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Phylogenic versus selection effects on growth development, egg laying and egg quality in purebred laying hens

Phylogenetische und Selektionseffekte auf die Wachstumsentwicklung, Legeleistung und Eiqualität von Reinzuchtlegehennen

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Introduction

Efficiency of poultry production is affected by several factors like feed costs, animal health and welfare, and a wide range of environmental conditions (YALCIN et al., 2005; DARMANI KUHI et al., 2010). Main objectives in breeding of laying hens are to achieve a large number of saleable eggs, great persistency in laying performance, good inner and outer egg quality and a low feed to egg mass ratio. In addition, efforts have been made to improve health and therefore welfare, and to guarantee a good adaptation to different kinds of housing systems (PREISINGER, 2012). Due to efficient selection the egg production has grown dynamically, and the world's annual egg production is estimated to be 1284 million (FAO, 2014). HORN and SÜTÖ (2000) demonstrated that the breeding process of the last two decades of the 20th century improved the egg production of white layers by two eggs per year. The poultry market of today is dominated by only a few breeding companies worldwide, whereas about 100 years ago nearly 40 chicken breeds were used in breeding stations in Germany (KNISPEL, 1908). World's egg consumption is covered to 50% by white egg layer hybrids (HORN and SÜTÖ, 2000), which have been derived from one single breed, the White Leghorn (CRAWFORD, 1990).

While directional genetic selection is the major contributor to the changes in performance potential (HAVENSTEIN et al., 2003), it has been reported that selection for high production efficiency in livestock species is associated with undesirable side-effects such as deficiencies in physiological, immunological and reproduction traits as well as behavioral problems (DUNNINGTON, 1990; MILLER et al., 1992; LIU et al., 1995; RAUW et al., 1998). Such undesirable side-effects might be related to an imbalance in resource allocation (GODDARD and BEILHARZ, 1977). Due to adaptation of genotypes, the metabolic resources used by an animal should be optimally distributed between maintenance to cope with the environment in which they are kept, and production traits (BEILHARZ et al., 1993). As selection aims at minimizing the metabolic resources not needed for maintenance, VAN DER WAAIJ (2004) and MIRKENA et al. (2010) hypothesized that high performing genotypes have a reduced capacity to compensate unexpected environmental changes like limited resources compared to low performing genotypes. To approach this hypothesis we have started a comprehensive collaboration at the Friedrich-Loeffler-Institut to study the effect of selection on performance efficiency towards the adaptability of laying hens under varying environmental conditions in a phylogenetic context. The design of this ongoing research activity is formed by four purebred layer lines differing in performance level and phylogenetic origin (Fig. 1). Two high performing, commercial genotypes (WLA and BLA) taken from breeding program of Lohmann Tierzucht GmbH are contrasted to two low performing ones (R11 and L68). R11 and L68 chicken lines are maintained as non-selected resource populations at the Institute of Farm Animal Genetics, Friedrich-Loeffler-Institut, at Mariensee. The line R originated from the Cornell Line K (COLE and HUTT, 1973), and has been introduced to the Institute in the 1960 s (HARTMANN, 1987). Line L68 is a New Hampshire line, which was founded in the 1970 s in the former German Democratic Republic (VEG Vogelsang). The two white layer lines (WLA and R11) are of White Leghorn

origin and phylogenetically closely related, but distant from the Rhode Island Red higher performing line (BLA) and its low performing counterpart L68 (LYIMO et al., 2014).

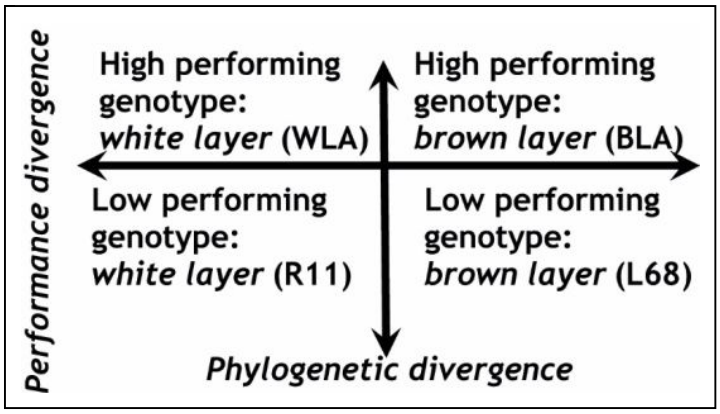


Figure 1. Experimental design of purebred laying hens differing in performance level and phylogenetic relationship

Versuchsdesign von Reinzuchtlegehennen unterschiedlichen Leistungsniveaus und phylogenetischer Verwandtschaft

As a first study, we report here on the characterization of the experimental model of four chicken lines towards the effects of phylogeny and selection on growth and laying performance from hatch to the end of the 74th week of age.

Material and Methods

Rearing trial

After hatch a total of 516 one day-old female chicks were housed over a period of 16 weeks in a floor-range system. Due to diverging hatch results of the different genotypes (data not shown) the number of housed day-old chicks varied between the four genotypes (140 chicks of WLA, 76 chicks of BLA, 147 chicks of R11 and 153 chicks of L68). Light was provided for 24 hours on day 1–2. From day 3 onwards light was reduced to 15 hours in the first week of age. From week 1 to 7 light period was reduced stepwise by one hour a week to 9 hours and maintained until the end of rearing (16th week of age). Temperature programme followed usual specifications and the animals were vaccinated against MD, ND and IB.

After hatch every chick was equipped with an individual wing-tag, and genotypes were placed separately to a single compartment of a floor-range system with nipple drinkers and a feeding trough. During the whole trial feed and water were provided *ad libitum*. Chicks were fed with a commercial grain-soybean meal diet (Table 1) from week one to seven (approx. 170 g crude protein and 11.5 MJ AME_N/kg diet). From week eight to 16 growing pullets were also fed with a commercial grain-soybean meal diet (approx. 135 g crude protein and 11.3 MJ AME_N/kg diet). Diets were formulated to meet nutrient requirements according to the recommendations of the National Research Council (NRC, 1994) and Society of Nutrition Physiology (GFE, 1999).

Table 1. Composition, calculated and analyzed nutrient contents of the experimental diets.

Zusammensetzung, kalkulierte und analysierte Inhaltsstoffe der Versuchsrationen.

