

Maternal genetic effects on body weight and breast morphological traits in duck population under selection

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Abstract

Direct and maternal additive genetic and mitochondrial variances of duck meat performance traits were estimated using AI-REML algorithm. Records of 3 099 (5 010 pedigreed birds) from six consecutive generations were included. The following four traits were investigated: body weight at 3rd week, body weight at 7th week, sternum crest length at 7th week (in cm), and breast muscles thickness at 7th week (in cm). The data were analysed via three single trait linear animal models: I - additive genetic model, II - model extended to additive maternal effects; III – as model II with mitochondrial effects as random. Adequacy of the models was examined by Akaike's information criterion (AIC). Relatively high direct additive heritability estimates were obtained for body weight at 3rd week (0.4326-0.4546) and body weight at 7th week (0.5322-0.6088) whereas lower estimates were obtained for sternum crest length (0.1756-0.2744) and breast muscles thickness (0.1369-0.2932). The maternal heritabilities were moderate and also considerably depended on the model used. For all of the studied traits a negative covariance between direct and maternal genetic effects was found. Mitochondrial heritabilities were very low. Generally, on the basis of criteria employed, the model III can be suggested for analysis of body weight whereas for other traits model II seems to be suitable.

Keywords: ducks, meat performance traits, mitochondrial effects, heritability, model adequacy

Zusammenfassung

Maternal-genetische Einflüsse auf einige Eigenschaften der Fleischproduktion bei Langzeitselektion in Entenbeständen

Mithilfe des AI-REML-Algorithmus wurden direkt- und maternal-additiv genetische und mitochondriale Varianzen der Fleischleistungseigenschaften der Enten bewertet. Die Analysen umfassten insgesamt 3 099 Datensätze (5 010 reinrassige Vögel) aus sechs aufeinanderfolgenden Generationen. Bewertet wurden Züge der Fleischleistung wie Körpermasse in der 3. Lebenswoche (BW3), Körpermasse in der 7. Lebenswoche (BW7), Länge des Brustbeinkamms in der 7. Lebenswoche (in cm) (SCL7) und Brustmuskeldicke in der 7. Lebenswoche (in cm) (BMT7). Die Analyse der Daten erfolgte anhand drei linearer Einzelmerkmalmodelle: I – additiv genetisches Modell, II – Modell I erweitert um additiv

maternale Effekte, III – wie Modell II, erweitert um mitochondriale Effekte als Zufallseffekte. Die Angemessenheit der Modelle wurde mittels Akaikes Informationskriterium (AIC) überprüft. Für Körpermasse in der 3. Lebenswoche (0,4326-0,4546) und Körpermasse in der 7. Lebenswoche (0,5322-0,6088) ergaben sich relativ hohe Schätzwerte der direkt-additiven Erblichkeit. Hingegen waren die Schätzwerte für die Länge des Brustbeinkamms (0,1756-0,2744) und die Brustmuskeldicke (0,1369-0,2932) deutlich niedriger. Die Bewertung der maternalen Erblichkeit zeigte mittelmäßige und modellabhängige Ergebnisse. Für alle untersuchten Merkmale war die Kovarianz zwischen direkt- und maternal-genetischen Effekten negativ. Die mitochondriale Erblichkeit war sehr gering. Basierend auf den angewandten Kriterien kann Modell III als am besten geeignet für Analysen der Körpermasse empfohlen werden. Für Bewertungen der anderen Merkmale erzielt Modell II die besten Ergebnisse.

Schlüsselwörter: Enten, Fleischleistungseigenschaften, mitochondriale Effekte, Heritabilität, Adäquanz des Modells

Introduction

Over the last years a number of duck flocks and duck meat production has been increasing around the world. According to FAO (<http://faostat.fao.org>), duck meat production increased from 3 019 329 tons (in 2003) to 3 779 899 (in 2007). Unfortunately, the genetic studies on duck performance traits are still not advanced compared to chickens and livestock. Majority of them were performed in Germany (PINGEL 1990) and France (ROUVIER *et al.* 1994, MIGNON-GRASTEAU 1998) and China (CHENG *et al.* 1995, HU *et al.* 2006, HUANG *et al.* 2007). From breeders' point of view, the most important duck traits are related to body weight composition (e.g. weight gain, sternum crest length, breast muscles thickness).

