

BREEDING AND GENETICS

Genetic Correlations Between Body Weight of Cocks and Production Traits in Laying Hens, and Their Possible Use in Breeding Schemes

C. HAGGER

*Institute of Animal Sciences, Swiss Federal Institute of Technology,
ETH-Zentrum, WEN, CH-8092 Zurich, Switzerland*

ABSTRACT Genetic and phenotypic (co)variances between body weight of cocks ($n_m = 1,138$), BWM, and production traits of hens ($n_f = 8,844$), i.e., egg number (EN), egg weight (EW), feed intake (FI), and body weight (BWF) were estimated by the restricted maximum likelihood method for an animal model. Six multivariate analyses were carried out to get all desired components. Resulting heritabilities were .292, .754, .682, .732, and .790 for EN, EW, FI, BWF, and BWM, respectively. Estimated genetic correlations between BWM and EN, EW, FI, and BWF, were $-.161$, .338, .645, and .841, respectively. The corresponding estimates between BWF and EN, EW, and FI, were $-.036$, .294, and .787, respectively. The additional expected selection response in traits of hens from including BWM into the selection criterion of cocks is given for a particular structure with full- and half-sister information and different correlations between BWM and traits of hens.

(*Key words:* sex differences, body weight, production traits, genetic relationships, selection)

1994 Poultry Science 73:381-387

INTRODUCTION

In breeding schemes designed to improve sex-limited traits, e.g., egg production in poultry, traits of males are usually not included into the selection criteria. Male breeders are selected on information from their full- and half-sisters. If the genetic correlations between traits of females and traits of males were known, it would be possible to combine the information on both sexes into selection criteria in an optimal way. A fraction of the genetic variation in the selection criterion in the male sex could, thus, be exploited without the need of offspring information. The genetic variation between full- and half-sib males cannot be used in a breeding scheme, if their selection is based on full- and half-sister information only, because in this case, all male full-sibs would have identical selection criteria. Selection of

males from offspring information would double the generation interval of cocks in layer breeding. In breeding schemes of laying chickens, only a limited number of males is usually raised. Therefore, recording some traits on them, e.g., body weight, could be done with little additional costs. It might even be of interest to investigate traits that are expensive to measure, e.g., feed intake and, thus, create the possibility to put direct selection pressure on it (Katie and Kolstad, 1992). One might also choose to raise more cocks to increase selection intensity to some extent. Including additional information correctly into a selection criterion usually increases its accuracy and, therefore, a higher selection response will be achieved. An attempt to include body weight of cocks into a layer breeding experiment has already been demonstrated by Hagger and Abplanalp (1988).

Knowledge of the genetic correlation between analogous traits of males and females, e.g., body weight, as well as their genetic and phenotypic variances provide information about the genetic similarity of

Received for publication July 19, 1993.

Accepted for publication October 14, 1993.

such traits. A genetic correlation clearly deviating from 1 would strongly indicate a genetic difference. If this is supported by the estimated correlation, treating the traits of the two sexes as two different traits of a selection criterion would definitely be preferable over their use as one trait with an adjustment for the sex difference of the means. This distinction would also be important if genetic correlations with other traits would be different between sexes or even show different signs, as found by Tixier-Boichard *et al.* (1992).

The introduction of the animal model (Quaas and Pollak, 1980) and increasing computing power enable the multivariate estimation of genetic (co)variances for sizable data sets. For this type of analysis it is a prerequisite that a minimum of the genetic relationships between animals of a population are known. This condition certainly poses no problems in poultry breeding operations or experiments because complete pedigrees are known for many generations. In such a favorable case, it is relatively easy to estimate the genetic covariance between traits not observed on all animals, e.g., male body weight and egg weight. However, it has to be remembered that under the circumstances addressed, the maximum genetic relationship between informative pairs of animals is one half (full-sibs, sire-daughter, dam-son). Thus, a considerable number of informative animals is necessary to reduce the inherently large variance of the estimated genetic correlations.

The aim of this investigation was to estimate genetic correlations between body weight of cocks and several production traits of hens using data from an experimental layer flock and to check the consequences of including this information into a selection scheme to improve sex-limited traits in hens.

