a micrometric screw at 42 different points on the egg. Its value was positively correlated with eggshell breaking strength ($r=0.34$; $p<0.01$). The authors showed that eggshell thickness measured exactly at the pointed end of the egg exhibited the highest similarity to the average total egg thickness; hence, measurement at this point can be a good predictor in assessment of eggshell quality. The thinnest point on the eggshell was located near the blunt egg end, where hatching chicks pierce the eggshell [Sun *et* *al*. 2012]. Similar conclusions were formulated by Kibala *et al*. [2015] in their analyses of eggshell thickness at 15 different points of the shell performed with an ultrasonic technique. Simultaneously, they stated that the measurement of eggshell thickness at an angle of 45° from the blunt egg end was the best predictor of its strength due to the highest heritability among all the measurement points and due to negotiating the needs of hatching ease in the breeding farms and table egg safe handling, in the production ones. The heritability of shell thickness ranged from 0.09 to 0.37 depending on the measurement point and layer breed [Kibala *et al*. 2015, 2018]. To calculate UET, Yan *et al*. [2014] also employed non-destructive approach to measure the eggshell thickness basing on ultrasonic technology (echometer/ultrasonic defectoscopy) in accordance with the methodology proposed by Sun *et al*. [2012]. Besides strength, eggshell thickness affects eggshell conductance reflecting its capability of gas exchange and water loss during egg incubation [Paganelli 1980]. Investigations results indicate that eggs with thicker eggshell are characterised by greater hatchability (r_p=0.30; Liao *et al*. 2013). Hatchability rates in eggs with a thin shell is from 3 to 9% lower [Bennett 1992] than that in eggs with a normal shell, i.e. between 0.35 and 0.40 mm [Icken *et al*. 2006]. Presumably, such eggs have longer pores, which should reduce eggshell conductance and protect the egg from excessive evaporation during the incubation period, thereby increasing heritability values [McDaniel *et al*. 1979,Wilson 1991]. Additionally, thicker shell protects the egg from microbial penetration [Sauter and Petersen 1974] and mechanical damage [Bain 1991, Khatkar *et al*. 1997]. Heritability of destructive eggshell thickness ranged from 0.16 to 0.57 (Table 1). Genetic correlation coefficient between shell thickness and albumen height (-0.11 to -0.25; 0.03-0.08), egg weight (-0.15 to 0.36), egg production (-0.16 to -0.22; 0.24) and sexual maturity (-0.09) were low positive or negative depending on statistical method and hen's line and age (Tab. 3). Positive correlation between shell thickness and albumen height were observed in brown and white layers female line at the age of 32-36 and 67-70 weeks of age [Blanco *et al*. 2014]. These lines had also lower egg weight, breaking strength and shell thickness (white egg line) compared to male lines. Positive genetic correlation between shell thickness and egg production was observed only in native fowl which was characterized by low egg weight and egg number [Salehinasab *et al*. 2014].

Rapid and non-destructive assessment of eggshell strength leaving the eggs intact can be performed with the acoustic resonance method proposed by Coucke [1998] and improved by other researchers [Coucke *et al.* 1999, De Ketelaere *et al*. 2002, Wang *et al*. 2004, Lin *et al*. 2011]. The technique involves excitation of eggshell vibrations by hitting it with a small hammer as well as analysis thereof and defining the resonance frequency. Next, the resonance frequency is used for estimation of eggshell strength in an intact egg. In this way, Coucke [1998] defined a new parameter determining eggshell strength, i.e. dynamic stiffness (Kdyn). It is estimated by measurements of vibrations at 4 points located at equal distances on the equatorial part of the egg.

The results obtained by different research groups investigating eggshell strength with acoustic resonance differ from one another. This is probably caused by the different weight and type of material used for construction of the hammer used for excitation of resonance [Lin *et al*. 2009, Attar and Fahti 2014]. As suggested by Blanco *et al*. [2014], the method, in contrast to measurement of eggshell thickness and breaking strength, is not suitable for comparison of different genetic lines or sets of layer hens with each other. Furthermore, the Kdyn value increases with age, while the breaking strength declines; therefore, comparison of this trait between eggs laid by hens of different age is problematic [De Ketelaere *et al*. 2002, Molnár *et al*. 2016]. The relatively high repeatability of the measurements of this trait, i.e. 0.68 to 0.71, is noteworthy [Blanco *et al*. 2014].