It is well known that these traits are determined by direct and maternal genetic effects and environmental conditions. Considerable maternal (indirect) genetic effects on production traits have been reported in mammals (BRADE and GROENEVELD 1999, MANIATIS and POLLOT 2002, NÄSHOLM 2004, KESBI *et al.* 2008, REINSH and KALM 1995, VOSTRY *et al.* 2007) and poultry (KOERHUIS and THOMPSON 1997, PAKDEL *et al.* 2002, SCHÜLER *et al.* 1996). By contrast to many livestock species, there are few studies on maternal effects in ducks. Generally, the maternal effects have been defined as any influence from a dam on its progeny, excluding the effects of directly transmitted genes (see e.g. ALBUQUERQUE *et al.* 1998). Although the maternal effects (and in consequence maternal variability) are more exhibited in mammals (because of within uterus development, maternal care until weaning and milk feeding), the development of an embryo (and in consequence, its body weight) depends on egg environment during incubation. KOERHUIS *et al.* (1997) reported that one gram difference in egg weight is reflected in about ten grams gain of body weight of a juvenile broiler. The so-called »egg environment« is determined by both dam genotype and the external environment (maternal environmental effects eg. age and nutrition of the dam). It should be recalled that from the standpoint of the offspring, indirect maternal effects are considered as environmental. Therefore, by analogy to the genotype by environment

interaction, attention should be given to the dependence between direct and maternal effects. If a negative relationship exists between the direct and maternal effect, the dam either gives her offspring a plus set of genes for the direct effect and a poor maternal effect or the other way around.

However, genetic information is situated not only in the nucleus, but also in mitochondria, which contain their own DNA, and inheritance is exclusively from the female parent (without Mendelian segregation). MANNEN *et al.* (1998) suggested that cytoplasmic genetic effects are an important source of variation for carcass traits in cattle. The main argument in favour of mitochondrial contribution to phenotypic variability of body weight and its composition is that the mitochondria are essential to cellular function in energy metabolism, especially in muscles (OPALKA *et al.* 2004). Furthermore, GIBSON (1997) reported that mitochondrial DNA has about 10 fold higher mutation rate than nuclear DNA. In consequence, it creates mitochondrial genetic variability. To our knowledge no estimates of mitochondrial effects of meat performance traits in ducks are available.

Because the correct modelling of maternal effects enables more accurate estimation of additive genetic effects and therefore higher selection response, the objective of this study was to estimate maternal and direct additive genetic effects as well as mitochondrial genetic effects for body weight at 3rd week and three traits measured at 7th week: body weight, sternum crest length and breast muscles thickness in duck population under selection.

Material and methods

A total of 3 099 recorded individuals of Pekin duck (strain P-44) from six consecutive generations (2000-2005) from one pedigree farm located in the north of Poland were analysed. The pedigree included 5 010 birds. The pedigree and production records were extracted from a database of the Division of Poultry Breeding and Assessment of the Polish National Poultry Council. The birds were naturally mated and kept on litter. The population studied is typical for domestic fowl with hierarchic structure, where each sire is mated to 4-9 dams. The environmental conditions (e.g. feeding level) did not change considerably over time. Average inbreeding level for this population was 0.5 % (BOROWSKA *et al.* 2007) under a complete pedigree information. The selection procedure was based on a classical selection index called SELEKT described by WĘŻYK (1978). The following four traits were analysed:

- body weight at 3rd week (in g) [BW3],
- body weight at 7th week (in g) [BW7],
- sternum crest length at 7th week (in cm) [SCL7] – from first to final rib,
- breast muscles thickness at 7th week (in cm) [BMT7] – the measurement was performed by the use of special needle cram 1.5 cm distance from sternum crest.

A brief description of the data set is given in Table 1. The material was classified according to year and sex classes included in the further analysis as fixed effects. To estimate mitochondrial variance, 166 maternal lineages (each group with at least two individuals) were created. It led to reduction of a number of recorded individuals (from 4 798 to 3 099).

