602. Heterosis of egg-laying performance in chickens

A.X. Ni[1,2*], M.P.L. Calus[2], H. Bovenhuis[2], Y.Y. Sun[1] and J.L. Chen[1]

[1]Institute of Animal Sciences, Chinese Academy of Agricultural Sciences, 100193 Beijing, China; [2]Wageningen University & Research, P.O. Box 338, 6700 AH Wageningen, the Netherlands; aixin.ni@wur.nl

Abstract
Heterosis is the phenomenon that hybrids display better performance than the parental average. In this study, we aimed to quantify egg-laying performance, and heterosis for a complete diallel cross of Beijing-You and White leghorn chickens. Egg weight, egg production and egg quality traits were measured, and heterosis was estimated. We found significant heterosis for egg weight, egg number and age at first egg in the cross lines. Favourable heterosis was also observed for egg quality traits except albumen height and Haugh unit. Moreover, for egg weight, heterosis tended to be higher if Beijing-You was the sire line and White Leghorn was the dam line which was in contrast to egg production traits.

Introduction
Heterosis is the phenomenon that performance in hybrids is superior to the average performance of their parents. At present, most eggs, chicken meat, and pork are produced from hybrid animals. Utilization of heterosis in commercial breeding schemes relies on investigating the best crossbreeding combinations performance from extensive cross-examination Therefore, in this study, a complete diallel cross of Beijing-You (Y) and White Leghorn (W) was constructed to evaluate heterosis of egg-laying performance in chickens.

Materials & methods
Population. Two breeds (Y, Beijing-You, a Chinese local breed; W, White Leghorn, a high productive breed) with a large difference in egg-laying performance were chosen. The two breeds were mated to generate four genetic groups: (1) 30 Y roosters were mated with 150 Y hens to generate YY offspring; (2) the same roosters were mated with 150 W hens to generate YW offspring; (3) 30 W roosters were mated with 150 W hens to generate WW offspring; and (4) the same roosters were mated with 150 Y hens to generate WY offspring.

Egg-laying performance. Egg laying characteristics measured were age at first egg (AFE), egg number until 43 weeks of age (EN43), average clutch length (ACL), and oviposition period (OP), weight of first egg (FEW), egg weight every 4 week from 28 weeks of age till 68 weeks of age, and egg quality traits at 32 weeks of age: shell colour (SC), shell strength (SI), shell thickness (ST), albumen height (Alh), Haugh unit (HU), egg shape index (ESI), yolk ratio (YR), and shell ratio (SR).

Statistics analysis. Heterosis and genetic parameters were estimated using the following model:

$$y_{ijk} = \mu + b_i + a_j + e_{ijk}$$

Where y_{ijk} is the phenotypic value, μ is the population average, b_i is the fixed effect of genetic group (YY, YW, WW and WY), a_j is the random animal effect with 2,485 animals included in the pedigree, e_{ijk} is the random error.

Estimated differences between YW and mid-parent value (MPV), between WY and MPV, and between YW and WY and their Wald F statistics were obtained by ASReml.

DOI: 10.3920/978-90-8686-940-4_602, © A.X. Ni *et al.* 2022

Results

Descriptive statistics. The mean egg weight increased with aging (Table 1). The standard deviation for egg number at 43 weeks of age and age at first egg were higher than oviposition period and average clutch length (Table 1). Descriptive statistics for egg quality traits is provided in Table 2.

Genetic parameter analysis. Estimated heritability for egg weight at 28 to 64 weeks of age was high (0.56-0.77), with the highest value at 52 and 64 weeks of age (Table 3). Genetic correlations between egg weight at different ages were high (0.86-0.98), especially for consecutive time points. Age at first egg was negatively correlated with egg number until 43 weeks of age (r_g=-0.47, Table 3). The heritability for all egg quality traits at 32 weeks of age was moderate (0.31-0.50, Table 4). Shell thickness had a strong genetic correlation with both shell ratio (r_g=0.85), and shell strength (r_g=0.69, Table 4).