MATERIALS AND METHODS

Data

Data for the investigation arose from a selection experiment with the aim to genetically improve the trait of income minus feed cost between 21 and 40 wk of age in brown

egg layers (Hagger, 1990, 1992). The experiment consisted of two selection lines (replicates) and a control line of 20 male and 80 female breeders each. Hens were selected for five generations on their performance followed by two generations on a restricted best linear unbiased prediction (Quaas and Henderson, 1976) animal model breeding value for the same trait. The restriction built into the selection criterion was for no genetic change in average egg weight during the test period from 21 to 40 wk of age. An average selection intensity of 18.9% among hens was realized during the experiment. Males were selected randomly within half-sib families.

The base population consisted of 905 hens with known pedigree that were obtained from matings between 50 Rhode Island Red males and 303 White Plymouth Rock females. Full-sib hens of this population were, if possible, equally distributed to all three lines before the first selection. The same 20 males were used as sires for the first selected generation in all lines. This procedure created additional genetic ties between the lines. Later on, the lines were closed. Between two and three male chicks from each half-sib family were raised and saved until the end of the breeding period. Hens were kept in three-tier single cage batteries of 1,350 cm² floor space from 14 wk of age on. Egg number and egg weight were recorded daily from onset of lay to 25 wk of age and on 6 d/wk thereafter until 60 wk. Egg production data were adjusted to 28-d periods for missing test days based on the hen's own information on rate of lay and egg weight. Individual feed consumption from *ad libitum* access was recorded continuously for all hens between 21 and 60 wk. All birds were weighed at 10, 20, 30, 40, and 60 (hens only) wk. More details on husbandry of birds and the selection criterion are given elsewhere (Hagger, 1990, 1992).

Altogether, 8,844 hens that had survived to 40 wk and that had eaten less than 10 kg of feed/kg of egg mass produced and records of 1,138 cocks were included in this investigation. Data of hens were adjusted for effects of hatch and laying house within year prior to the analysis. Results are presented for some important traits that determine the economic success of egg

production in the test period of the experiment. These are: egg number to 40 wk (EN), average egg weight to 40 wk (EW), feed intake to 40 wk (FI), body weight at 40 wk of females (BWF) and of males (BWM).

Genetic Analyses

Genetic and phenotypic (co)variances were estimated multivariately with the restricted maximum likelihood (REML) method (Patterson and Thompson, 1971) for an animal model containing the fixed effect of generation and the random effects of animal and residual. The complete additive genetic relationship matrix back to the grandparents of the base population was available. For the estimation of the genetic covariances between traits of males and traits of females it is most informative if the genetic relationships between the males and females that were recorded are known and these individuals are close relatives. The genetic ties between the lines established at the beginning of the experiment in conjunction with the relationship matrix made it possible to combine the data from the three lines. Analyses for several combinations of the traits of interest had to be performed. If BWM is to be treated jointly with traits of females, one has to keep in mind that the residual covariance between pairs of these traits is zero. The same model was valid for all traits. The parameters estimated as outlined are the expected parameters of the first generation in the pedigrees, i.e., in the present case, the grandparents of the base population. The DFREML computer programs of Meyer (1991), which provide the necessary capabilities, were used.

Variance-covariance matrices between simple, untransformed traits, per definition, have to be positive definite, i.e., all eigenvalues positive. Therefore, if multivariate selection is to be applied in a breeding scheme (e.g., a selection index), care should be taken that the matrices fulfill this condition (Hayes and Hill, 1980; Foulley and Ollivier, 1986). Matrices of (co)variance components estimated multivariately and simultaneously by the REML method are positive definite, but the condition may not hold if (co)variance components from several independent multivariate estima-

tions have to be combined to obtain the desired matrix. For such cases, methods exist to transform a matrix to the necessary form (Hayes and Hill, 1981; Mielenz and Wagenknecht, 1992). The genetic (co)variance matrix for the traits EN, EW, FI, BWF, and BWM had to be assembled from components resulting from several analyses and, thus, had to be tested for the condition mentioned.