Ingredients, g/kg diet	Chicks (week 1–7)	Pullets (week 8–16)	Layers (week 17–74)
Corn	235.6	–	49.9
Wheat	200.0	389.2	470.0
Barley	200.0	300.0	200.0
Soybean meal	165.0	100.0	159.0
Soybean oil	2.0	2.5	7.5
Field Peas	100.0	120.0	–
Lucerne pellets	50.0	50.0	–
Wheat bran	22.0	–	–
Calcium phosphate	15.0	10.0	8.0
Calcium carbonate (limestone)	–	16.0	92.5
Premix [1]	9.5	–	–
Premix [2]	–	10.0	–
Premix [3]	–	–	10.0
DL-methionine	0.4	0.3	0.6
Sodium chloride	–	2.0	2.5
Anticoccidal (Sacox 12%)	0.5	–	–
Chemical composition, g/kg dry matter			
Dry matter [4]	888.1 ± 0.4	883.6 ± 0.6	911.7 ± 0.5
Crude ash [4]	50.45 ± 0.83	67.53 ± 0.85	152.41 ± 3.57
Crude protein [4]	189.61 ± 1.17	151.67 ± 2.41	168.11 ± 1.61
Crude fat [4]	31.38 ± 0.58	30.21 ± 1.43	29.43 ± 0.77
Crude fiber [4]	53.33 ± 1.57	45.91 ± 1.72	30.55 ± 0.19
Neutral detergent fiber [4]	223.26 ± 13.73	186.20 ± 4.41	161.13 ± 8.70
Acid detergent fiber [4]	67.46 ± 1.09	57.09 ± 4.00	50.11 ± 5.99
Starch [4]	501.69 ± 1.00	538.24 ± 2.42	459.06 ± 2.07
Sucrose [4]	44.51 ± 0.05	34.45 ± 0.27	30.55 ± 0.17
Phosphorous [4]	6.94 ± 0.28	8.11 ± 0.29	5.06 ± 0.21
Calcium [4]	9.14 ± 0.36	15.83 ± 0.44	50.05 ± 0.81
AME_N (MJ/kg DM) [5]	12.97 ± 0.05	12.82 ± 0.06	11.68 ± 0.05
Methionine [6]	3.23	2.77	2.82
Lysine [6]	9.91	8.45	7.87

[1] premix – chicks: feed additives (per kg premix): Vitamin A, 1,200,000 IU; Vitamin D_3, 350,000 IU; Vitamin E, 4,000 mg; Vitamin B_1, 250 mg; Vitamin B_2, 800 mg; Vitamin B_6, 600 mg; Vitamin B_{12}, 3,200 µg; Vitamin K_3, 450 mg; Nicotin amide, 4,500 mg; Calcium-D-pantothenate, 1,500 mg; Folic acid, 120 mg; Biotin, 5,000 µg; Choline chloride, 55,000 mg; Fe, 3,200 mg; Cu, 1,200 mg; Mn, 10,000 mg; Zn, 8,000 mg; I, 160 mg; Se, 40 mg; Co, 20 mg; Butylated hydroxy toluene (BHT), 10,000 mg

[2] premix – pullets: feed additives (per kg premix): Vitamin A, 1,000,000 IU; Vitamin D_3, 200,000 IU; Vitamin E, 2,500 mg; Vitamin B_1, 250 mg; Vitamin B_2, 500 mg; Vitamin B_6, 400 mg; Vitamin B_{12}, 1,850 µg; Vitamin K_3, 300 mg; Nicotin amide, 3.000 mg; Calcium-D-pantothenate, 900 mg; Folic acid, 80 mg; Biotin, 2,100 µg; Choline chloride, 30,000 mg; Fe, 4,000 mg; Cu, 1,500 mg; Mn, 8,000 mg; Zn, 8,000 mg; I, 160 mg; Se, 32 mg; Co, 20 mg; Butylated hydroxy toluene (BHT), 10,000 mg

[3] premix – hens: feed additives (per kg premix): Vitamin A, 1,000,000 IU; Vitamin D_3, 250,000 IU; Vitamin E, 2,000 mg; Vitamin B_1, 250 mg; Vitamin B_2, 700 mg; Vitamin B_6, 400 mg; Vitamin B_{12}, 2,000 µg; Vitamin K_3, 400 mg; Nicotin amide, 4,000 mg; Calcium-D-pantothenate, 1,000 mg; Folic acid, 60 mg; Biotin, 2,500 µg; Choline chloride, 40,000 mg; Fe, 4,000 mg; Cu, 1,000 mg; Mn, 10,000 mg; Zn, 8,000 mg; I, 120 mg; Se, 25 mg; Co, 20.5 mg; Butylated hydroxy toluene (BHT), 12,500 mg; Beta-carotene, 400 mg; Canthaxanthin, 400 mg

[4] analyzed

[5] apparent metabolizable energy concentrations corrected to zero nitrogen balance (AME_N), calculated according to the energy estimation equation of the WPSA (VOGT, 1986)

[6] calculated

In the first half of the rearing trial (hatch to eighth week of age) the animals were weighed once a week, while in the second half (eighth to 16th week of age) they were weighed every second week. Feed not consumed was recorded weekly. The daily weight gain and the feed to gain ratio were calculated.

Performance trial of laying hens

At the end of the rearing trial, 192 17-week-old pullets (48 of each genotype) were moved to a layer facility with single cages in a three-floor cage system in random order. Each genotype was allocated to one experimental group. The single cages enabled individual records of laying performance and feed intake. Each cage (50 cm × 46 cm × 43 cm) was equipped with a feeding trough, a nipple drinker and a perch. Feed and water were provided *ad libitum*. From 17th week of age the light duration was increased by half an hour per week to 14 hours of light at 23rd week of age.

After a pre-laying period from week 17 to 22, the performance trial was subdivided into thirteen 28-day laying periods. The trial ended at week 74. Hens were fed with a commercial grain-soybean meal diet (approx. 150 g crude protein and 10.6 MJ AME_N/kg diet; Table 1). The diets were formulated to meet nutrient requirements according to the NRC (1994) and GFE (1999) recommendations for high performing laying hens.

Hens were weighed at the end of every 28-day laying period. Eggs were recorded daily. Defective eggs (shell-less, cracked, double eggs) were also recorded. For each laying period the egg weight was monitored by collecting all laid eggs of each hen on three consecutive days in a two-week interval. Feed not consumed was recorded weekly. Based on the feed intake and egg mass the feed to egg mass ratio was calculated.

Egg quality parameters

In the 40th, 65th and 74th week of age eggs of each hen were collected on three consecutive days (40th week: 416 eggs, 65th week: 328 eggs, 74th week: 250 eggs). Eggs were weighed and egg yolk and albumen were separated. Weight of the shell, including the inner shell membrane, and weight of yolk were recorded. The weight of albumen was determined by subtracting yolk and shell weight from the original egg weight; yolk to albumen ratio was calculated. Weights of the egg components are presented in percentage as proportions of the whole egg weight. Yolk color was estimated by using a Roche-fan (15 fans, F. Hoffmann-La Roche Ltd., Basel, Switzerland).

Dry matter and crude nutrients of feed

Diets (Table 1) were analyzed for dry matter, crude ash, crude fat, crude fiber, neutral and acid detergent fiber, starch, sucrose, phosphorous, calcium and Kjeldahl N according to the methods of the Association of German Agricultural Analytic and Research Institutes (VDLUFA; NAUMANN and BASSLER, 1993). Crude protein of the diets was calculated by multiplying the Kjeldahl N by 6.25. The apparent metabolizable energy concentrations corrected to zero nitrogen balance (AME_N) of the diets were calculated according to the energy estimation equation of the World's Poultry Science Association (VOGT, 1986).

Modelling of growth curves

The time-dependent individually recorded growth data (cumulative growth; n = 48 per genotype) were fitted to the growth function of GOMPERTZ (1825) regressively from hatch to the end of the 74th week of age. That data were analyzed by means of the procedure "nonlinear regression" of the software package "Statistica 10.0 for the Windows™ Operating System" (STATSOFT INC., 2011). The method of parameter estimation was calculated using the iterative Quasi-Newton method.

$$y(t) = a \cdot e^{-b \cdot e^{-c \cdot t}}$$

Where y(t) = body weight (g) of the hen at time t, expressed as a function of a; a = adult body weight (g) of the hen (asymptotic limit); b, c = parameters of the function (regression coefficients); and t = time (weeks) taken to reach the maximum rate of maturity.

