QUANTITATIVE GENETIC STUDIES
ON GROWTH AND REPRODUCTIVE TRAITS
IN BROILER CHICKENS

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Declaration

I hereby declare that this thesis is my own composition and is an account of research performed whilst studying for the degree of Doctor of Philosophy at the University of Edinburgh. I am the senior author of the publications arising from this thesis (listed below). I wrote the first manuscripts and conducted the analyses.

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[redacted]

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Chapter	Author(s)	Journal
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ABSTRACT

This thesis considers three major quantitative genetic topics characteristic of growth and reproductive traits in broiler breeding, *i.e.* (1) the estimation of maternal effects in juvenile body weight (JBWT), (2) selection for food conversion into growth defined as a ratio (FCR), and (3) non-normality and curvilinearity of heritability of egg production distributions and the genetic relationships of those reproductive traits with juvenile growth. Restricted maximum likelihood (REML) methods based on the individual animal model were utilised in the estimation of variance components to make optimum use of the data and take account of selection.

Estimates of the maternal additive genetic variation were small relative to the direct additive genetic variation of JBWT for two broiler populations investigated. The negative estimates of the direct-maternal genetic correlation (r_{AM}) were unexpected and prompted the investigation of more appropriate and detailed statistical models taking account of direct-maternal environmental covariation, estimated either as the covariance between the environmental maternal and the environmental residual effects or as a maternal phenotypic effect through regression on the mother's phenotype. Whilst the goodness-of-fit of these alternative models was superior, the estimates of r_{AM} were not much affected. The choice of the fixed effect structure was shown to be paramount in the estimation of maternal effects. Thus far, maternal effects were lumped together into a single component. Next, the results were described of an experiment conducted to identify individual pathways related to the egg causing maternal variation in JBWT and to establish their effect on offspring-parental regressions. Antagonistic maternal pathways of egg weight at the start and at the 18th day of incubation were observed. Their effects largely offset each other and hence biased the offspring-dam regression only slightly. A high loss in egg weight during incubation, indicative of poor egg shell quality, was identified as the likely cause for the negative estimates of r_{AM}.

Direct versus indirect selection for FCR after selection for JBWT, a sequential scheme often applied in broilers, was considered. It was shown that, with large differences in heritabilities or genetic and environmental correlations of food consumption (FC) and weight gain (WG), selection for a linear representation of FCR, with weights for FC and WG based on statistical differentiation, can lead to additional progress in FCR. Similar heritabilities for FC and WG in the literature suggest a small loss by direct selection for the ratio. REML proved robust to the non-normality in FCR and hence transformation does not seem necessary to enable accurate selection and estimation of response using best linear unbiased predicted (BLUP) breeding values.

A marked skewness in egg production distributions of female line broiler hens was observed. A mixture model of two Gaussian distributions with different dispersion and location fitted the phenotypic data best. Sexual maturity closely followed a log-normal distribution after a shift in location. Elimination of outliers, on the basis of either outlier theory on the phenotypic mixture model or the hypothetical underlying genetic variability, and/or data transformation improved normality of errors and linearity and size of heritability. In spite of appreciable decreases, curvilinearity of heritability was still significant after transformation by comparison of effective heritabilities in the up and down direction of selection. The genetic relationships among these reproductive data and JBWT revealed substantial differences in comparison to earlier literature estimates. This illustrates the importance of contemporary, population specific estimates for the optimal construction of selection indices or multivariate BLUP breeding values and indicates possible effects of changes in management on genetic relationships.

These studies demonstrate the scope for more efficient broiler breeding programmes and indicate important areas for further research.

CHAPTER 1

GENERAL INTRODUCTION

Broiler growth and maternal effects

The primary demand of broiler growers in attempting to satisfy market demand has always been rapid growth, with a maximum weight for age, or a minimum number of days to the desired market weight (Hunton, 1990). A high selection pressure and reasonable accuracy of selection decisions for growth to a fixed age provided rapid and consistent gains over the years. Progress was facilitated by the introduction of family indices after Osborne (1957). Unfortunately, these gains were not without cost, particularly in terms of traits concerned with reproduction. For instance, negative relationships have been observed for high body weight with egg production, fertility and hatchability of fertile eggs as a result of impaired egg shell quality (Marks, 1985; Siegel and Dunnington, 1985; Robinson *et al.*, 1993). Chambers (1990) summarised heritability estimates for body weight based on the analysis of variance components in nested mating designs. Average estimates based on dam components were considerably higher than the estimates based on the sire (0.70 *versus* 0.41), and although non-additive and sex-linked genetic variation might be partially responsible, both environmental and genetic maternal effects should not be underestimated. The genotype of the dam might affect the phenotype of her progeny through a sample of half her direct additive genes for growth as well as through her genotype for maternal effects on growth (Willham, 1963; Koch, 1972; Meyer, 1992a). Potential maternal pathways involved might be the size of the egg and its shell quality. Depending on their relationship with the direct genetic variation in body weight, partitioning of the variance into direct and maternal components might be required to achieve optimum progress in body weight and these reproductive traits (Baker, 1980; Meyer, 1992a). In Chapter 2 the estimation of maternal effects for juvenile body weight (JBWT) data of two meat-type chicken populations was considered assuming unknown maternal performances. Standard analyses (Meyer,

1989) based on the (reduced) biometrical model of Willham (1963) were performed. Extension of these models with an environmental dam-offspring covariance was investigated. Furthermore, the goodness-of-fit of a model assuming a phenotypic maternal effect through regression on the dam's phenotype as proposed by Falconer (1965), and integrated Falconer-Willham models were investigated in a mixed model setting. The present sizeable data sets possibly increase the scope for these detailed genetic models to partition several highly correlated components.