Table 1

Description of the data set

Beschreibung des Datensatzes

Trait	Recorded individuals	Average	SD
BW3	3 099	1 078.72	128
BW7	3 099	2 705.02	234
SCL7	3 099	12.14	0.697
BMT7	3 099	1.05	0.180

BW3 body weight at 3rd week (in g), BW7 body weight at 7th week (in g), SCL7 sternum crest length at 7th week (in cm), BMT7 breast muscles thickness at 7th week (in cm)

BW3 Körpermasse in der 3. Woche (in g), BW7 Körpermasse in der 7. Woche (in g), SCL7 Länge des Brustbeinkamms in der 7. Woche (in cm), BMT7 Brustmuskeldicke in der 7. Woche (in cm)

By contrast to statistical inference in classical experimental designs, evaluation of significance of effects studied under an animal model may be done only via comparison of respective models. Hence, three single trait linear models were employed:

$$\text{Model I: } \mathbf{y} = \mathbf{X}_1 \boldsymbol{\beta}_1 + \mathbf{X}_2 \boldsymbol{\beta}_2 + \mathbf{Z}_1 \mathbf{a} + \mathbf{e} \quad (1)$$

$$\text{Model II: } \mathbf{y} = \mathbf{X}_1 \boldsymbol{\beta}_1 + \mathbf{X}_2 \boldsymbol{\beta}_2 + \mathbf{Z}_1 \mathbf{a} + \mathbf{Z}_2 \mathbf{m} + \mathbf{e} \quad (2)$$

$$\text{Model III: } \mathbf{y} = \mathbf{X}_1 \boldsymbol{\beta}_1 + \mathbf{X}_2 \boldsymbol{\beta}_2 + \mathbf{Z}_1 \mathbf{a} + \mathbf{Z}_2 \mathbf{m} + \mathbf{Z}_3 \mathbf{c} + \mathbf{e} \quad (3)$$

where \mathbf{y} is the vector of observations, $\boldsymbol{\beta}_1$ is the vector of fixed effects of sex, $\boldsymbol{\beta}_2$ is the vector of fixed effects of year, \mathbf{a} is the vector of random direct additive genetic effects, \mathbf{m} is the vector of random maternal additive genetic effects, \mathbf{c} is the vector of random mitochondrial genetic effects, \mathbf{e} is the vector of random errors and $\mathbf{X}_1, \mathbf{X}_2, \mathbf{Z}_1, \mathbf{Z}_2, \mathbf{Z}_3$ are the respective incidence matrix for fixed and random effects.

Normal distribution of residuals for single traits was assumed. For models II and III, the covariance between direct and maternal genetic effects was assumed as follows: $\text{cov}(\mathbf{a}, \mathbf{m}) = \mathbf{A}\boldsymbol{\sigma}_{am}$. Covariances between other random effects were assumed as null.

The following parameters were estimated:

$$\text{– direct additive heritability} \quad h_a^2 = \sigma_a^2 / \sigma_p^2 \quad (4)$$

$$\text{– maternal additive heritability} \quad h_m^2 = \sigma_m^2 / \sigma_p^2 \quad (5)$$

$$\text{– covariance between direct and maternal effects as a proportion to phenotypic variance} \quad d_{am} = \sigma_{am} / \sigma_p^2 \quad (6)$$

$$\text{– mitochondrial heritability} \quad h_c^2 = \sigma_c^2 / \sigma_p^2 \quad (7)$$

$$\text{– total heritability} \quad h_T^2 = (\sigma_a^2 + 0.5\sigma_m^2 + 1.5\sigma_{am} + \sigma_c^2) / \sigma_p^2 \quad (8)$$

where σ_a^2 is the additive genetic variance, σ_m^2 is the maternal additive genetic variance, σ_{am} is the covariance between direct and maternal effects, σ_c^2 is the mitochondrial variance, σ_p^2 is the phenotypic variance.

The computations were performed using the AI-REML algorithm in the DFREML program (MEYER 2000). Akaike's information criterion (AIC) was applied to check the fit of the models (AKAIKE 1974):

$$AIC = 2k - 2\ln L \quad (9)$$

where k is a number of parameters included in the model, L is a likelihood function. In fact AIC is not considered as a statistical test, because significance level is not controlled. However, the smallest AIC indicates the best model.