The age at maximum body weight gain (t_{max}), that is equivalent to the point of inflection of the cumulative, sigmoid growth curve, was calculated by the second derivative of the cumulative growth function:

$$t_{max} = \frac{\ln b}{c}$$

The maximum daily weight gain was computed by substituting the genotype specific calculated t_{max} in the derivative of the cumulative growth function of the associated genotype.

Statistical analyses

Statistical analysis of performance traits was carried out by means of a two factorial analysis of variance (ANOVA) with genotype, age and their interaction as fixed effects. For traits measured repeatedly on the same animal (e.g. body weight, feed intake and egg weight) a "repeated" statement was considered in the statistical model to account for similarities within subjects. Statistical analysis of calculated growth function parameters was carried out by means of a one factorial ANOVA with genotype as fixed effect. In both cases the Tukey-Kramer test was applied for a multiple comparison of means. Data were reported as least square mean values and standard error. Differences between genotypes were considered to be statistically significant for $P < 0.05$. ANOVA of performance traits was performed using the procedure MIXED and ANOVA of calculated growth function parameters was performed using procedure ANOVA of the software package SAS 9.2 (SAS Institute Inc., 2010).

Results

Rearing trial

During the 16 weeks rearing trial genotype, age and their interaction affected body weight, daily weight gain, daily feed intake and feed to gain ratio significantly ($p \leq 0.001$; Table 2).

Table 2. Growth performance of different genotypes from hatch to 16th week of age (LSMeans; SEM; n = 140 (WLA), 76 (BLA), 147 (R11), 153 (L68)).

Wachstumsleistung verschiedener Genotypen vom Schlupf bis zur 16. Lebenswoche.

	Body Weight (g/chick)					Daily Weight Gain (g/chick/d)				Daily Feed Intake (g/chick/d)				Feed to gain ratio (g/g)				
Genotype (GT)	Hatch	wk 4	wk 8	wk 12	wk 16	wk 1–4	wk 5–8	wk 9–12	wk 13–16	wk 1–4	wk 5–8	wk 9–12	wk 13–16	wk 1–4	wk 5–8	wk 9–12	wk 13–16	wk 1–16
WLA	38	209 ^{b}	538 ^{b}	919 ^{b}	1107 ^{c}	6.3 ^{b}	11.9 ^{b}	13.8 ^{b}	7.0 ^{b}	19.6 ^{a}	39.9 ^{b}	63.9 ^{b}	71.2 ^{b}	3.1 ^{ab}	3.4 ^{b}	4.6	10.2 ^{a}	5.2
BLA	38	224 ^{b}	535 ^{b}	923 ^{b}	1180 ^{b}	6.8 ^{b}	11.3 ^{b}	14.1 ^{ab}	9.4 ^{a}	21.5 ^{a}	43.4 ^{ab}	67.7 ^{a}	78.4 ^{a}	3.2 ^{ab}	3.8 ^{ab}	4.8	8.3 ^{b}	5.1
R11	32	157 ^{c}	386 ^{c}	695 ^{c}	854 ^{d}	4.5 ^{c}	8.3 ^{c}	11.2 ^{c}	5.8 ^{c}	16.3 ^{b}	33.8 ^{c}	52.9 ^{c}	60.1 ^{c}	3.6 ^{a}	4.1 ^{a}	4.7	10.4 ^{a}	5.5
L68	34	251 ^{a}	607 ^{a}	1005 ^{a}	1249 ^{a}	7.9 ^{a}	12.9 ^{a}	14.5 ^{a}	8.9 ^{a}	20.2 ^{a}	46.1 ^{a}	70.5 ^{a}	77.4 ^{a}	2.6 ^{b}	3.6 ^{b}	4.9	8.7 ^{b}	4.9
SEM	5	5	5	5	6	0.2	0.2	0.2	0.2	1.3	1.3	1.4	1.5	0.2	0.2	0.3	0.4	0.4

^{a,b,c,d}: LSMeans within columns with no common superscripts are significantly different ($p < 0.05$)

Body weight of different genotypes showed a time-dependent increase ($p \leq 0.001$) over the 16 weeks trial. The mean hatch weight (32 to 38 g/chick) did not differ statistically between the genotypes. After 16 weeks L68 achieved the highest body weight (1249 g/chick) of the four genotypes ($p < 0.05$). The high performing BLA (1180 g/chick) and WLA (1107 g/chick) differed significantly from each other, while R11 had the lowest body weight (854 g/chick) after 16 weeks. From week four onwards L68 started to differ significantly from the other genotypes and line R11 showed the lowest body weight ($p < 0.05$). Until the end of the trial the high performing genotypes did not differ from each other.

According to the development of body weight, genotype also significantly influenced daily weight gain ($p \leq 0.001$; Table 2). All genotypes showed highest daily weight gain at the tenth week of age ($p < 0.05$). The highest weight gain of 14.5 g/chick/d was recorded in line L68 from week nine to twelve. In the first half of the trial line L68 differed significantly from the other genotypes and WLA and BLA did not differ significantly from each other. During the entire rearing R11 line achieved lowest daily weight gain of all four lines. In the second half both brown lines did not differ from each other. Age also affected this trait high significantly ($p \leq 0.001$), as daily weight gain increased until week 10, and then strongly decreased to end of the trial.

Daily feed intake also showed a time-dependent increase ($p \leq 0.001$; Table 2) over the 16 weeks rearing trial. In the first four weeks all genotypes excluding R11 had a similar daily feed intake. In the consecutive course, the brown genotypes

showed a higher daily feed intake than the white ones until 16th week of age ($p < 0.05$), in which R11 achieved the significantly lowest daily feed intake of all four genotypes.

Feed to gain ratio of the genotypes also showed a time-dependent increase ($p \leq 0.001$; Table 2) over 16 weeks of rearing. In the first eight weeks only L68 and WLA achieved significantly lower feed to gain ratios than R11. While no differences between genotypes occurred from the ninth to the twelfth week of age, brown genotypes showed lower feed to gain ratios than white ones in the last four weeks ($p < 0.001$). Cumulative feed to gain ratio of genotypes across the entire period did not differ.

Adaptation of growth data to the Gompertz function

Non-linear regression of growth data fitted to the Gompertz function (GOMPERTZ, 1825) is summarized in Table 3. Genotype affected the equation parameters (a, b and c) as well as t_{max} and its associated maximum daily weight gain high significantly ($p \leq 0.001$). t_{max} was achieved at 8.04 to 9.54 weeks of age. WLA reached maximum daily weight gain after 8.04 weeks firstly ($p < 0.05$). In contrast, BLA (9.25 weeks) and R11 (9.54 weeks) showed the slowest growth rates ($p < 0.05$). R11 achieved the lowest and L68 the highest maximum daily weight gains at their specific t_{max} ($p \leq 0.001$), respectively.

Table 3. Influence of genotype on the parameters of the Gompertz growth curve[1] from hatch to 74th week of age and the accuracy of data fit (LSMeans, SEM; n = 48 per genotype).