Table 1. Descriptive statistics for egg weight and egg production traits of all populations.

Trait[1]	EWt28	EWt40	EWt52	EWt64	EN43	AFE	OP	ACL
n	1,141	989	868	774	928	1,194	1,104	936
Mean	51.28	55.85	58.05	60.85	110.86	167.92	25.27	7.55
SD	4.86	4.99	4.85	5.01	18.40	11.83	1.11	5.95

[1] EWtx = egg weight at x weeks of age, n = number of test animals, SD = standard deviation.

Table 2. Descriptive statistics for egg quality traits of all populations.

Trait	SC	SI	ST	Alh	HU	ESI	YR	SR
n	1,075	1,068	1,074	1,074	1,071	1,074	1,071	1,065
Mean	64.46	3.79	0.34	4.53	67.29	1.31	29.00	9.98
SD	12.90	0.57	0.02	0.80	6.69	0.04	2.18	0.59

Table 3. Estimated genetic parameters for egg weight and egg production traits.

Trait category	Egg weight					Egg production			
Trait[1]	EWt28	EWt40	EWt52	EWt64	Trait	EN43	AFE(d)	OP	ACL
EWt28	0.56	0.89	0.84	0.86	EN43	0.22	-0.47	-0.30	0.36
EWt40	0.67	0.67	0.97	0.97	AFE(d)	-0.62	0.54	-0.28	0.24
EWt52	0.62	0.80	0.77	0.98	OP	-0.35	-0.01	0.38	-0.74
EWt64	0.60	0.75	0.81	0.77	ACL	0.47	0.03	-0.39	0.06

[1] Values in bold are heritability estimates, the upper triangles are genetic correlations and lower triangles are phenotypic correlations.

Table 4. Estimated genetic parameters for egg quality traits.

Trait	SC(%)	SI(kg/cm²)	ST(mm)	Alh(mm)	HU	ESI	YR	SR
SC (%)	0.31	-0.22	-0.44	-0.44	-0.46	0.00	0.27	-0.37
SI (kg/cm²)	-0.17	0.38	0.69	-0.14	-0.13	-0.06	0.03	0.74
ST (mm)	-0.33	0.55	0.42	-0.12	-0.10	0.00	-0.08	0.85
Alh (mm)	-0.07	-0.01	-0.03	0.32	0.97	-0.11	-0.32	-0.13
HU	-0.04	-0.02	-0.07	0.92	0.31	-0.09	-0.26	-0.09
ESI	-0.02	0.07	-0.01	0.01	-0.04	0.44	-0.03	-0.07
YR	0.10	-0.05	-0.19	-0.44	-0.35	0.00	0.44	0.07
SR	-0.20	0.61	0.76	-0.28	-0.19	-0.03	0.09	0.50

Predicted values. Both YW and WY showed significant heterosis (1.07%-6.65%) for egg weight throughout the laying period. The heterosis for egg weight increased with advancing age, and was higher for YW than for WY (Figure 1). Age at first egg and egg number until 43 weeks of age showed favourable heterosis, and the heterosis for egg number was higher for WY than for YW. While oviposition period differed between WY and MPV, and between YW and WY. Except for albumen height and Haugh unit, all egg quality traits presented favourable heterosis. For shell colour, yolk weight, shell strength, and shell thickness, hybrid performance was higher than MPV, while the reverse was observed for Haugh unit. Heterosis for yolk weight, yolk ratio, and egg shape index in YW was higher than in WY (Table 5).

Discussion

Egg-laying performance is an important economic trait. The pedigree-based heritability estimates for egg weight and egg quality traits were slightly higher than those in a Rhode Island Red (RIR) population (Liu *et al.*, 2018a, 2018b). The estimate of egg number and age at first egg were similar to RIR population (Liu *et al.*, 2019). The genetic and phenotypic correlation among all egg-laying traits were similar to previously reported estimates (Liu *et al.*, 2018a, 2018b, 2019).With the extension of the laying period egg weight increases which confirms results of other studies (Ledur *et al.*, 2002).