Results

The genetic parameter estimates (and their standard deviations) are shown in Table 2. Generally, the estimates of heritability and covariance between direct and maternal effects varied across the models studied. Relatively high direct additive heritability (h_a^2) estimates were obtained for BW3 (0.43-0.45) and BW7 (0.53-0.61). Lower and more varied heritability was estimated for SCL7 (0.18-0.27) and BMT7 (0.14-0.28). The maternal heritabilities (h_m^2) were moderate and not exceed 0.2. They were also considerably depended on the model used. The least variable maternal heritability was estimated for SCL7. It should be stressed that for all of the studied traits a negative covariance between direct and maternal effects was found. The covariance estimates differed across the traits and the models. However, inconsistent tendencies were observed. Exclusion of maternal genetic or mitochondrial effects does not lead to overestimation of the direct heritability. Contrary, in case of BW7, SCL7 and BMT7, estimates of h_a^2 from model I were lower compared to other models. The differences between the direct heritability estimates for a particular trait (except BMT7) were negligible. Mitochondrial heritabilities were very low (h_c^2 about 0.01) for BW3 and SCL7. Approximated standard deviations of these estimates ranged from 0.030 to 0.079 (for direct heritability), 0.018 to 0.039 (from maternal heritability) and 0.008 to 0.050 (for mitochondrial heritability). It confirms that mitochondrial heritabilities can be considered negligible. A negative covariance between direct and maternal effects for all models and characters studied should be further investigated. From a genetic improvement program perspective, it confirms a necessity to incorporate maternal effects in genetic evaluation of ducks. Selection is based on rankings of individuals according to their predicted genetic (direct vs maternal) effects. Therefore, negative correlation between these effects may affect the ranking of birds depending on the linear model applied.

As already mentioned, the Akaike's information criterion was used for the evaluation of goodness of fit of the analysed linear models. The AIC values are listed in Table 3. In general, they correspond with the above given remarks. For SCL7 and BMT7 the model II (with the smallest AIC values) can be recommended whereas for both body weight measurements, model III seems to be the best.

Table 2

Genetic parameters of the analysed traits

Genetische Parameter der analysierten Merkmale

Trait model	h_a^2	h_m^2	d_{am}	h_c^2	h_t^2
BW3					
I	0.450 ± 0.055				
II	0.433 ± 0.054	0.157 ± 0.032	-0.122 ± 0.028		
III	0.435 ± 0.067	0.124 ± 0.036	-0.109 ± 0.033	0.009 ± 0.009	0.341 ± 0.059
BW7					
I	0.532 ± 0.059				
II	0.537 ± 0.059	0.138 ± 0.030	-0.127 ± 0.029		
III	0.613 ± 0.079	0.154 ± 0.039	-0.179 ± 0.043	0.006 ± 0.008	0.437 ± 0.067
SCL7					
I	0.191 ± 0.036				
II	0.266 ± 0.042	0.048 ± 0.018	-0.082 ± 0.023		
III	0.274 ± 0.053	0.069 ± 0.023	-0.124 ± 0.036	0.010 ± 0.010	0.183 ± 0.043
BMT7					
I	0.137 ± 0.030				
II	0.247 ± 0.041	0.087 ± 0.024	-0.130 ± 0.029		
III	0.278 ± 0.053	0.097 ± 0.031	-0.152 ± 0.039	<0.001 ± 0.050	0.108 ± 0.033

BW3 body weight at 3rd week (in g), BW7 body weight at 7th week (in g), SCL7 sternum crest length at 7th week (in cm), BMT7 breast muscles thickness at 7th week (in cm), h_a^2 direct heritability, h_m^2 maternal heritability, d_{am} covariance between direct and maternal effects as proportion to phenotypic variance, h_c^2 mitochondrial heritability, h_t^2 total heritability

BW3 Körpermasse in der 3. Woche (in g), BW7 Körpermasse in der 7. Woche (in g), SCL7 Länge des Brustbeinkamms in der 7. Woche (in cm), BMT7 Brustmuskeldicke in der 7. Woche (in cm), h_a^2 direkte Heritabilität, h_m^2 maternale Heritabilität, d_{am} Kovarianz zwischen direkten und maternalen Effekten als Verhältnis zu phänotypischer Varianz, h_c^2 mitochondriale Heritabilität, h_t^2 gesamte Heritabilität

Table 3

Comparison of the employed models by the use of Akaike's information criterion

Vergleich der angewandten Modelle mittels Akaikes Informationskriterium

Trait	Model	AIC
BW3	I	45.636
	II	45.582
	III	29.694
BW7	I	52.791
	II	52.753
	III	34.512
SCL7	I	-255.21
	II	-273.66
	III	-150.60
BMT7	I	-9.336
	II	-9.379
	III	-7.746

BW3 body weight at 3rd week (in g), BW7 body weight at 7th week (in g), SCL7 sternum crest length at 7th week (in cm), BMT7 breast muscles thickness at 7th week (in cm)