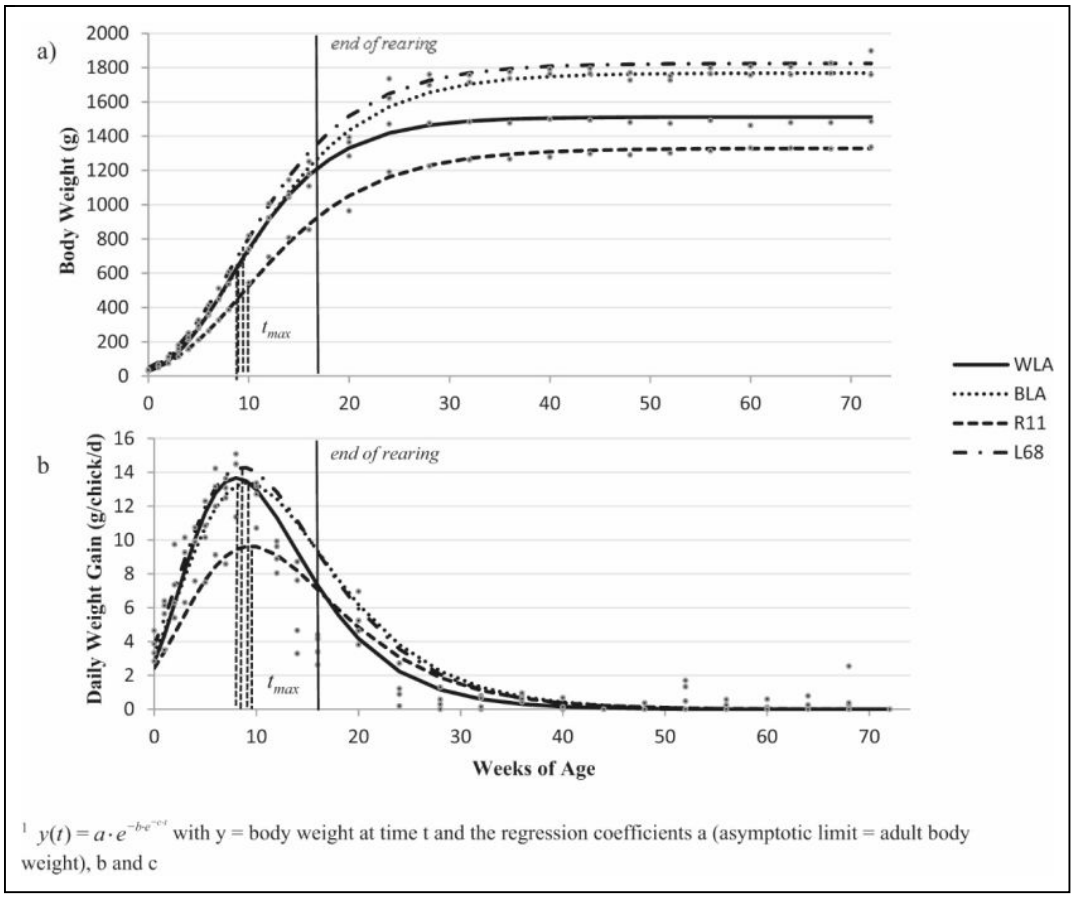
Einfluss des Genotyps auf die Parameter der Gompertz-Wachstumskurve[1] vom Schlupf bis zur 74. Lebenswoche sowie die Genauigkeit der Datenanpassung.

Genotype	Estimated adult body weight (a) [g]	b	c	t_{max} [weeks]	R^2	RSD (g)	Estimated maximum DWG (g/chick/d)	Achieved average maximum DWG (g/chick/d)
WLA	1512 ^{b}	3.98 ^{a}	0.172 ^{a}	8.04 ^{c}	0.999	12	13.7 ^{ab}	14.5 ^{a}
BLA	1769 ^{a}	3.73 ^{b}	0.144 ^{bc}	9.25 ^{a}	0.998	14	13.4 ^{b}	14.5 ^{a}
R11	1329 ^{c}	3.68 ^{b}	0.138 ^{c}	9.54 ^{a}	0.997	10	9.6 ^{c}	11.3 ^{b}
L68	1825 ^{a}	3.62 ^{b}	0.149 ^{b}	8.69 ^{b}	0.998	15	14.3 ^{a}	15.2 ^{a}
SEM	24	0.042	0.003	0.13			0.3	0.4

[1] with y = body weight at time t and the regression coefficients a (asymptotic limit = adult body weight), b and c
t_{max} is equivalent to the point of inflection (time of maximum weight gain)

R^2 = coefficient of determination
RSD = residual standard deviation
SEM = standard error of mean
DWG = daily weight gain
[a,b,c,d]: LSMeans within columns with no common superscripts are significantly different ($p < 0.05$)

Growth curves and their derivative, identical to the course of daily weight gain, are presented in Figure 2a and 2b. The asymptotic limit of the curves, which is equal to the estimated adult body weight, demonstrated highly significant ($p \leq 0.001$) differences between brown and white genotypes, while L68 (1825 g) and BLA (1769 g) showed no statistical differences. In contrast, the average adult body weight of white genotypes was calculated to be 1512 g (WLA) and 1329 g (R11) which differed significantly from each other ($p \leq 0.001$; Table 3). The course of daily weight gain showed a strong increase until the genotype-specific calculated t_{max} and strongly decreased in the further course of the rearing trial. After the 40th week of age, daily weight gain curves of the genotypes approached the ordinate axis asymptotically.



[1] $y(t) = a \cdot e^{-b \cdot e^{-c \cdot t}}$ with y = body weight at time t and the regression coefficients a (asymptotic limit = adult body weight), b and c

Figure 2. Non-linear regression of growth data from hatch to the 74th week of age of 48 purebred laying hens of each genotype fitted to the Gompertz equation[1] (a) and the derived course of daily weight gain (b) with emphasis of the genotype specific t_{max}

Nichtlineare Regression der Wachstumsdaten vom Schlupf bis zur 74. Lebenswoche von 48 Reinzuchtlegehennen jeden Genotyps angepasst an die Gompertz-Gleichung[1] (a) und der daraus abgeleitete Verlauf der täglichen Zunahmen (b) mit Hervorhebung des Genotyp-spezifischen t_{max}

Growth, feed intake and laying performance

Growth development and laying performance of the genotypes from the 23rd to the 74th week of age are summarized in Table 4, divided into four periods of 13 weeks each, and were significantly affected by genotype, age and their interaction ($p \leq 0.001$). To obtain a better overview, each performance trait is shown over time in Figure 3a-e.

Table 4. Growth and laying performance of different genotypes from 23rd to 74th week of age subdivided in four periods of 13 weeks each (I: week 23 – 35; II: week 36 – 48; III: week 49 – 61; IV: week 62 – 74) (LSMeans, SEM; n = 48 per genotype).

Wachstums- und Legeleistung verschiedener Genotypen von der 23. bis zur 74. Lebenswoche unterteilt in vier Perioden á 13 Wochen.