Lande and Kirkpatrick (1990) advocated identification and inclusion of individual networks of maternal effects, rather than combining all non-Mendelian inheritance into a single maternal effect. Therefore, Chapter 3 presents the results of an experiment that was conducted in order to identify individually observed maternal pathways relating to the egg which might be responsible for the heterogeneous offspring-sire and offspring-dam regression estimates of JBWT. Additional direct selection for those traits with sufficient genetic variation could improve JBWT more effectively; and could prevent sometimes unfavourable genetic changes in response to selection for only JBWT.

Efficiency of broiler growth defined as a ratio

Food represents about 70% of the costs of broiler production (Pym, 1990). Therefore, efficient conversion of food into growth, often expressed as a ratio (food conversion ratio, FCR), is paramount from an economic point of view. The higher efficiency of birds selected for JBWT mainly originates from the decrease in energy needed for maintenance due to the shorter growing period (Hunton, 1990). Pym (1979; 1983; 1985) showed that substantial scope exists for improvement of FCR independent of JBWT, which prompted breeding companies to select for this trait directly. The feed efficiency can be defined in several different ways, but FCR is probably most commonly used. Although FCR is only a measure of gross efficiency (Pym, 1985), a breed's commercial efficiency is generally judged by this measure which makes it the efficiency trait of direct economic importance. Selection for a ratio might be sub-optimal. Linear selection for the component traits allows us to take into consideration their covariation resulting in extra accuracy, but increases genetic evaluations by one dimension (two components instead of a ratio). In Chapter 4 these two alternative selection methods were compared in predicted response considering both single- and two-step selection for JBWT and FCR. The effects of differences in heritabilities and/or correlations of the component traits were investigated. Genetic and phenotypic (co)variances of FCR with the other traits were approximated by statistical differentiation (Pearson, 1897), which makes the present study more straightforward in its approach than Gunsett's (1984) comparison of selection for ratio and linear index.

Reproductive ability of broiler parents

The downward trend in reproductive performance of broiler parents was initially compensated for by managemental changes in nutrition and lighting. However, as the industry progressed and competition intensified, most breeders began to develop specialised male and female lines (Hunton, 1990). The loss in reproductive performance could be (partially) counterbalanced by direct selection for those traits, although the scope was limited due to their sex-limited character and low heritabilities. Furthermore, selection was hampered by the non-normality of the egg production distributions (Clayton, 1975). Ibe and Hill (1988) and Besbes *et al.* (1993) suggested a power-transformation due to Box and Cox (1964). This transformation procedure substantially improved normality and linearity of heritability, which are prerequisites for the efficient use of selection index and BLUP methods. It was not clear, however, whether Box-Cox transformation was sufficient to bring us back on "usual grounds". Prior to analyses, Ibe and Hill (1988) made an arbitrary decision as regards the elimination of potential outliers, whereas Besbes *et al.* (1993) failed to report the statistical reasoning behind the identification and subsequent elimination of outliers. Chapter 5 considered identification of outliers more formally on the basis of outlier theory (Barnett and Lewis, 1994) and the hypothetical underlying genetic variability of egg production distributions. Further, Chapter 5 investigated whether elimination of outliers and data transformation were able to restore fully the usual assumptions by testing curvilinearity of heritability, which can be indicative of several potential problems in the data (Robertson, 1977).

The success of specialised female lines in providing sufficiently prolific broiler parents, yet with acceptable broiler characteristics very much depends on the genetic antagonism between those traits. Contemporary, population specific estimates of their genetic relationships are relevant for the optimal construction of selection indices or multivariate BLUP breeding values. Also, our understanding of changes in genetic correlations due to differences in environments (*eg.* restricted *versus ad libitum* feeding regimes) is of the utmost importance, as this can have direct bearing on (underlying) genetic trends of economic traits. Therefore, in Chapter 6 genetic relationships between reproduction traits and JBWT and among the reproduction traits were studied (with or without data transformation) for a modern meat-type female line, and were compared to earlier literature estimates.

Scope of this thesis

In summary the aim of this thesis was to investigate the quantitative genetic problems of both scientific and commercial interest characteristic of three economically highly important traits in broiler breeding (1) the estimation of maternal genetic and environmental effects in JBWT (Chapters 2 and 3), (2) selection for food conversion into growth defined as a ratio (Chapter 4); and (3) non-normality and curvilinearity of heritability of egg production distributions (Chapter 5) and the genetic relationships of those traits with JBWT (Chapter 6). All Chapters are preceded by a more detailed introduction specific to the respective topic.