An undeniable advantage of this method is the short time of a single analysis (ca. 10 ms). Hence, multiple measurements of ca. 200 eggs per hour can be performed [Dunn *et al*. 2005a]. For this reason, the method is of growing popularity and has new practical applications, e.g. monitoring of eggshell strength in layer hen farms, which can be decreased by stress or disease [Lin *et al*. 2004, Mertens *et al*. 2007]. Messens *et al*. [2007] also showed that eggs with a higher Kdyn value were penetrated by *Salmonella enteritidis* bacteria to a lesser extent and exhibited a lower rate of damage throughout the production process. As reported by Dunn *et al*. [2005b], the lower the Kdyn value, the higher the probability of eggshell damage during the packaging process. Dynamic stiffness has moderate to high heritability (0.16 to 0.70 – Tab. 1). The estimates of genetic correlation of Kdyn with presence of microcracks (-0.46 to -0.62) were negative and substantial (Tab. 3).

Slight negative genetic correlation was noted between dynamic stiffness and egg weight (-0.06 to -0.20), albumen height (-0.03 to -0.01), fertility rate (0.08 to -0.11) hatching rate of eggs set (-0.10 to -0.17) and hatching rate of fertile eggs (-0.09 to -0.17, Tab. 3). Dunn *et al*. [2005a,b] showed a small negative genetic correlation between dynamic stiffness and egg production between the 26^{th} and 50^{th} weeks of age and a moderate negative correlation between Kdyn and egg production at the age of 58-74 weeks (Tab. 3). These values, however, were burdened with a relatively large standard error and also depended on statistical model employed for calculation. Majority of the studies showed slight negative genetic correlation between dynamic stiffness and egg weight although Balnco *et al*. [2014] reveal positive correlation between these traits in Leghorn male line. This line was characterized by lower dynamic stiffness than the female line but higher egg weight, breaking strength and shell thickness.

Each of the presented eggshell quality traits and each measurement method have their advantages and drawbacks. The choice of the best method depends on whether it is to be employed for identification of cracked eggs or selection of the best individuals in terms of the eggshell quality traits.

Conclusions

Unfavourable genetic correlations between breaking strength and other economically important traits such as albumen height, and, in particular, egg production and egg weight support the choice of braking strength as the breeding goal component.

Table 4 presents most popular or promising indirect and non-destructive methods which may be used as an index for breaking strength in selection of laying hens for stronger eggshell.

Table 4. Advantages and disadvantages of indirect methods used for eggshell quality evaluation

Indirect method	Genetic correlation with breaking strength	Advantages	Disadvantages
Specific gravity	high	• non-destructive • time efficient • cost efficient	• sensitivity to environment factors • inability for hatching and sale after measurement • hairline cracks do not affect the measurement result
Non-destructive deformation	high negative	• non-destructive • multiple measurements possible	• sensitivity to environment factors • high costs of equipment
Dynamic stiffness	moderate to high	• non-destructive • detection of microcracks • time efficient • cost efficient • multiple measurements possible	• depends on material used for hammer construction (excitation of resonance) • increase with hen's age (BS decrease)
Ultrasonic eggshell thickness	high	• non-destructive • multiple measurements possible • time efficient cost efficient	• depend on the measurement point • hairline cracks do not affect the measurement result

The most common indirect method of eggshell strength evaluation is specific gravity. However, many authors have challenged its reliability. In turn, non-destructive deformation requires an expensive recording equipment. The advantages of dynamic stiffness recording include rapid and multiple measurements of an egg, high heritability and repeatability, and high correlation with the target eggshell breaking strength. However, the Kdyn value increases with the age of the stock, whereas eggshell strength declines. Therefore, comparison between different-age bird groups should be avoided. Among all presented in Table 4 measurements the ultrasonic eggshell thickness is characterised by high heritability and positive genetic correlation with eggshell breaking strength. The measurement is non-destructive and can be performed at many points on the egg. No statistically significant differences were observed between shell thickness measurements performed at the same points using a micrometre screw and the ultrasound device [Kibala *et al*. 2015]. To reduce the time of recording even more, measurement at one point on an egg can be carried out [*ibidem*]. Hence, from the breeder's point of view ultrasonic eggshell thickness measurement should be considered as a good choice selection criterion.

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