Geno-type (GT)	Body weight (g/chick)				Feed intake (g/hen/d)				Laying intensity (%)				Egg weight (g/egg)				Egg mass (g/hen/d)				Feed to egg mass ratio (kg/kg)			
	I	II	III	IV	I	II	III	IV	I	II	III	IV	I	II	III	IV	I	II	III	IV	I	II	III	IV
WLA	1477 c	1492 b	1484 c	1480 c	104 b	101 b	102 b	106 a	94.8 a	94.1 a	87.9 a	83.1 a	53.0 b	55.4 b	56.3 c	59.1 a	50.3 a	52.2 a	49.5 a	49.1 a	2.07 a	1.93 a	2.06 a	2.16 a
BLA	1678 b	1755 a	1741 b	1761 b	115 a	112 a	109 a	108 a	90.2 a	89.9 a	84.8 a	78.0 b	54.6 a	59.2 a	59.3 a	60.2 a	49.3 a	53.2 a	50.3 a	47.0 a	2.33 a	2.11 a	2.17 a	2.30 a
R11	1226 d	1280 c	1302 d	1336 d	75 d	76 d	76 d	75 c	51.3 c	61.2 b	53.4 b	43.8 c	43.6 d	49.6 d	52.3 d	54.0 b	22.4 c	30.4 c	27.9 b	23.7 c	3.35 b	2.50 b	2.72 b	3.16 b
L68	1748 a	1787 a	1770 a	1829 a	92 c	93 c	92 c	94 b	60.7 b	65.4 b	53.6 b	46.8 c	46.5 c	53.9 c	58.0 b	60.5 a	28.2 b	35.2 b	31.1 b	28.3 b	3.26 b	2.64 b	2.96 b	3.32 b
SEM	25	25	25	25	2	2	2	2	3.0	3.0	3.0	3.0	0.5	0.5	0.5	0.5	1.6	1.6	1.6	1.6	0.25	0.25	0.25	0.25

a,b,c,d: LSMeans within columns with no common superscripts are significantly different ($p < 0.05$)

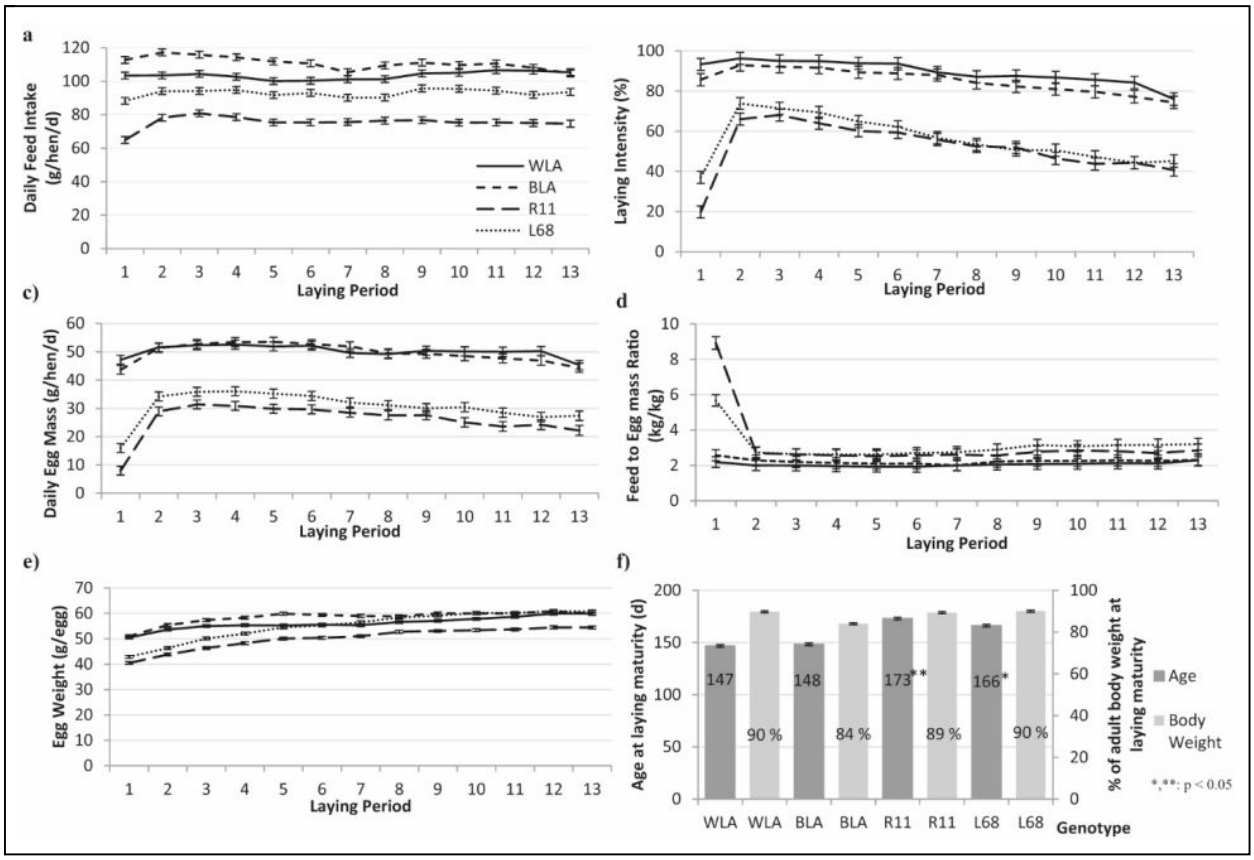


Figure 3. Time-dependent course of performance parameters over 13 laying months (a-e) as well as age and body weight at laying maturity (f) of the four genotypes during the 13 laying months (LSMeans ± SE; n = 48 of each genotype).

Zeitabhängiger Verlauf der Leistungsparameter über 13 Legemonate (a-e) sowie Alter und Lebendmasse bei Legereife (f) der vier Genotypen

Body weight of the hens increased significantly with age ($p \leq 0.001$). During the whole trial, both brown layer lines were significantly heavier than both white layer lines (Table 4, Figure 2). Within the brown genotypes L68 and within the white genotypes WLA weighed more than their counterparts. From week 23 to 74 brown genotypes gained more

than 80 g body weight. In low performing R11 body weight even increased by more than 110 g/hen. Only the high performing WLA did not alter body weight over the entire period.

During 13 laying months, daily feed intake (Table 4, Figure 3a) of the hens was nearly constant, but significant differences were observed between all four genotypes ($p < 0.05$). The high performing ones had a significantly higher daily feed intake compared to the low performing genotypes. Highest daily feed intake of 115 g/hen/d was recorded for BLA during week 23 to 35. Thereafter, daily feed intake of BLA decreased slightly up to the end of the trial, and did not differ from WLA feed intake at the end of the trial. During the entire trial WLA ingested approximately 100 g/hen/d, constantly. The low performing genotypes differed significantly from each other with a constant daily feed intake of approximately 75 g/hen/d (R11) and 92 g/hen/d (L68).

Laying maturity, defined as age at the first egg laid, was firstly reached by the hens of the high performing genotypes (Figure 3f). In comparison to the low performing genotypes, the high performing lines reached laying maturity four to five weeks earlier, in the 20th week of age ($p < 0.05$). On reaching maturity age, all genotypes but BLA (84%) weighed 90% of their adult body weight (Figure 3f).