CHAPTER 2

MODELS TO ESTIMATE MATERNAL EFFECTS ASSUMING UNKNOWN MATERNAL PERFORMANCES APPLIED TO JUVENILE BODY WEIGHT IN BROILER CHICKENS

INTRODUCTION

At present, estimation of maternal genetic variances in animal breeding is mainly based on the biometrical model suggested by Willham (1963). This model of maternal inheritance assumes a single (unobserved) maternal trait, inherited in a purely Mendelian fashion, producing a non-Mendelian effect on a separate trait in the offspring. For instance, the dam's milk production and mothering ability might exert a combined non-Mendelian influence on early growth rate of beef cattle (Meyer, 1992a). The practical application of such models has been greatly facilitated and hence encouraged by derivative-free IAM-REML programs of Meyer (1989), in which estimation of genetic maternal effects according to Willham (1963) forms a standard feature. Meyer (1989), however, uses a 'reduced' model by assuming absence of an environmental dam-offspring covariance, which is likely to improve the precision of the often highly confounded components to be estimated but which might at the same time lead to biased estimates of the correlation between the direct and the maternal genetic effects (r_{AM}) in particular (Koch *et al.*, 1972; Thompson, 1976; Meyer, 1992a,b). Often the types of covariances between relatives available in the data do not have sufficiently different expectations to allow all components of Willham's (1963) model to be estimated (Thompson, 1976; Meyer, 1992b). For a data set (of size 8 000) based on a genetic parameter structure typical to a growth trait in beef cattle, Meyer (1992b) found that the environmental dam-offspring covariance should amount to at least 30% of the permanent environmental variance due to the dam before a likelihood ratio test would be expected to distinguish it from zero. Greater data sets, however, including multiple generations of observations and a variety of types of covariances between relatives might provide sufficient contrast for the higher number of components in an extended model to be estimated more precisely.

Falconer (1965) considered the case where the phenotypic value of the mother for the character in question influenced the value of the offspring for the same character, which results in an environmentally caused dam-offspring resemblance. To account for this resemblance statistically, he included a partial regression coefficient in the model which related daughters' to mothers' phenotypic values in the absence of genetic variation among the mothers. The genetic basis of the maternal effect is ignored in such a model. Thompson (1976) investigated Falconer's (1965) approach, using maximum likelihood methods, as an alternative to Willham's (1963) model with low precision and high sampling covariances between some estimates.

Lande and Kirkpatrick (1990) showed that Willham's (1963) model fails to account for cycles of maternal effects as in Falconer's (1965) model. Robinson (1994) demonstrated by simulation that a negative dam-offspring covariance, as in Falconer's model with a maternal coefficient of -0.2, was fitted by Willham's model partially as a negative r_{AM} and as a permanent environmental effect using Meyer's IAM-REML programs. Consequently, she argued that maternal action according to these, Falconer-type, models might explain the often disputed negative r_{AM} estimates.

Because of these mutual limitations it might be interesting to integrate Falconer's and Willham's models in a mixed model setting to enable consideration of both the genetic basis of the maternal effect and the maternal action through regression on mother's phenotype (corrected for Best Linear Unbiased Estimator solutions of fixed effects).

A great amount of work has been carried out on the estimation of maternal effects among domestic livestock, in particular for mammals (for reviews see Willham, 1980; Mohiuddin, 1993). In poultry, however, where maternal (egg) effects on juvenile broiler body weight (JBWT) are apparent (Chambers, 1990), no major attempts have been made to partition this maternal variance into genetic and environmental components. Also the sign and magnitude of r_{AM} has not been estimated according to Willham's (1963) model. Many studies, however, have shown a positive (phenotypic) effect of egg weight on JBWT (Chambers, 1990). Poultry data may be suitable for the estimation of maternal genetic variances due to their size and structure with many offspring per dam and often many recorded generations available.

The objectives of the present study were to investigate 1) the effect of estimation of the environmental dam-offspring covariance on the other (co)variance components and resulting parameters (particularly r_{AM}) and on the likelihood of the sizeable data sets for JBWT in two meat-type chicken populations by IAM-REML methods and 2) the goodness-of-fit of Falconer-type and integrated Falconer-Willham models to simulated data and these JBWT data and the resulting estimated components and parameters.

MATERIAL AND METHODS

Data

Field data The data on JBWT originated from two commercial broiler populations. Summary statistics are illustrated in Table 2.1. The data on strain A and B represented approximately 6 and 3 overlapping generations, respectively. Male and female JBWT SDs were somewhat heterogeneous, presumably due to a scale effect. Some heterogeneity of raw CVs was apparent, but disappeared after correction for effects of hatch week and age of the dam. Some data structure aspects are shown in Table 2.2

Simulated data Data was simulated to study the goodness-of-fit of the various models to estimate maternal effects (see following) and the differences between simulated and estimated (co)variance components. The genetic model was similar to the one assumed by Robinson (1994), with a direct genetic effect, a maternal genetic effect and a temporary environmental effect, sampled from N(0,100), N(0,20) and N(0,280), respectively. Furthermore, a regression of -0.1 on the dam's phenotype was assumed. The base population consisted of 110 animals. Ten sires were mated to a hundred dams in a nested design with ten full sib offspring produced by each sire-dam combination. Parental candidates were randomly chosen from these thousand offspring to generate the next generation. This hierarchical mating scheme was repeated for eight generations.

