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Heterosis in egg production in different parts of the laying period of layers of Rhode Island Red origin selected by RRS selection in two environments Part I. Heterosis in egg production in the original populations after few generations of RRS selection

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ABSTRACT

Heterosis in hen day egg production was studied in four independent 90 day part periods of the 360 day laying cycle. All parental purebred and their reciprocal crossbred progeny were housed 2 and 4 hens per cage. The parental strains were Rhode Island competitive commercial populations selected by RRS since few generations only. From each pure strain 9 random selected unrelated cocks mated to 15 unrelated pullets produced the purebred and crossbred progeny. The experiment was conducted as an orthogonal randomised factorial trial, sires were regarded as random, mating system (cross vs. pure) and density (2 vs. 4 hens/cage) as fixed effects. A total of 18 paternal half-sib groups of 64 birds each completed the trial. Heterosis was significant (P<0.001) in all part periods in both environments. The heterosis in hen day egg production during the part periods 1-90, 91-180, 181-270 and 271-360 days in production respectively were: 2 birds per cage: 4.75, 4.99, 6.12 and 4.58 eggs, 4 birds per cage: 4.12, 3.14, 5.24, 7.96 eggs. In both environments the mean heterosis across production periods in eggs produced was the same: 5.11 eggs. The relative (%) magnitude of heterosis tended to increase in the second part of the egg production period, this tendency was more pronounced when 4 hens were kept to a cage, simulating a production environment which is very close to that practised on intensive commercial farms. The increased stocking rate depressed egg production significantly (P<0.01-0.001) only in the second part of the laying cycle, interactions mating × density were not significant.
(Keywords: heterosis, egg production, part periods, commercial strains, RRS selection)

ÖSSZEFOGLALÁS

A tojástermelésben mutatkozó heterózis az RRS módszerrel szelektált Rhode Island Red tojótyúkok különböző termelési periódusában, két eltérő környezetben I. Heterózis az eredeti populációban néhány generációra terjedő RRS szelekció után

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360 napos tojóciklus, 4 független 90 napos periódusa alatt, tanulmányoztuk a tojástermelésben jelentkező heterózis nagyságát. A szülői fajtatiszta vonalakat és a reciprok keresztezett *populációkat 2 és 4 férőhelyes ketrecekben helyeztük el. A Rhode Island Red szülővonalak olyan átlagos tenyészetekből származtak, amelyekben csak néhány generáción keresztül szelektáltak RRS módszerrel. Mindegyik vonalból 9 véletlenszerűen kiválasztott, egymással rokonságban nem lévő kakast, 15 rokonságban nem lévő tisztavérű és keresztezett jércével párosítottunk. A kísérletet ortogonális, véletlenszerű, faktoriális módon állítottuk be és értékeltük. Az apákat véletlen hatásnak tekintettük, a párosítási módja (keresztezett vagy tisztavérű), valamint a telepítési sűrűség (2 és 4 tojótyúk/ketrec) volt a fix hatás. A heterózis a 360 napos periódus mindegyik részében, valamint mindkét környezetben szignifikáns volt (P<0,001). A következőkben felsorolt szakaszok alatt (1-90, 91-180, 181-270 és 271-360 nap) a tojástermelésben tapasztalt heterózis az alábbiak szerint alakult: 2 madár/ketrec: 4,75; 4,99; 6,12 és 4,58 tojás; 4 madár/ketrec: 4,12; 3,14; 5,24 és 7,96 tojás. Mindkét környezetben a heterózis átlagos nagysága mindegyik populációnál azonos volt (5,11) tojással. A relatív heterózis % nagysága a második tojástermelési periódusban növekedett, ez a tendencia növekedett 4 tojó / ketrec esetén kifejezetten erős volt. Ez az elhelyezés azt a környezetet modellezte, amely rendkívül közel áll a gyakorlatban alkalmazott intenzív tojástermelési viszonyokhoz. A nagyobb állatsűrűség csak a termelés második felében csökkentette szignifikánsan (P<0,01; 0,001) a tojástermelést. A párosítás×telepítési sűrűség interakció növekedett nem volt szignifikáns.*