Moreover, in the 364 days of the laying trial the high performing genotypes achieved an average number of 310 (BLA) to 325 (WLA) eggs, while the low performing genotypes reached 200 (R11) to 205 (L68) eggs. On average, 1.4 ± 0.5% (WLA), 2.7 ± 0.5% (BLA), 1.6 ± 0.5% (R11) and 0.8 ± 0.5% (L68) of the eggs showed defects such as shell-less, cracked-broken and double yolk eggs ($p = 0.0523$).

Due to the different age at laying maturity, egg production differed significantly at the beginning of the performance trial. In the first laying month high performing genotypes reached an egg production of more than 85 to 90% (Figure 3b), whereas the low performing hens showed an egg production of approximately 20% (R11) and 37% (L68), respectively, at the same time. All but R11 genotypes reached their maximum egg production in the second laying month. Hens of R11 reached their maximum egg production one month later. The maximum egg production of the high performing genotypes ranged from 93% (BLA) to 96% (WLA). Both low performing genotypes showed a lower egg production ($p < 0.05$) of maximal 67% (R11) and 74% (L68). In the following laying months egg production slightly decreased and persisted at approximately 75% in the high performing genotypes and 41 to 44% in the low performing genotypes until the end of the experiment. Results in Table 4 showed that the laying intensity of the high performing genotypes already started to decrease slightly after week 23 to 35, while the laying intensity of low performing genotypes increased until week 36 to 48 and decreased considerably thereafter.

Furthermore, the weight per egg (Figure 3e) ranged from approximately 40 g (R11, L68) to 50 g (WLA, BLA) at the beginning of the performance trial. In the following laying months egg weight slowly increased in all genotypes ($p \leq 0.001$). At the end of the trial, the eggs weight ranged from 54.0 g (R11) to 61.0 g (WLA, BLA, and L68).

Daily egg mass is illustrated in Figure 3c. In the first laying month the low performing genotypes began the trial with a significantly lower daily egg mass than the high performing ones. Maximum daily egg mass production was achieved by R11 in the third (31.4 g/hen/d), WLA (52.5 g/hen/d) and L68 (36.1 g/hen/d) in the fourth and BLA (53.6 g/hen/d) in the fifth laying month. To the end of the experiment, daily egg mass slowly decreased to 44.4 to 45.3 g/hen/d in the high performing genotypes and to 22.2 to 27.4 g/hen/d in the low performing layers. During the entire trial, high performing genotypes showed a higher daily egg mass production than the low performing ones ($p < 0.05$) while no differences were found neither between WLA and BLA nor between R11 and L68.

Due to the different age at laying maturity, feed to egg mass ratio (Figure 3d) of the low performing genotypes (L68: 5.68; R11: 8.92) differed significantly from the one of the high performing hens (WLA: 2.19; BLA: 2.58) in the first laying month (Figure 3d). From the second laying month, feed to egg mass ratio showed a nearly constant course. The four genotypes achieved their lowest level at the fourth to sixth laying month. In particular, the high performing WLA reached a feed to egg mass ratio of less than 1.95. The high performing BLA achieved its lowest feed to egg mass ratio of 2.02. Low performing genotypes showed significantly higher feed to egg mass ratios of more than 2.55. At the end of the experiment the feed to egg mass ratio of all genotypes slightly increased. The high performing hens (2.30) differed significantly from the low performing hens (R11: 2.85, L68: 3.20).

During the entire trial an average mortality of 8.9% was recorded. The losses for each individual genotype are listed in the following ascending order: BLA 4.3% – R11 8.3% – L68 10.4% and WLA 12.5%.

Egg quality at the 40th, 65th and 74th week of age

Total egg weight, proportions of shell, yolk and albumen, the yolk color and the calculated yolk to albumen ratio (Table 5) were significantly influenced by genotype, age and genotype × age ($p \leq 0.001$).

Table 5. Effect of genotype on egg quality in the 40th, 65th and 74th week of age[1].

Effekt des Genotyps auf die Eiqualität in der 40., 65. und 74. Lebenswoche.

Geno-type (GT)	Egg weight (g/egg)			Shell (% of egg)			Yolk (% of egg)			Albumen (% of egg)			Yolk to albumen ratio			Yolk colour (Roche fan)		
	wk 40	wk 65	wk 74	wk 40	wk 65	wk 74	wk 40	wk 65	wk 74	wk 40	wk 65	wk 74	wk 40	wk 65	wk 74	wk 40	wk 65	wk 74
WLA	55.3 ^{b}	57.1 ^{b}	58.9 ^{a}	13.6 ^{a}	11.8 ^{ab}	11.2 ^{b}	29.3 ^{c}	29.4 ^{c}	29.8 ^{c}	57.1 ^{b}	58.8 ^{b}	59.0 ^{b}	0.516^{c}	0.503^{c}	0.507^{c}	12.7 ^{b}	13.5 ^{a}	13.1 ^{a}
BLA	59.6 ^{a}	60.0 ^{a}	59.1 ^{a}	12.9 ^{b}	11.6 ^{b}	10.3 ^{c}	27.1 ^{d}	26.8 ^{d}	27.3 ^{d}	60.0 ^{a}	61.6 ^{a}	62.4 ^{a}	0.453^{d}	0.436^{d}	0.439^{d}	12.4 ^{c}	13.6 ^{a}	12.9 ^{a}
R11	49.3 ^{c}	53.9 ^{c}	53.2 ^{b}	12.5 ^{b}	12.4 ^{a}	10.8 ^{bc}	30.3 ^{b}	32.3 ^{b}	31.8 ^{b}	57.2 ^{b}	55.3 ^{c}	57.4 ^{c}	0.532^{b}	0.587^{b}	0.557^{b}	12.3 ^{c}	12.4 ^{b}	12.6 ^{b}
L68	54.2 ^{b}	59.7 ^{a}	59.6 ^{a}	11.9 ^{c}	10.8 ^{c}	11.8 ^{a}	31.7 ^{a}	33.5 ^{a}	32.6 ^{a}	56.4 ^{c}	55.7 ^{c}	55.6 ^{c}	0.565^{a}	0.611^{a}	0.605^{a}	13.0 ^{a}	13.5 ^{a}	12.9 ^{a}
SEM	0.6	0.6	0.7	0.1	0.1	0.1	0.3	0.3	0.3	0.3	0.3	0.3	0.007	0.007	0.007	0.1	0.1	0.1

[1] Each value represents the least square mean of the laid eggs of 48 hens on three consecutive days each of three replicates
[a,b,c,d]: LSMeans within columns with no common superscripts are significantly different ($p < 0.05$)

In the 40th week of age, BLA eggs (59.6 g/egg) were significantly heavier eggs than those of other genotypes (WLA 55.3 g/egg; L68 54.2 g/egg; R11 49.3 g/egg). At the second and third examination date, eggs of all genotypes had increased their total egg weight, as age affected the absolute egg weight highly significantly ($p \leq 0.001$). At week 74, only R11 eggs (53.2 g/egg) differed from those of other genotypes (58.9 to 59.6 g/egg; $p < 0.05$).

In contrast to the absolute egg weight, WLA (13.6%) showed a significantly higher relative proportion of egg shell in week 40 compared to the other genotypes (BLA 12.9%; R11 12.5%; L68: 11.9%). From week 40 to 74 the relative proportion of egg shell decreased significantly in WLA, BLA and R11 (about 1.7 to 2.6% of total egg weight; $p \leq 0.001$), while the egg shell of L68 remained constant at 11.8% at last examination date.