Models of analyses

Effects of location Fixed effects fitted were hatch week (198 and 90 levels for strain A and B, respectively), sex (2 levels) and age of the dam when the egg was laid in 3-week intervals (7 levels) representing effects on eggs (*eg.* size).

Considering male and female JBWT as separate traits Table 2.1 gave some evidence that the differential SDs of both sexes are due to the dependence of variance and mean, since adjusted CVs were homogeneous. To fully justify evaluation of male and female JBWT as one trait in the analysis of maternal effects, however, the two sexes were considered as separate traits in a bivariate analysis in order to investigate the genetic relationship between these traits and hence the importance of segregation of sex-linked genes affecting JBWT in the present broiler populations. In matrix notation the bivariate model can be presented as:

$$\begin{bmatrix} \mathbf{y}_1 \\ \mathbf{y}_2 \end{bmatrix} = \begin{bmatrix} \mathbf{X}_1 & 0 \\ 0 & \mathbf{X}_2 \end{bmatrix} \begin{bmatrix} \mathbf{b}_1 \\ \mathbf{b}_2 \end{bmatrix} + \begin{bmatrix} \mathbf{Z}_{a1} & 0 & \mathbf{Z}_{p1} & 0 \\ 0 & \mathbf{Z}_{a2} & 0 & \mathbf{Z}_{p2} \end{bmatrix} \begin{bmatrix} \mathbf{a}_1 \\ \mathbf{a}_2 \\ \mathbf{p}_1 \\ \mathbf{p}_2 \end{bmatrix} + \begin{bmatrix} \mathbf{e}_1 \\ \mathbf{e}_2 \end{bmatrix} \qquad [2.1]$$

where, for trait i (i = 1,2 ; representing JBWT on males and females), $\mathbf{y}_i$ is a vector of observations; $\mathbf{b}_i$ is a vector of fixed effects; $\mathbf{a}_i$ is a vector with random additive genetic animal effects; $\mathbf{p}_i$ is a vector with random maternal permanent environmental effects; $\mathbf{e}_i$ is a vector with random residual effects; and $\mathbf{X}_i$, $\mathbf{Z}_{ai}$ and $\mathbf{Z}_{pi}$ are incidence matrices relating the observations to the respective fixed and random effects. The assumed variance-covariance structure is:

$$V\begin{bmatrix}\mathbf{u}\\ \mathbf{e}\end{bmatrix} \equiv V\left[\begin{array}{c}\mathbf{a}_1\\ \mathbf{a}_2\\ \mathbf{p}_1\\ \mathbf{p}_2\\ \hline \mathbf{e}_1\\ \mathbf{e}_2\end{array}\right] = \left[\begin{array}{cccc|cc} \mathbf{A}\sigma^2_{a1} & \mathbf{A}\sigma_{a12} & 0 & 0 & 0 & 0\\ \mathbf{A}\sigma_{a12} & \mathbf{A}\sigma^2_{a2} & 0 & 0 & 0 & 0\\ 0 & 0 & \mathbf{I}_1\sigma^2_{p1} & \mathbf{B}\sigma_{p12} & 0 & 0\\ 0 & 0 & \mathbf{B}\sigma_{p12} & \mathbf{I}_2\sigma^2_{p2} & 0 & 0\\ \hline 0 & 0 & 0 & 0 & \mathbf{I}_1\sigma^2_{e1} & 0\\ 0 & 0 & 0 & 0 & 0 & \mathbf{I}_2\sigma^2_{e2}\end{array}\right]$$

where σ^2_{ai}, σ^2_{pi} and σ^2_{ei} are the additive genetic, the maternal permanent environmental and the residual environmental variances for trait i; σ_{a12} and σ_{p12} are the corresponding covariances between the male and female JBWT; **A** is the relationship matrix; $\mathbf{I}_i$ is an identity matrix; and **B** is a rectangular incidence matrix linking male and female progeny records to the dam. The algorithm of Thompson *et al.* (1995) was used. Their method reduces the model to univariate forms by scaling and transformation, which diminishes dimensionality and speeds up convergence.

A 'reduced' Willham model Initially six different genetic models, optional in Meyer's (1989) programs, were considered for both strains. Table 2.3 exhibits the random effects fitted and the (co)variance components estimated in each model. Model 1 was a purely direct additive model, while model 2 (with sub-models a,b and c) allowed for dams' permanent environmental effects in addition. This environmental maternal component was slightly expanded by distinguishing between a covariance of maternal half sibs (model 2a) and full sibs (model 2b). Fitting both simultaneously was considered also (model 2c). Model 3 included a maternal genetic effect in addition to the animals' direct genetic effects, assuming zero direct-maternal covariance (σ_{AM}). Model 4 was as model 3 but allowed for a non-zero σ_{AM}. Models 5 and 6 (a, b and c) corresponded to models 3 and 4, respectively, but included maternal permanent environmental effects in addition (on maternal HSs and/or FSs). The sub-models (1 to 5) follow from the full mixed linear model (model 6), which in matrix notation is:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Z}_A\mathbf{u}_A + \mathbf{Z}_M\mathbf{u}_M + \mathbf{Z}_C\mathbf{c} + \mathbf{e} \qquad [2.2]$$