The consequences of including the performance of males (M) as a part of their selection criterion to improve a sex-limited trait of females (F) on expected response and accuracy of selection were investigated with the application of selection index theory (e.g., Falconer, 1982). If selection is for trait F and if the mean of m full-sisters, \overline{FS} , and the mean(s) of one (several) half-sister group(s) (each of m full-sisters), \overline{HS}_i , are available, the true breeding value of a male, H, can be estimated by a selection index, $I_{1,[2]} = b_1\overline{FS} + b_2\overline{HS}_i + [b_3M]$ (one half-sister group). The additional increase of the correlation between true and estimated breeding value, r_{HI} , and the expected additional genetic gain, ΔG , in F from including M into the selection criterion of males, I, can now easily be found. To calculate b_i , r_{HI} , and ΔG , the following (co)variances will be needed (additive inheritance):

$$\text{Var}(M) = \sigma_{pM}^2$$

$$\text{Var}(\overline{FS}) = \text{Var}(\overline{HS}_i) = \frac{1}{2}\sigma_{gF}^2 + \frac{\sigma_{pF}^2 - \frac{1}{2}\sigma_{gF}^2}{m}$$

$$\text{Cov}(M, \overline{FS}) = \frac{1}{2}\sigma_{gMF}$$

$$\text{Cov}(M, \overline{HS}_i) = \frac{1}{4}\sigma_{gMF}$$

$$\text{Cov}(\overline{FS}, \overline{HS}_i) = \frac{1}{4}\sigma_{gF}^2$$

$$\text{Cov}(\overline{HS}_i, \overline{HS}_j) = \frac{1}{4}\sigma_{gF}^2$$

$$\text{Cov}(H, M) = \sigma_{gMF}$$

$$\text{Cov}(H, \overline{FS}) = \frac{1}{2}\sigma_{gF}^2$$

$$\text{Cov}(H, \overline{HS}_i) = \frac{1}{4}\sigma_{gF}^2$$

where: σ_{pM}^2 and σ_{pF}^2 = phenotypic variances of M and F; σ_{gF}^2 = additive genetic variance of F; σ_{gMF} = additive genetic covariance between M and F.

RESULTS AND DISCUSSION

Means for the traits of the population used in the investigation, their phenotypic and genetic standard deviations, together with the number of recorded hens and cocks with complete records are given in Table 1. The values show that the mean performance of the three experimental lines used in this investigation was not far from the performance of commercially available brown egg layers. Cocks were on average more than 1 kg heavier at 40 wk than hens, with a 40% larger standard deviation of their body weight. Differences between sexes in body weight and its standard deviation of the same magnitude were observed by Bordas *et al.* (1992) in an experimental flock of Rhode Island Red chickens. The differences in means and standard deviations between body weight of the two sexes may be taken as indication for a genetic difference between the two traits. This remains true, even if the larger standard deviations of BWM are explained as a scale effect.

The estimated genetic (co)variances for the five traits are given in Table 2. These entries were assembled from six independent multivariate analyses. The resulting matrix turns out positive definite. Table 3 contains the estimated heritabilities of the traits on the diagonal, the phenotypic correlations above, and the genetic correlations below the diagonal. The values show that the genetic and the phenotypic

correlations between all combinations of female traits do not differ much from each other.

Slightly lower genetic and phenotypic correlations between BWF and FI were observed by Pauw *et al.* (1986) in White Leghorn hens. The heritabilities of the traits given are in the upper range of published estimates. This may partly be a consequence of the model and the estimation procedure employed. The heritability of BWM turned out slightly higher than the estimate for BWF. The genetic correlation between these two traits, although high, is substantially lower than 1.0; therefore, strongly indicating a genetic difference between the two traits. This observation is supported by a difference between the genetic standard deviation of the two traits, which is 45% higher for BWM than for BWF. The genetic correlations between BWM and EN, EW, and FI were all in the same direction and of similar size as the corresponding correlations of BWF with EN, EW, and FI.

It is remarkable that such high genetic correlations between BWM and EW and FI were found. From an analysis of full-sib means, Hagger and Abplanalp (1988) found a correlation between BWM and EW of .47 in an experimental flock of White Leghorns with large eggs. For combinations of residual feed intake of either cocks or hens with other traits of hens, Tixier-Boichard *et al.* (1992) also observed different signs for some of the corresponding pairs of genetic correlations. In such a case, including a male trait into a selection criterion, say an index, but using the same parameters as for the analogous female trait could lead to a cancellation of selection responses or even

TABLE 1 Means and phenotypic (s_x) and genetic (σ_x) standard deviations of egg number (EN), egg weight (EW), and feed intake (FI) until 40 wk, and body weight of 8,844 females (BWF) and of 1,138 males (BWM) at 40 wk