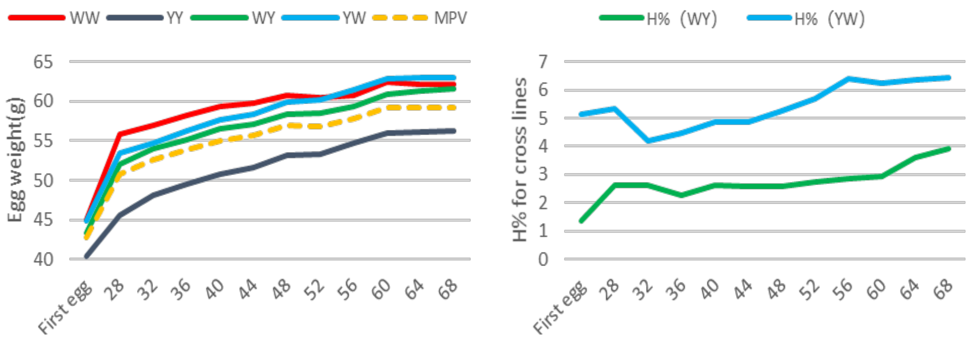

Figure 1. Predicted egg weight for the four genetic groups and heterosis for the two reciprocal crosses.

Table 5. Predicted values for egg production and egg quality traits.

Trait		MPV	H%(WY)	H%(YW)	*P*-value		
					WY vs MPV	YW vs MPV	WY vs YW
Egg production	EN43	109.97	3.01	1.87	<0.01	<0.01	<0.01
	AFE	169.21	-1.96	-0.99	0.01	<0.01	<0.01
	OP	25.26	-0.62	0.03	0.02	0.69	<0.01
	ACL	9.04	-24.29	-26.07	<0.01	<0.01	0.02
Egg quality	SC (%)	63.00	8.33	5.88	0.50	<0.01	<0.01
	SI (kg/cm^2)	3.62	5.08	10.71	<0.01	<0.01	0.32
	ST (mm)	0.33	1.08	2.65	0.01	<0.01	0.09
	Alh (mm)	4.62	-2.20	-4.28	0.04	0.22	0.50
	HU	68.49	-3.21	-3.66	<0.01	<0.01	0.75
	ESI	1.31	0.56	0.36	0.08	<0.01	0.03
	YR	28.58	1.91	2.08	<0.01	0.05	<0.01
	SR	9.86	1.32	3.00	<0.01	<0.01	0.21

In this experiment, significant heterosis was observed for egg weight, egg number, average clutch length and Haugh unit, which was consistent with other studies (Abplanalp *et al.* 1984; Ledur *et al.* 2000; Emmerson *et al.* 2002; Ledur *et al.* 2002). But heterosis for egg number and age at first egg was smaller than Williams *et al.* results in fowl (2002) and Emmerson *et al.* in turkey (2002). Our results showed that the level of heterosis is both dependent on the trait and the reciprocal cross.

Throughout the experimental period, we found higher heterosis for egg number in WY than YW, and higher for egg weight in YW than WY. There was a strong divergence in heterosis for these traits, illustrating the complexity of non-additive genetic variation and the difficulty in predicting heterosis. Sutherland *et al.* (2018) also found differences between reciprocal crosses for growth traits in chickens, and suggested that one or more Z-linked genes may underlie this difference.

In conclusion, favourable heterosis was observed for most egg-laying performance traits in a cross between Beijing-You and White Leghorn chickens. Moreover, a considerable difference in heterosis between the two reciprocal crosses was observed. The molecular mechanisms underlying heterosis will be further explored in a subsequent genome-wide association study.

Acknowledgements

This work was supported by the National Natural Science Foundation of China (32172721), and scholarships from the China Scholarship Council (202103250072).

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