where **y**, **b**, $\mathbf{u}_A$, $\mathbf{u}_M$, **c** and **e** are vectors of observations, fixed effects, direct breeding values, maternal breeding values, random maternal permanent environmental effects, and random environmental residual effects, respectively; and **X**, $\mathbf{Z}_A$, $\mathbf{Z}_M$ and $\mathbf{Z}_C$ are incidence matrices relating the observations to the respective fixed and random effects. The variance-covariance structure is

$$\text{var}\begin{bmatrix} u_A \\ u_M \\ c \\ e \end{bmatrix} = \begin{bmatrix} \mathbf{A}\sigma_A^2 & \mathbf{A}\sigma_{AM} & 0 & 0 \\ \mathbf{A}\sigma_{AM} & \mathbf{A}\sigma_M^2 & 0 & 0 \\ 0 & 0 & \mathbf{I}\sigma_C^2 & 0 \\ 0 & 0 & 0 & \mathbf{I}\sigma_E^2 \end{bmatrix}$$

An 'extended' Willham model Throughout the previous models a zero direct-maternal environmental covariance (σ_{EC}) was assumed, which is commonly practiced. However, the possibility of a non-zero σ_{EC} is real. The existence of a negative σ_{EC}, for example, has been suggested (*eg.* Koch, 1972). Ignoring a (non-zero) σ_{EC} is likely to bias the parameters involved in the estimation of maternal effects. In particular σ_{AM} might be biased in a downward direction when ignoring a σ_{EC} that is negative. Therefore, σ_{EC} was included in all models in a second series of runs to study changes in estimated components and parameters and goodness-of-fit. The (co)variance structure now is

$$\text{var}\begin{bmatrix} u_A \\ u_M \\ c \\ e \end{bmatrix} = \begin{bmatrix} \mathbf{A}\sigma_A^2 & \mathbf{A}\sigma_{AM} & 0 & 0 \\ \mathbf{A}\sigma_{AM} & \mathbf{A}\sigma_M^2 & 0 & 0 \\ 0 & 0 & \mathbf{I}\sigma_C^2 & \mathbf{B}\sigma_{EC} \\ 0 & 0 & \mathbf{B}\sigma_{EC} & \mathbf{I}\sigma_E^2 \end{bmatrix}$$

Consequently, three maternal environmental covariances were conceivable, a covariance amongst maternal half sibs, a covariance amongst full sibs and a covariance between dam and offspring.

The (direct) Falconer model Falconer (1965) suggested that a model for the phenotype of an individual, y, might be expressed as

$$y = A + F_m y' + D + C + E \qquad [2.3]$$

where A is the individual's breeding value; $F_m y'$ is the maternal effect as linear function F_m of the mother's phenotype y' ; D is the individual's dominance deviation; C is the effect of environmental factors common to full sibs that are not included in the maternal effect; and E represents all other environmental effects. The coefficient

F_m is a partial regression coefficient relating daughters' to mothers' phenotypic values in the absence of genetic variation among the mothers. When D, C and E are ignored and mother's phenotype is represented by $y' = A' + F_m y''$, the expectation of the dam-offspring covariance is

$$
\begin{aligned}
\mathrm{cov}(y, y') &= \mathrm{cov}(A, y') + F_m \,\mathrm{var}(y') \\
&= \mathrm{cov}(A, A') + F_m \,\mathrm{cov}(A, y'') + F_m \sigma_P^2 \\
&= \tfrac{1}{2}\sigma_A^2 + F_m \,\mathrm{cov}(A, y'') + F_m \sigma_P^2
\end{aligned}
$$

where

$$
\begin{aligned}
F_m \,\mathrm{cov}(A, y'') &= F_m(\mathrm{cov}(A, A'') + F_m \,\mathrm{cov}(A, y''')) \\
&= F_m(\mathrm{cov}(A, A'') + F_m(\mathrm{cov}(A, A''') + \mathrm{cov}(A, y''''))) \\
&= F_m \,\mathrm{cov}(A, A'') + F_m^2 \,\mathrm{cov}(A, A''') + F_m^3 \,\mathrm{cov}(A, A'''') + \ \ldots \text{ etc.} \\
&= (\tfrac{1}{4}F_m + \tfrac{1}{8}F_m^2 + \tfrac{1}{16}F_m^3 + \ldots)\,\sigma_A^2
\end{aligned}
$$

which is a geometric series with common ratio ½ F_m that can be summed as $\frac{F_m}{2(2-F_m)}\sigma_A^2$ and hence $\mathrm{cov}(y, y') = \frac{1}{2}\sigma_A^2 + \frac{F_m}{2(2-F_m)}\sigma_A^2 + F_m\sigma_P^2$ (Falconer, 1965; Thompson, 1976). Table 2.4 exhibits the expectations for σ_P^2 and σ_A^2 in terms of F_m for the sources of (co)variation frequently used for animal breeding data making inferences about y rather than ($y - F_m y'$). The variance of y in model 2.3 (ignoring dominance) can be described as