Statistical parameter	EN	EW	FI	BWM	
				BWF	BWM
\bar{x}	118.5	59.9	15.9	2.30	3.43
s_x	12.65	4.56	1.41	.264	.375
σ_x	6.91	3.58	1.20	.234	.339

TABLE 2. Genetic (co)variances of egg number (EN), egg weight (EW, grams), feed intake (FI, kilograms), female body weight (BWF, kilograms) and male body weight (BWM, kilograms)

	EN	EW	FI	BWF	BWM
EN	47.8				
EW	-6.61	12.8			
FI	2.36	1.65	1.44		
BWF	-.0585	.246	.220	.0546	
BWM	-.362	.383	.254	.0666	.115

drive a trait in an undesired direction. If, on the other hand, the estimated parameters for each of the two analogous traits were used, the index weight for the male trait would get the opposite sign of that of the female trait. The estimated genetic correlation between BWM and the selection criterion of females, i.e., income minus feed cost, was $-.032$ (Hagger, unpublished data). The corresponding correlation in hens was stronger, $-.162$, and caused a pronounced correlated genetic reduction in BWF (Hagger, 1992).

The magnitude of the correlations found between BWM and female traits strongly suggest that including the information on a male trait into their selection criterion would be worthwhile to improve sex-limited traits of hens. The expected increase of selection response from selection of males either with or without including their own body weight into the selection criterion was investigated by application of selection index theory. Indices I_1 for males were calculated for one female trait at a time using the means of five full-sisters and of three half-sister groups of five full-sisters each. For indices I_2 , the body weight of the selection candidates was also taken into account. The influence of the size of the genetic

correlation between BWM and the traits of females could be investigated also because different genetic correlations were found for the different combinations of the traits.

The parameters given in Tables 2 and 3 and a standardized selection differential of $i = 1.0$ were used for the calculations. Table 4 contains the correlations between the true and the estimated breeding values, r_{HI} , and the expected genetic changes in the female traits (ΔG) from selection of cocks on either of the two indices. From the results it is obvious that the additional genetic gains from selection on index I_2 relative to the gains from selection on index I_1 are closely related to the genetic correlation between BWM and the traits of hens. With a genetic correlation of $.338$ (Table 4), as observed between BWM and EW, the relative additional gain in EW from selection of cocks only would be 3.6%, an increase that could be achieved with very little additional input, i.e., only taking once the body weight of cocks. For trait combinations with higher correlations, the additional gain increases substantially, but in all cases due to the same additional input. These calculations could be done for multitrait indices in the same way, but then economic weights would be needed for the traits in the

TABLE 3. Heritabilities (diagonal), phenotypic (above diagonal), and genetic (below diagonal) correlations of egg number (EN), egg weight (EW), feed intake (FI), female body weight (BWF) and male body weight (BWM)

	EN	EW	FI	BWF	BWM
EN	.292				
EW	-.267	.754			
FI	.279	.391	.682		
BWF	-.036	.294	.787	.732	
BWM	-.161	.338	.645	.841	.790

TABLE 4. Correlation between true and estimated breeding values (r_{IH}) of cocks for an index of full- and half-sister information (I_1) or for an index of full- and half-sister information and own body weight (I_2), expected selection responses in female offspring (ΔG) with standardized selection differential $i = 1$, and relative superiority of selection on I_2 ($\Delta G\%$) for various genetic correlations between male body weight and female traits¹

Item	Female trait/correlation							
	EN/-.161		EW/.338		FI/.645		BWF/.841	
	I_1	I_2	I_1	I_2	I_1	I_2	I_1	I_2
r_{IH}	.519	.529	.624	.648	.613	.716	.620	.810
ΔG	1.80	1.83	1.12	1.16	.368	.429	.073	.095
$\Delta G\%$		1.7		3.6		16.6		30.1

¹EN = egg number; EW = egg weight; FI = feed intake; and BWF = female body weight.

aggregate genotype and they would influence the results. The relative increase in selection response due to including male body weight into the male selection criterion would increase with decreasing numbers of available full- and half-sister available records. The amount of information on relatives could, therefore, be reduced to attain the same response as from selection on index I_1 .