Eggs of high performing genotypes (27.1 to 29.8%) showed significantly lower proportions of yolk than the eggs of the low performing ones (30.3 to 33.5%) at all three examination times. Egg yolk proportion of high performing genotypes remained constant during the trial, while the eggs of low performing genotypes showed a slight increase in yolk proportion ($p \leq 0.001$).

A reverse situation was found in the albumen proportion. Eggs of WLA and BLA (57.1 to 62.4%) had a significantly higher albumen proportion than those of R11 and L68 (55.3 to 57.4%). The albumen proportion of the high performing genotypes increased by time ($p \leq 0.001$), while eggs of R11 and L68 remained largely constant in this proportion at the three examination times.

Purebred layers of the low performing genotypes showed a significantly higher yolk to albumen ratio than the high performing genotypes. The yolk to albumen ratio of the low performing hens increased by time, while that of the high performing hens remained constant across the three measurement dates ($p \leq 0.001$).

Finally, L68 eggs showed the most intensive yolk color with 13.0 on the Roche scale at the first examination time ($p < 0.05$). In course of the examination the time affected the yolk color ($p \leq 0.001$), as the eggs of WLA, BLA and L68 achieved their most intensive coloring at week 65 (13.4 to 13.5), while the R11 yolks (12.6) had their most intensive color at week 74. From the second to the third time of examination, yolk color of WLA, BLA and L68 declined again by 0.5 points on average to approximately 13.0 on the Roche scale.

Discussion

The objective of the present study was to examine the influence of divergent genotypes on performance related parameters. The experimental design allows to assess the effect of both components separately, performance divergence and phylogenetic divergence. Phylogenetic relationship between white layers and brown layers were described previously (GRANEVITZE et al., 2009; LYIMO et al., 2014).

Significant differences were found in the four genotypes studied concerning several performance parameters. In accordance with PREISINGER (2000), results of this study confirmed that brown layer genotypes had a higher body weight than white layers. Higher body weight went along with a significantly higher feed intake in brown genotypes in contrast to their white counterparts, resulting from an absolutely higher maintenance requirement of brown layers (PREISINGER, 2000).

Because of identical conditions in feeding and housing, differences in daily feed intake and laying performance are likely to result from the genetically determined performance potential of the studied genotypes. Besides the significant differences between high and low performing genotypes in several laying performance traits, also age at onset of laying was significantly different between the high and low performing genotypes. Laying maturity is an important trait which is affected by selection and has a great importance to the life output of laying hens (POGGENPOEL and DUCKITT, 1988). WLA and BLA in this trial reached laying maturity four to five weeks earlier than the low performing genotypes. As described by POGGENPOEL and DUCKITT (1988) the intensive selection on egg production was closely connected with the intensive selection on sexual maturity. This fits well to the findings of HORN and SÜTÖ (2000) that today's layers start to lay about 15 to 20 days earlier than 20 years ago.

Furthermore, these authors reported that the body weight of white layers remain constant, while the egg weight and the total egg mass increased. In case of body weight, the high performing brown layers (BLA) showed a significantly lower body weight than the low performing ones after four weeks of rearing. This significant difference remained until the end of the laying performance trial in the 74^{th} week of age. Within the high performance level the white layers (WLA) showed a significantly lower body weight than BLA. This circumstance is also well depicted by the calculated growth curves in our study. The Gompertz equation is frequently used in poultry (GOUS et al., 1999; SAKOMURA et al., 2005). Body weight data of all four genotypes were adapted to the Gompertz equation and its derivative, and showed a good fit to the chosen model with R^2 ranging from 0.997 (R11) to 0.999 (WLA). As a result, this growth equation (Figure 2, Table 3) could be useful for further experiments under changing environmental conditions to determine the efficiency of nutrient utilization, or to predict daily energy, protein and mineral requirements (DARMANI KUHI et al., 2010) of the genotypes studied. Significant differences were observed among the genotypes for several curve parameters, especially the age at maximum daily weight gain (t_{max}). In contrast to BLA, WLA achieved the maximum weight gain first and reached, as well as R11 and L68, 90% of its adult body weight at age of laying maturity. These findings emphasize the fast development of high performing White Leghorn layers regarding their body weight. Intensive selection on early sexual maturity reduced the age at first egg (POGGENPOEL and DUCKITT, 1988) and age at reaching the asymptotic body weight (SZYDLOWSKI and SZWACZKOWSKI, 2001).

In addition to the laying performance, egg quality was analyzed. It shows that genotype, age and their interaction had a highly significant influence on the evaluated parameters. According to the findings of several other authors (HEIL and HARTMANN, 1997; LEDVINKA et al., 2000; VITS et al., 2005), in week 40 and week 65 the examined eggs of brown hens were heavier than those of white hens, while at week 74, differences between BLA, L68 and WLA were no longer statistically detectable. In agreement with RIZZI and CHIERICATO (2005) and JOHNSTON and GOUS (2007), the absolute egg weight increased with the age of the hens in the studied genotypes. Concerning the effect of age on egg proportions, there are contradicting findings reported in the literature (ROSSI and POMPEI, 1995; SUK and PARK, 2001; SILVERSIDES and SCOTT, 2001; YANNAKOPOULOS et al., 1994). In our study, eggs of high performing hens showed a decreasing proportion of shell and yolk with age, but increasing proportion of albumen. In comparison, eggs of low performing hens decreased in proportion of egg shell, but increased for egg yolk, and remained constant in albumen content.

Beside the time-dependent effect and the differences between high and low performing genotypes on egg quality, several authors made statements about the effects of phylogeny. LEYENDECKER et al. (2001b) found significantly higher yolk proportions in white eggs than in those of brown layers. Our results indicate that the eggs of high performing brown layers had lower yolk proportions than those of the high performing white layers. In case of the low performing genotypes, however an opposite relation was found between white and brown layers. Furthermore, the white hens of present study showed a significantly higher egg shell proportion than brown hens. The findings of LEDVINKA et al. (2000) contradict our results, while BASMACIOGLU and ERGUL (2005) found no significant effect of genotype on shell percentage by comparing Babcock-300 (white layers) with Isa-Brown (brown layers). This suggested that general statements about egg quality parameter without consideration of the studied genotype should not be made, as genetic influence on egg quality parameters is very strong (BUSS and GUYER, 1982; STEINHILBER, 2005; FLOCK et al., 2007).

In addition to egg quality, proportion of defect eggs was recorded. In contrast to WOLC et al. (2012), the present study did not confirm the assumption that high producing hens had a lower frequency of egg defects in general. The lowest proportion of defect eggs was observed in low performing brown hens. While there was hardly any difference between white hens of WLA (1.4%) and R11 (1.6%), proportion of defect eggs differed markedly between brown hens of L68 (0.8%) and BLA (2.7%).

Genotypes of same performance level and with a distant phylogenetic relationship (WLA/BLA and R11/L68) showed similarities in several traits with differences less than five percentage. Other traits differed significantly between five and ten percentage in high performing genotypes (e.g. egg yolk proportion, daily feed intake and feed to egg mass ratio) and between 20 and 40 percentage in low performing genotypes (e.g. body weight, daily feed intake, egg weight and daily egg mass). Considering the phylogenetic relationship (WLA/R11 and BLA/L68), differences of about 30 to 100 percentage could be found in performance related traits. However, differences in egg quality parameters were much lower (four to nine percentage) between closely related strains.