$$\mathrm{var}(y) = \sigma_P^2 = \sigma_A^2 + 2F_m \,\mathrm{cov}(A, y') + F_m^2 \,\mathrm{var}(y') + \sigma_C^2 + \sigma_E^2$$

where

$$
\begin{aligned}
\mathrm{cov}(A, y') &= \mathrm{cov}(A, A') + F_m \,\mathrm{cov}(A, A'') + F_m^2 \,\mathrm{cov}(A, A''') + \ \ldots \text{ etc.} \\
&= (\tfrac{1}{2} + \tfrac{1}{4}F_m + \tfrac{1}{8}F_m^2 + \ \ldots \text{ etc.})\,\sigma_A^2 \\
&= \frac{1/2\sigma_A^2}{1 - F_m/2} = \frac{\sigma_A^2}{2 - F_m}
\end{aligned}
$$

and thus

$$\sigma_P^2 = \sigma_A^2 + \frac{2F_m}{2-F_m}\sigma_A^2 + F_m^2\sigma_P^2 + \sigma_C^2 + \sigma_E^2$$

$$(1 - F_m^2)\,\sigma_P^2 = \sigma_A^2 + \frac{2F_m}{2-F_m}\sigma_A^2 + \sigma_C^2 + \sigma_E^2$$

$$\sigma_P^2 = \left[\sigma_A^2 + \tfrac{2F_m}{2-F_m}\sigma_A^2 + \sigma_C^2 + \sigma_E^2\right] \;/\; (1 - F_m^2)$$

In a mixed model setting the Falconer model (ignoring the dominance component) can be formulated in matrix notation as

$$\mathbf{y} = \mathbf{Xb} + F_m(\mathbf{y}_P - \mathbf{X}_P\mathbf{b}) + \mathbf{Z}_A\mathbf{u}_A + \mathbf{Z}_C\mathbf{c} + \mathbf{e} \qquad [2.4]$$

where $\mathbf{y}_P$ is a vector with the dams' observations and $\mathbf{X}_P$ is the incidence matrix relating these observations to the respective fixed effects. Two complications may arise when considering estimation of the Falconer parameter (F_m): i) some (non-base) dams may have their records missing and ii) offspring of base animals with missing values have different variance. The first complication can be resolved by filling in the missing values prior to any REML analyses. Healy and Westmacott (1956) use an iterative approach in which they are initially setting the missing values to the grand mean whereafter the analysis is repeated with the estimate for each missing value adjusted each time to set its residual to zero. By insertion of a dummy factor in **X** for every dam with a missing record, the Falconer parameter estimate remains unaffected by these Ordinary Least Squares (OLS) expected values. The second complication is due to the offspring of base animals being uncorrected for $F_m(\mathbf{y}_P - \mathbf{X}_P\mathbf{b})$ since their dams' observations are unknown, which creates extra noise among these individuals. These animals' residual variances need to be scaled to produce constant variance across all individuals. The residual variance of those individuals is

$$\begin{aligned}
\sigma_{E*}^2 &= \sigma_P^2 - \sigma_A^2 - \sigma_C^2 \\
&= \left[\sigma_A^2 + \tfrac{2F_m}{2-F_m}\sigma_A^2 + \sigma_C^2 + \sigma_E^2 - (1 - F_m^2)\,\sigma_A^2 - (1 - F_m^2)\,\sigma_C^2\right] \;/\; (1 - F_m^2) \\
&= \left[F_m^2\sigma_A^2 + \tfrac{2F_m}{2-F_m}\sigma_A^2 + F_m^2\sigma_C^2 + \sigma_E^2\right] \;/\; (1 - F_m^2) \\
&= \left[\left\{ (F_m^2 + \tfrac{2F_m}{2-F_m})\tfrac{\sigma_A^2}{\sigma_E^2} + F_m^2\,\tfrac{\sigma_C^2}{\sigma_E^2} + 1\right\} \;/\; (1 - F_m^2)\right]\sigma_E^2
\end{aligned}$$

from which the scaling factor (s_F) emerges as a function of the variance components and the parameter F_m:

$$s_F = \left[(F_m^2 + \tfrac{2F_m}{2-F_m})\tfrac{\sigma_A^2}{\sigma_E^2} + F_m^2\,\tfrac{\sigma_C^2}{\sigma_E^2} + 1\right] \;/\; (1 - F_m^2) \qquad [2.5]$$

Without C in model 4 the term $F_m^2\sigma_C^2/\sigma_E^2$ cancels out.