(Kulcsszavak: heterózis, tojástermelés, részperiódusok, kereskedelmi vonalak, RRS szelekció)

INTRODUCTION

Heterosis in poultry has been studied in numerous experiments. *Fairfull* (1990) presents an excellent survey summarising experimental evidence regarding the factors affecting heterosis of many traits in poultry considering age related aspects, genetic background of populations and some environmental aspects. Overall it can be stated that there are very few experiments published in which competitive commercial or highly productive egg type chicken were tested in distinctly different environments except those published by *Gowe and Fairfull* (1982), *Horn et al.* (1980, 1982) and *Muir* (1995). The situation did not change lately (*Horn et al.,* 1998). No data were published on egg production of commercial egg producing strains regarding the changes of heterosis in the case when the total egg production period is divided to several independent part periods.

In the experiment reported here we present data on heterosis in egg production for 4 independent part periods of 90 days duration each.

MATERIALS AND METHODS

The pure lines and their reciprocal crosses used in this experiment are internationally competitive highly productive commercial Rhode Island type layers. In the present report we summarise evaluations on heterosis in egg production as influenced by 4 part periods of the 12 months laying cycle in two environments. In Part I. of this publication we evaluate the data collected during 1977-1978. In this experiment the Rhode Island strains tested originated directly from the nucleus herd of the primary breeder. The pure lines were selected only a few generations by Reciprocal Recurrent Selection *(Lorenz,* 1996*)*.

In Part II. of this paper we present data of an experiment conducted in 1997-1998 and which was an exact replication of the first trial, the difference being, that 20 years of RRS selection was practised on the same lines, using RRS in its purest form *(Lorenz,* 1996). This generation we may designate as a long term RRS selected population.

Stocks and treatments

In the experiment reported two commercial Rhode Island type commercial layer strains were used (R and Q). Both strains were utilised for producing commercial layer hybrid hens for only a few generations. Both pure lines R and Q and their reciprocal crossbred progeny were originating from 9-9 unrelated cocks mated to randomly selected 15-18 hens to each cock to produce the purebred and crossbred progeny at the same time.

All purebred and crossbred pullets were reared on the floor intermingled and housed at 16 weeks of age in cages at two density levels. Pullets housed 2 per cage represented the populations producing under optimal environment, and those housed 4 per cage were regarded as producing under suboptimal (commercial) environment. In the first case 800 cm^2 cage floor area and 200 mm trough length per pullet was provided per pullet, in latter case only 400 cm^2 floor area and 100 mm trough length. Previous experiments showed that the latter density treatment can be regarded as maximal for the medium sized layer type hens used in this experiment (*Horn*, 1978). Each pure strain and the crosses consisted of 144 pullets in each of the environments. In the experiment recorded a total of 8x144=1152 hens were included. Individual cages represented the subgroups, total 432. Each cage belonging to the various treatment combinations was randomised within one 4 tier battery of the environmentally controlled windowless house.

Within each of the cages the number of the hens were kept constant throughout the experiment, this was possible because from each pure strain and the crosses 25% surplus pullets were reared and housed at the same time and the same building at two density levels. Each time a hen was lost in any of the experimental cages, on the same day in the evening a reserve hen was randomly chosen to replace it, belonging to the same genotype/density level as the dead one. This procedure does not influence significantly the mean productivity of the subgroup (*Horn,* 1978; *Bessei et al*., 1979). This way subgroup sizes and density treatments could be kept constant. All managemental factors were identical to commercial practice and standards.

Egg production data collection

Data on egg production were collected daily for the entire experimental period for all 432 cages. Egg production period started as each subgroup reached 50% egg production. It was measured on cage basis. The egg production mean had to reach or surpass 50% for three consecutive days, and the second day of this cycle was the starting day of the 360 day egg production cycle.

Statistical procedures

To be able to arrange the experiment as on orthogonal balanced trial, and ensure that irrespective of density treatments 4 hens should be the standard unit as for egg records the date of those cages in which 2 hens were housed we used the pooled data of randomly allotted paired cages.