Conclusions

The results of this study fitted well with the intended performance divergence between high and low performing genotypes in the established experimental design (Fig. 1). Firstly, recorded data of daily feed intake, growth and laying performance under conditions of identical feeding and housing gave an initial impression of the performance potential of the studied genotypes. Secondly, such data could be used to calculate performance-dependent nutrient requirements of the four genotypes in further experiments. In those studies the genotypes should be stressed by changing environmental conditions (e.g. via nutrition, infectious diseases, challenging housing conditions) and their physiological reactions could be studied concerning the adaptation ability to such new conditions.

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Summary

The aim of the present study was to assess the performance traits of chicken lines with different performance level and phylogenetic origin. Selection for high performances may change unselected traits related to animal health and well-being. However, long before intense selection started to act leading to contemporary high performing genotypes, founder populations on egg laying breeds with white and brown egg shell had been separated for many generations and have evolved independently. We have started to set up a comprehensive collaborative effort at the Friedrich-Loeffler-Institut to approach research question related to the capacity of high selected chicken lines to cope with limited metabolic resources. As a first step, four genotypes of purebred laying hens (WLA, BLA, R11 and L68) were used, which were divided by their divergence in performance and phylogeny. For the first time these genotypes were characterized according to their performance and growth development in the first 16 weeks of age in a rearing trial, a pre-laying period of 6 weeks and a following performance trial of 13 laying months (23^{rd} to 74^{th} week of age). The investigated performance traits were significantly affected by genotype, age and their interaction ($p \leq 0.001$). As a result of selection for high laying performance, selected strains showed a significantly higher performance than the non-selected ones. The high performing genotypes had an average laying intensity of 85 to 90%, a daily egg mass production of approximately 50 g/hen/d and a feed to egg mass ratio of 2.1 to 2.3 kg/kg. However, the low performing genotypes had an average laying intensity of 52 to 56%, a daily egg mass production of approximately 26 to 31 g/hen/d and a feed to egg mass ratio of approximately 3.0 kg/kg. Concerning average egg weight only R11 (50 g/egg) differed from the other experimental lines (55 to 58 g/egg). Independently of their performance brown hens showed a significantly higher body weight than white hens during the whole trial.

Egg quality analyses showed that high performing lines had a significantly higher albumen proportion (57.1 to 62.4%) and a significantly lower yolk proportion (26.8 to 29.8%) than the low performing lines (albumen: 55.3 to 57.4%, yolk: 30.3 to 33.5%). White hens (10.8 to 13.6%) had significantly higher proportion of egg shells than brown hens (10.3 to 12.9%).

In summary, the studied genotypes showed clear differences in performance level that made them well suitable for the established experimental design. With that design further studies should be carried out under varying environmental conditions (e.g. feeding, housing, infectious diseases). Thereby the studies will examine the question whether selection on high performance (WLA, BLA) leads to a reduced adaptability to varying environmental conditions.

Key words

Experimental design, chicks, pullets, laying hens, genotypes, growth, laying performance, egg quality, Gompertz equation

Zusammenfassung

Phylogenetische und Selektionseffekte auf die Wachstumsentwicklung, Legeleistung und Eiqualität von Reinzuchtlegehennen

Das Ziel der vorliegenden Untersuchung war die Entwicklung eines Versuchsdesign zur Beurteilung von Leistungsmerkmalen bei Hühnerlinien unterschiedlicher Leistungsniveaus und phylogenetischer Herkunft. Selektion auf hohe Leistung könnte nicht-selektierte Eigenschaften bezüglich Tiergesundheit und Wohlbefinden verändern. Lange bevor eine intensive Selektion zu den gegenwärtigen hochleistenden Genotypen hin durchgeführt wurde, trennte man Gründerpopulationen von Legezuchten mit weißer und brauner Eischale für mehrere Generationen, die sich daraufhin unabhängig voneinander entwickelten. Daher haben wir eine umfangreiche Zusammenarbeit am Friedrich-Loeffler-Institut begonnen, um uns Forschungsfragen zu nähern, die sich mit der Leistungsfähigkeit stark selektierter Hühnerlinien im Umgang mit begrenzten metabolischen Ressourcen befassen. Als erster Schritt wurden vier Genotypen von Reinzuchtlegehennen (WLA, BLA, R11 und L68) ausgewählt, die hinsichtlich ihrer Divergenz in Leistung und Phylogenie unterteilt wurden. Zum ersten Mal wurden diese Genotypen bezüglich ihrer Leistung und Wachstumsentwicklung in den ersten 16 Lebenswochen in einem Aufzuchtversuch, einer sechswöchigen Vorlegephase und einem angeschlossenen Leistungsversuch über 13 Legemonaten (23. – 74. Lebenswoche) charakterisiert. Die untersuchten Leistungsmerkmale wurden durch den Genotyp, das Alter sowie deren Interaktion höchst signifikant beeinflusst ($p \leq 0.001$). Als Folge der Selektion auf hohe Legeleistung zeigten selektierte Linien eine signifikant höhere Leistung als Nichtselektierte. Die hochleistenden Genotypen hatten eine Legeintensität von durchschnittlich 85 bis 90%, eine tägliche Eimasseproduktion von ca. 50 g/Henne/d sowie eine Futterverwertung von 2.1 bis 2.3 kg/kg. Die minderleistenden Genotypen hatten hingegen eine Legeintensität von durchschnittlich 52 bis 56%, eine tägliche Eimasseproduktion von 26 bis 31 g/Henne/d sowie eine Futterverwertung von ca. 3.0 kg/kg. Hinsichtlich des durchschnittlichen Eigewichtes unterschied sich lediglich R11 mit 50 g/Ei von den übrigen Versuchslinien mit 55 bis 58 g/Ei. Unabhängig von ihrer Leistung zeigten braune Hennen über den gesamten Versuch eine signifikant höhere Lebendmasse als weiße Hennen.

Untersuchungen der Eiqualität zeigten, dass hochleistende Linien einen signifikant höheren Eiklaranteil (57.1 bis 62.4%), gleichzeitig aber einen signifikant niedrigeren Eidotteranteil (26.8 bis 29.8%) aufwiesen als minderleistende Linien (Eiklar: 55.3 bis 57.4%, Dotter: 30.3 bis 33.5%). Weiße Hennen (10.8 bis 13.6%) besaßen einen signifikant höheren Schalenanteil als braune Linien (10.3 bis 12.9%).

Zusammenfassend zeigten die untersuchten Genotypen deutliche Unterschiede hinsichtlich des Leistungsniveaus, welche sie für das etablierte Versuchsdesign sehr gut geeignet machen. Mit diesem Design sollen weitere Studien unter variierenden Umweltbedingungen (z.B. Fütterung, Haltung, Infektionen) durchgeführt werden. Dabei soll der Frage näher nachgegangen werden, ob eine Selektion auf hohe Leistung (WLA, BLA) zu einer verminderten Anpassungsfähigkeit an variierende Umweltbedingungen führt.

Stichworte

Versuchsdesign, Küken, Junghennen, Legehennen, Genotypen, Wachstum, Legeleistung, Eiqualität, Gompertz-Funktion

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