An integrated Falconer-Willham model To account for possible maternal pathways through the dam's phenotype as well as the genetic origin of maternal effects an integrated approach was investigated. The matrix representation of the full linear integrated Falconer-Willham model that was considered is

$$\mathbf{y} = \mathbf{Xb} + \mathrm{F}_m(\mathbf{y}_P - \mathbf{X}_P\mathbf{b}) + \mathbf{Z}_A\mathbf{u}_A + \mathbf{Z}_M\mathbf{u}_M + \mathbf{Z}_C\mathbf{c} + \mathbf{e} \qquad [2.6]$$

which is model 2.2 and model 2.4 amalgamated. The variance of y amounts to

$$\sigma_P^2 = \sigma_A^2 + \sigma_M^2 + \sigma_{AM} + 2\mathrm{F}_m \operatorname{cov}(A, y') + 2\mathrm{F}_m \operatorname{cov}(M, y') + \mathrm{F}_m^2\sigma_P^2 + \sigma_C^2 + \sigma_E^2$$

where

$$\begin{aligned}
\operatorname{cov}(A, y') = {} & \operatorname{cov}(A, A') + \mathrm{F}_m \operatorname{cov}(A, A'') + \mathrm{F}_m^2 \operatorname{cov}(A, A''') + \;\ldots\ldots \text{ etc.} \\
& + \operatorname{cov}(A, M') + \mathrm{F}_m \operatorname{cov}(A, M'') + \mathrm{F}_m^2 \operatorname{cov}(A, M''') + \;\ldots\ldots \text{ etc.} \\
& = (\tfrac{1}{2} + \tfrac{1}{4}\mathrm{F}_m + \tfrac{1}{8}\mathrm{F}_m^2 + \;\ldots\ldots \text{ etc.})\,\sigma_A^2 \\
& + (\tfrac{1}{4} + \tfrac{1}{8}\mathrm{F}_m + \tfrac{1}{16}\mathrm{F}_m^2 + \;\ldots\ldots \text{ etc.})\,\sigma_{AM} \\
& = \frac{1/2\sigma_A^2 + 1/4\sigma_{AM}}{1 - \mathrm{F}_m/2} = \frac{2\sigma_A^2 + \sigma_{AM}}{2(2 - \mathrm{F}_m)}
\end{aligned}$$

and

$$\begin{aligned}
\operatorname{cov}(M, y') = {} & \operatorname{cov}(M, A') + \mathrm{F}_m \operatorname{cov}(M, A'') + \mathrm{F}_m^2 \operatorname{cov}(M, A''') + \;\ldots\ldots \text{ etc.} \\
& + \operatorname{cov}(M, M') + \mathrm{F}_m \operatorname{cov}(M, M'') + \mathrm{F}_m^2 \operatorname{cov}(M, M''') + \;\ldots\ldots \text{ etc.} \\
& = (1 + \tfrac{1}{2}\mathrm{F}_m + \tfrac{1}{4}\mathrm{F}_m^2 + \;\ldots\ldots \text{ etc.})\,\sigma_{AM} \\
& + (\tfrac{1}{2} + \tfrac{1}{4}\mathrm{F}_m + \tfrac{1}{8}\mathrm{F}_m^2 + \;\ldots\ldots \text{ etc.})\,\sigma_M^2 \\
& = \frac{\sigma_{AM} + 1/2\sigma_M^2}{1 - \mathrm{F}_m/2} = \frac{4\sigma_{AM} + 2\sigma_M^2}{2(2 - \mathrm{F}_m)}
\end{aligned}$$

and hence

$$\sigma_P^2 = \left[\sigma_A^2 + \sigma_M^2 + \sigma_{AM} + \left\{\frac{2\sigma_A^2 + 5\sigma_{AM} + 2\sigma_M^2}{2 - \mathrm{F}_m}\right\}\mathrm{F}_m + \sigma_C^2 + \sigma_E^2\right] / (1 - \mathrm{F}_m^2)$$

The factor (s_F) to scale the residual variances of the individuals with their dams' observations missing becomes

$$s_F = \left[\mathrm{F}_m^2\frac{\sigma_A^2}{\sigma_E^2} + \mathrm{F}_m^2\frac{\sigma_M^2}{\sigma_E^2} + \mathrm{F}_m^2\frac{\sigma_{AM}}{\sigma_E^2} + \left\{\frac{2\sigma_A^2 + 5\sigma_{AM} + 2\sigma_M^2}{2 - \mathrm{F}_m}\right\}\frac{\mathrm{F}_m}{\sigma_E^2} + \mathrm{F}_m^2\frac{\sigma_C^2}{\sigma_E^2} + 1\right] / (1 - \mathrm{F}_m^2) \qquad [2.7]$$

For models with a maternal effect the fraction of the selection differential that would be realised if selection were on phenotypic values (h_{A+M}^2), *i.e.* the regression of the sum of direct and maternal genotypes on the phenotype was calculated as (Willham, 1963):

$$h^2_{A+M} = (\sigma^2_A + 1.5\sigma_{AM} + 0.5\sigma^2_M) / \sigma^2_P$$

where σ^2_A is the direct additive genetic variance, σ^2_M is the maternal additive genetic variance and σ^2_P is the phenotypic variance.