BW3 Körpermasse in der 3. Woche (in g), BW7 Körpermasse in der 7. Woche (in g), SCL7 Länge des Brustbeinkamms in der 7. Woche (in cm), BMT7 Brustmuskeldicke in der 7. Woche (in cm)

Discussion

In the present study, models including direct and maternal additive genetic effects and mitochondrial effects were employed. However, body weight is a complex trait for which also single loci with considerable effects were identified. Some of them were detected in ducks (HUANG *et al.* 2007), for example QTLs were suggested for six body weight traits in the Pekin ducks. It is well known that sexual dimorphism of the studied traits exists. As noted by CHAMBERS (1990), other additional genetic effects (as dominance) could be considered in genetic analysis of body weight and carcass composition. The first suggestion on a complex background of body weight was reported many years ago based on a simple comparison between sire and dam components. Is the inclusion of all hypothetical genetic and environmental effects in statistical model possible? Unfortunately, there is an antagonism between data (size and structure) and accuracy in estimation of many genetic and environmental effects. Moreover, many assumptions and limitations of sophisticated statistical methodology meet real, sometimes incomplete production and pedigree records.

As already mentioned, a number of reports on genetic parameters of body weight and composition are available in the literature. The majority of them concerns mammals and chicken. In poultry, maternal effects are related to the egg. Generally, genetic parameters vary across methods, genetic models and first of all across specific factors that affect the given population. Therefore, direct comparison of results from literature should be focused on general tendencies. Do the results of this study correspond with the ones reported by other authors? MIGNON-GRASTEAU *et al.* (1998) found that heritability estimates of BW in Muscovy ducks ranged from 0.33 to 0.67, whereas according to CHENG *et al.* (1995) for Brown Tsaiya laying ducks the estimated heritabilities were between 0.39 and 0.48. Investigation carried out by TAI *et al.* (1989) on the basis of the sire-dam model suggested maternal influences on duck body weight. As already mentioned, estimated covariances between direct and maternal additive effects for all four traits according to all models were negative. They are in agreement with many of the results obtained for chickens (KOERHUIS and THOMPSON 1997). However, SZWACZKOWSKI *et al.* (2007) found positive covariances between direct and maternal additive effects for body weight in two goose populations. Genetic antagonism between these effects was found in most of the other studies carried out for body weight in livestock species. These unfavourable covariances imply that genetic improvement would be more difficult as an increase in direct additive component would result in a decline in maternal one and vice versa.

The participation of mitochondrial genetic variance in the total variance in the present study is negligible. However, it should be remembered that estimation of cytoplasmic variance based on maternal lineages seems to be very difficult. One of the main problems is that in the model a lack of mutations within the groups is assumed. Moreover, from the statistical perspective an assumption of the independence of lineages is necessary. According to ROUGHSEGE *et al.* (2001) underestimation of maternal lineage variance is the result of tracing insufficient number of generations of maternal pedigree, which to some extent can be overcome by a more detailed pedigree recording. It should be recalled, that recorded individuals from five consecutive generations were included. This population has an undesirable structure to estimate the mitochondrial effects on the basis of maternal lineage

groups because their size is relatively small and differentiated (2-143). So, the cytoplasmic variances can be underestimated. Therefore, it seems that a further study should be based on mitochondrial DNA polymorphism.

Which model is the best for genetic evaluation of the population? In general, by contrast to a classical experimental design, an evaluation of significance of the effects in animal models (with complex variance-covariance matrices for random genetic effects) is not straightforward. Several comparison criteria were described in literature. Some of them (e.g. likelihood ratio test) are statistical tests (unfortunately, usually with small number of degrees of freedom). Other ones (e.g. Akaike's or Bayesian information criterion), also based on likelihood functions, do not allow for control of significance level. Additionally, the field collected data have unbalanced structure and missing pedigree information. It influences the precision of genetic evaluation (NILFOROOSHAN *et al.* 2008, ROUGHSEGE *et al.* 2001, KOMINAKIS 2008, CLEMENT *et al.* 2001).

Although the applied Akaike's information criterion indicates model III for analysis of BW3 and BW7, and model II for SCL7 and BMT7, it seems that an evaluation of mitochondrial genetic effects requires further investigations. However, the obtained results in the current study clearly indicate that a model including maternal genetic effects should be applied in further routine genetic evaluation.

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