The expected additional genetic gains in Table 4 clearly show that taking the body weight of cocks and including this information into the selection procedure would be a means to improve the efficiency of a layer breeding scheme, once the necessary correlations of trait combinations between sexes are available. In this particular case, taking the same relationships between body weight of cocks and traits of hens as between body weight of hens and other traits of hens would probably not harm the selection decisions too much because the genetic correlation between both weights is high and the correlations to the other traits are in the same direction and of similar magnitude. However, if these relationships are clearly different, as found by Tixier-Boichard *et al.* (1992) for other traits, then using the same relationships for equivalent male and female traits to other female traits (Katlé, 1992) would not be advisable. Therefore, it seems to be essential that correlations between male and female traits be estimated from adequate sets of data before traits of males can safely be included into

their selection indices to improve traits of females. Taking body weight of cocks would not be expensive. Justification for measurement of more expensive traits on cocks, e.g., feed consumption, needs further investigation. This problem has been studied by Katlé (1992), but analogous traits of males and females were treated as the same trait.

ACKNOWLEDGMENTS

The excellent technical assistance of D. Steiger-Stafl and the continuous support of G. Stranzinger are gratefully acknowledged.

REFERENCES

- Bordas, A., M. Tixier-Boichard, and P. Mérat, 1992. Direct and correlated responses to divergent selection for residual food intake in Rhode Island Red laying hens. *Br. Poult. Sci.* 33: 741-754.
- Falconer, D. S., 1982. *Introduction to Quantitative Genetics*. 2nd ed. Longman, London, England, and New York, NY.
- Foulley, J. L., and L. Ollivier, 1986. A note on criteria of coherence for the parameters used to construct a selection index. *J. Anim. Breed. Genet.* 103:81-86.
- Hagger, C., 1990. Response from selection for income minus food cost in laying hens, estimated via the animal model. *Br. Poult. Sci.* 31:701-713.
- Hagger, C., 1992. Two generations of selection on restricted best linear unbiased prediction breeding values for income minus feed cost in laying hens. *J. Anim. Sci.* 70:2045-2052.
- Hagger, C., and H. Abplanalp, 1988. Selection with restriction in a poultry breeding scheme with different selection procedures in both sexes: Direct responses. *Br. Poult. Sci.* 29:251-263.

- Hayes, J. F., and W. G. Hill, 1980. A reparametrization of a genetic selection index to locate its sampling properties. *Biometrics* 36:237-248.
- Hayes, J. F., and W. G. Hill, 1981. Modification of estimates of parameters in the construction of genetic selection indexes ("bending"). *Biometrics* 37:483-493.
- Katle, J., 1992. Genetic and economic consequences of including residual food consumption in a multi-trait selection program for laying hens. *Acta Agric. Scand.* 42:63-70.
- Katle, J., and N. Kolstad, 1992. Residual food consumption recorded on cocks from egg-laying strains. *Proceedings XIX World's Poultry Congress, Amsterdam, September 20-24, Vol. 2: 206.*(Abstr.)
- Meyer, K., 1991. Estimating variances and covariances for multivariate animal models by restricted maximum likelihood. *Genet. Sel. Evol.* 23:67-83.
- Mielenz, N., and M. Wagenknecht, 1992. Korrektur von geschätzten Varianz-Covarianz-Matrizen durch Optimierung im Raum der positiv definiten Matrizen. *Arch. Tierz. Dummerstorf* 35:611-618.
- Patterson, H. D., and R. Thompson, 1971. Recovery of interblock information when block sizes are unequal. *Biometrika* 58:545-554.
- Pauw, R., J. Petersen, and P. Horst, 1986. Comparison of several indicators of food conversion efficiency in laying hens from genetic point of view. Pages 104-108 *in: Proceedings VII European Poultry Conference, Vol. 1. Paris, August 24-28. M. Larbier, ed. Tours, France.*
- Quaas, R. L., and C. R. Henderson, 1976. Selection criteria for altering the growth curve. *J. Anim. Sci.* 43:221.(Abstr.)
- Quaas, R. L., and E. J. Pollak, 1980. Mixed model methodology for farm and ranch beef cattle testing programs. *J. Anim. Sci.* 51:1277-1287.
- Tixier-Boichard, M., D. Boichard, A. Bordas, and E. Groeneveld, 1992. Genetic parameters of residual feed intake in adult males and females from a layer Rhode Island Red population. *Proceedings XIX World's Poultry Congress, Amsterdam, September 20-24. Vol. 2: 209.*(Abstr.)