The data were analysed by ANOVA using a completely randomised factorial design. In the statistical analyses sires were regarded as random, mating (pure lines vs. crosses) and density (2 vs. 4 hens per cage) as fixed effects. The procedure for calculating expected mean squares was based on model by *Anderson and Mc Lean* (1974*)*. The following linear model was used:

$$Y_{ijkr}=\mu+\alpha_i+\beta_j+\gamma_k+\alpha\beta_{ij}+\alpha\gamma_{ik}+\beta\gamma_{jk}+\alpha\beta\gamma_{ijk}+\varepsilon_{r(ijk)}$$

In this equation Y_{ijkr} is individual performance of r-th progeny from i-th mating system (1 to 2), j-th. Density (1 to 2), k-th sire (1 to 18), and the independent variables of the equation are defined as; μ=population mean, α_i=sire effect, β_j=mating system, γ_k=density effect, $\varepsilon_{r(ijk)}$=unknown errors.

The expected mean squares are shown in *Table 1*.

Table 1

General model of the analysis of variance elaborated for the statistical evaluation of the data

FACTORS	i	j	k	r	EMS
α_i	1	2	2	4	$\square_e^2 + 2*2*4\square_e^2$
β_j	18	0	2	4	$\square_e^2 + 2*\square^2_{\square\square} + 2*18*4\square^2_{\square}$
$(\alpha\beta)_{i\,j}$	1	0	2	4	$\square_e^2 + 2*4\square^2_{\square\square}$
γ_k	18	2	0	4	$\square_e^2 + 2*4\square^2_{\square\square} + 2*18*4\square^2_{\square}$
$(\alpha\gamma)_{i\,k}$	1	2	0	4	$\square_e^2 + 2*4\square^2_{\square\square}$
$(\beta\gamma)_{j\,k}$	18	0	0	4	$\square_e^2 + 2*4\square^2_{\square\square\square} + 18*4\square^2_{\square\square}$
$(\alpha\beta\gamma)_{i\,j\,k}$	1	0	0	4	$\square_e^2 + 4\square^2_{\square\square\square}$
$\varepsilon_{r(i\,j\,k)}$	1	1	1	1	$\square_e^2$

α_i: Sire effect (1-18 sires) as random effect (*Apai hatás (1-18 kakas), mint véletlenszerű hatás)*; β_j: Mating system effect (pure-bred vs. cross-bred) as fix effect (*Párosítási rendszer hatása (fajtatiszta, keresztezett), mint fixhatás)*; $(\alpha\beta)_{i\,j}$: Interaction between sires and mating system (*Interakció a szülői és a párosítási rendszer között)*; γ_k Density effect (two hens per cage vs. four hens per cage) as fix effect (*Telepítési sűrűség (2 tojó/ketrec, 4 tojó/ketrec*), mint fixhatás); $(\alpha\gamma)_{i\,k}$: the interaction between sires and density (*Interakció a szülők és a telepítési sűrűség között)*; $(\beta\gamma)_{j\,k}$ the interaction between mating system and density (*Interakció a párosítási rendszer és a telepítési sűrűség között)*; $(\alpha\beta\gamma)_{i\,j\,k}$: the interaction between sires, density and mating system (*Interakció a szülők és a telepítési sűrűség és a párosítás között)*.

1. táblázat: Az adatok statisztikai értékelésére alkalmazott varianciaanalízis általános modellje

The variance components of each effect have been calculated by expected mean squares (EMS) as;

$$\sigma_e^2 = MS_\varepsilon \qquad \varepsilon^2_{\alpha\beta\gamma} = \frac{MS_{\alpha\beta\gamma} - MS_\varepsilon}{4}$$

$$\sigma^2_{\beta\gamma} = \frac{MS_{\beta\gamma} - MS_{\alpha\beta\gamma}}{72} \qquad \sigma^2_{\alpha\gamma} = \frac{MS_{\alpha\gamma} - MS_\varepsilon}{8}$$

$$\sigma^2_{\beta\gamma} = \frac{MS_{\beta\gamma} - MS_{\alpha\beta\gamma}}{72} \qquad \sigma^2_{\alpha\beta} = \frac{MS_{\alpha\beta} - MS_{\varepsilon}}{8}$$

$$\sigma^2_{\beta} = \frac{MS_{\beta} - MS_{\alpha\beta}}{144} \qquad \sigma^2_{\alpha} = \frac{MS_{\alpha} - MS_{\varepsilon}}{16}$$

The total variance component is calculated by summation of all components as:

$$\sigma^2_r = \sigma^2_\varepsilon + \sigma^2_{\alpha\beta\gamma} + \sigma^2_{\beta\gamma} + \sigma^2_{\alpha\gamma} + \sigma^2_\gamma + \sigma^2_\beta + \sigma^2_\alpha$$

The percentage of variance for each component has been calculated as:

$$\%\sigma^2_{\alpha\beta} = \frac{\sigma^2_{\alpha\beta}}{\sigma^2_T} \qquad \%\sigma^2_{\alpha\beta\gamma} = \frac{\sigma^2_{\alpha\beta\gamma}}{\sigma^2_T} \qquad \%\sigma^2_{\beta\gamma} = \frac{\sigma^2_{\beta\gamma}}{\sigma^2_T} \qquad \%\sigma^2_{\alpha\gamma} = \frac{\sigma^2_{\varepsilon\gamma}}{\sigma^2_T}$$

$$\%\sigma^2_{\varepsilon} = \frac{\sigma^2_{\varepsilon}}{\sigma^2_T} \qquad \%\sigma^2_{\gamma} = \frac{\sigma^2_{\gamma}}{\sigma^2_T} \qquad \%\sigma^2_{\beta} = \frac{\sigma^2_{\beta}}{\sigma^2_T} \qquad \%\sigma^2_{\alpha} = \frac{\sigma^2_{\alpha}}{\sigma^2_T}$$

RESULTS AND DISCUSSION

The hen day egg production means of the purebred (QQ and RR) and crossbred (QR and RQ) hen populations under optimal conditions are summarised on *Table 2* for the four 90 day part periods. On *Table 3* the same data are presented for the hen populations producing under sub-optimal conditions (4 hens per cage).

In *Table 4*. The main results of the ANOVA are summarised relevant to the data presented on *Table 2* and *Table 3*.

Table 2

Means of hen day egg production of the purebred and crossbred hen populations as affected by period of production under optimal environment

	Hen day egg production 2 hens/cage(1)					
Genotypes(2) / Periods (5)	QQ	RR	Av. purelines(3)	QR	RQ	Av. crosses (4)
1-90 day (6)	64.727	70.713	67.720	67.019	77.920	72.469
91-180 day	75.014	69.377	72.195	77.909	76.477	77.193
181-270 day	64.528	63.056	63.792	69.556	70.278	69.917
271-360 day	59.943	54.603	57.273	61.491	62.234	61.857

2. táblázat: Az átlagos tojástermelés optimális környezeti feltételek mellett a tisztavérű és keresztezett tyúkpopulációkban

2 Tojó/ketrec átlagos tojástermelése(1), Genotípus(2), Tisztavérű vonalak(3), Keresztezett vonalak(4), Szakaszok(5), Nap(6)

In our experiment the Sire component measures additive effects influencing egg production. Heterosis has two main components of variance namely Mating (pure lines vs crossbreds) and the interaction Sire × Mating, the first measuring general, the latter specific combining ability.

Table 3

Means of hen day egg production of the purebred and crossbred hens as affected by period of production under sub-optimal environment

	Hen day egg production 4 hens/cage(1)					
Genotypes(2) / Periods(5)	QQ	RR	Av. purelines(3)	QR	RQ	Av. crossbreds(4)
1-90 day(6)	63.085	70.913	66.999	65.450	76.784	71.117
91-180 day	72.974	68.721	70.847	74.096	73.882	73.989
181-270 day	64.917	58.803	61.858	66.493	67.712	67.102
271-360 day	55.033	45.571	50.302	58.391	58.133	58.262

3. táblázat: Az átlagos tojástermelés a szuboptomális környezeti viszonyok között tisztavérű és keresztezett tyúkpopulációkban

4 Tojó/ketrec átlagos tojástermelése(1), Genotípus(2), Tisztavérű vonalak(3), Keresztezett vonalak(4), Szakaszok(5), Nap(6)

Table 4

Mean squares (MS) and their significance based on ANOVA for hen day egg production by periods of lay

Sources(2)	**df**	**Periods (day)(1)** 1-90	91-180	181-270	270-360
Sires (S)(3)	17	514.378^{xxx}	160.86^{xxx}	129.66^{xx}	169.13^{xxx}
Mating (M)(4)	1	1415.52^{xxx}	1182.97^{xxx}	2315.23^{xxx}	2832.35^{xxx}
S×M	17	100.83^{xx}	64.33^{x}	84.84	158.3^{xxx}
Density(D)(5)	1	77.37	367.68^{xx}	387.28^{xx}	2009.73^{xxx}
S×D	17	75.47	51.93	110.15^{x}	89.24
M×D	1	7.19	64.12	13.18	205.18
S×M×D	17	36.25	43.34	79.65	130.87
Error(6)	216	50.35	39.17	55.58	65.81

$^{xxx:}$ P<0.001; $^{xx:}$ P<0.01; $^{x:}$ P<0.05

4. táblázat: Az ANOVA-szerint számolt négyzetátlagok és szignifikanciaszintek a tojástermelés különböző periódusaira

Periódus (nap)(1), Források(2), Szülők(3), Párosítási rendszer(4), Telepítési sűrűség(5), Hiba(6)

The Sire component was significant in all part periods (P<0.01-P<0.001) showing additive gene effect to be one major source of variation of hen day egg production. Mating system (pure vs. crossbreeding) influenced egg production in all part periods significantly (P<0.001) indicating the importance of general combining ability in determining heterosis in hen day egg production.

The Sire×Mating interaction was significant (P<0.05-P<0.01) in all part periods of egg production except the period between 181-270 days in production indicating that specific combining ability plays a considerable role in contributing to the magnitude of heterosis mostly during the first six and last 3 months of the egg production cycle together with general combining ability.

The Density component of variance was significant only (P<0.01-0.001) in the second part of the laying cycle, causing reduced egg production in both pure lines and crosses.

Although increasing the number of hens from 2 to 4 to a cage reduced egg production from the 2nd part period onwards (91-180, 181-270 and 271-360 days in lay) the effect of Density was only significant statistically for the 3rd and 4th part periods (P<0.01-P<0.001).

The various interactions between Density and the other main sources of variance (M and S) were not significant in a total of 12 ANOVA tests except one (S × D interaction part period 3). Overall it may be stated that Density exerted a direct linear significant effect in reducing egg production from the 7th month in lay onwards.

In *Table 5* the heterosis measured in egg production as affected by the part periods in absolute and relative (%) terms is presented in the two environments. The crossbred hens produced more eggs compared to purebreds (means) in all part periods tested, both in optimal and sub-optimal cage environment. It is interesting to note, that the deviations in the intensity of lay regarding superiority of crossbred hens between part periods is small compared to purebreds. The maximum deviation from the mean was +2.85 eggs (between 271-360 days of lay 4 hens/cage).

The relative (%) magnitude of heterosis tended to increase in the second part of the laying period, this tendency was most pronounced when 4 hens were kept in one cage simulating a production environment which is very close to that of intensive commercial units. The observed tendencies are well supported considering the results of the ANOVA, and analising the components of variance and their magnitude.

Table 5

Heterosis in absolute and relative terms in hen day egg production in the part periods as affected by density

	Heterosis egg/hen(1)		**Heterosis (%)(2)**	
Periods(3)	2 hens/cage(4)	4 hens/cage	2 hens/cage	4 hens/cage
1-90 days	4.75	4.12	7.01	6.15
91-180 days	4.99	3.14	6.92	4.43
181-270 days	6.12	5.24	9.60	8.47
271-360 days in production(5)	4.58	7.96	8.00	15.82
Mean(6)	5.11	5.11	7.88	8.72

5. táblázat: A telepítési sűrűség hatása a tojástermelés heterozísának abszolút és relatív mértékére

Heterózis tojás/tojótyúk(1), Heterózis (%)(2), Tojástermelési szakaszok(3), Tojótyúk/ketrec(4), Tojástermelési napok száma(5), Átlag(6)

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