Methods of analyses

Henderson-III and offspring-parent regression Henderson's Method III was applied to the data to produce estimates of variance due to sires (patHS) and sire-dam combinations (FS). A weighted average of the individual generation estimates was obtained by weighing them inversely proportional to their sampling variances. Covariances between offspring and sire and dam, respectively, were obtained by weighted regression analyses (with the degrees of freedom as weights) of average offspring on parental performances which were both deviated from OLS expectations based on the effects of location. The sources of (co)variation were equated to their expectations (Table 2.4) and the resulting system of linear equations was solved by multiple regression for a series of values for F_m, thereby locating the F_m that resulted in minimisation of the Mean Square Error or rather maximisation of the likelihood and the 'best' estimates for σ^2_P and σ^2_A and a residual component (σ^2_R).

IAM-REML IAM estimates of the (co)variance components for both data sets were obtained by a derivative-free REML algorithm based on programs written by Meyer (1989). The programs were adapted to include an environmental dam-offspring covariance component and to enable the estimation of Falconer's maternal phenotypic regression, either on its own or integrated in Willham's model. Equations in the mixed model matrix (MMM), the coefficient matrix and the RHS's augmented, were reordered using a multiple minimum degree reordering (George and Liu, 1980) to minimise fill-in, before Gaussian elimination was performed on MMM. The Downhill Simplex method was used to locate the maximum log-likelihood (log L). Convergence was assumed when the variance of the function values (-2log L) in the

Simplex was less than 10^{-8}. The Falconer parameter F_m maximising the likelihood was localised by quadratic approximation of the marginal log-likelihood surface of F_m. The first run was performed with a scaling factor (s_F) of unity since s_F is a function of the F_m and the (co)variances to be estimated. A second run was performed incorporating a scaling factor for the residual variances of animals with missing maternal observations as deduced from the estimated (co)variance components and F_m (see equations 2.5 and 2.7). In this second run the likelihood was remaximised and adjusted for the changes in the projected data and the variance component estimates.

Likelihood ratio tests, with error probability of 5%, were carried out to determine whether maternal genetic or permanent environmental effects contributed significantly to the phenotypic variance in JBWT for both strains. On the logarithmic scale, twice the difference between the log-likelihood of the null hypothesis and the log-likelihood of the alternative hypothesis approaches a χ^2 distribution with the number of degrees of freedom equal to the number of parameters tested.

Furthermore, the asymptotic sampling variances of σ_{AM} (models 6c and 12c) and σ_{EC} (model 12c) were obtained by fitting quadratic Taylor polynomials to their marginal log-likelihood profiles (Smith and Graser, 1986). The marginal likelihoods were $L_\eta(\sigma^2_{A\eta}, \sigma^2_{M\eta}, \sigma^2_{C\eta}, \sigma^2_{E\eta} \mid \sigma_{AM\eta}, y)$, $L_\eta(\sigma^2_{A\eta}, \sigma^2_{M\eta}, \sigma^2_{C\eta}, \sigma_{EC\eta}, \sigma^2_{E\eta} \mid \sigma_{AM\eta}, y)$ and $L_\eta(\sigma^2_{A\eta}, \sigma^2_{M\eta}, \sigma_{AM\eta}, \sigma^2_{C\eta}, \sigma^2_{E\eta} \mid \sigma_{EC\eta}, y)$ for σ_{AM} in the models 6 and 12 and for σ_{EC} in model 12, respectively, where η represents the fixed point for which the marginal log-likelihood was maximised.

RESULTS

Sex-linked variation in JBWT

Results of the bivariate analyses considering male and female JBWT as different traits are shown in Table 2.5. Differences in male and female phenotypic variances were substantial as might be expected because of the large differences in mean performances of both sexes (Table 2.1). Although not significant, the female heritabilities were somewhat greater than the male heritabilities. In birds the females are the heterogametic sex. Female offspring get their sex-linked genes only from their fathers. Therefore, if significant sex-linkage is present, higher male heritabilities might be anticipated which was not the case. Also, genetic relationships might be expected to deviate markedly from unity. However, the correlations were very high, although statistically just different from unity. We can now with more confidence say that sex-linked genes did not notably contribute to the differential variation of male and female JBWT in the present populations. Logarithmic transformation was considered to alleviate the variance-mean dependency. The comparison of genetic parameters of several models involving maternal effects did not reveal any important discrepancies between the data on the arithmetic and the geometric scales. Hence, analyses of the data on the arithmetic scale will be presented.

Conventional estimation of (co)variances, heritabilities and the Falconer parameter

Heritability estimates based on between sire variances (paternal HS) were equal for both populations (0.21) and very similar to the offspring-sire regression estimates (0.20 and 0.19 for populations A and B, respectively) (see Table 2.6). The heritability estimates based on FSs and offspring-dam regression were considerably higher. For population A the FS estimate was somewhat higher than the offspring-dam estimate, whereas population B showed the reverse. The components were equated to their expectations for several F_m values (Table 2.7). The 'optimum' F_m estimates were positive with 0.03 and 0.07 for populations A and B, respectively. The derived heritability estimates were 0.21 and 0.19 for populations A and B, respectively.

IAM-REML estimation of maternal genetic parameters

Simulated data The goodness-of-fit of Willham, Falconer and integrated models were tested to simulated data based on a genetic model assumed before by Robinson (1994). The results are shown in Table 2.8. The appropriate model to be fitted was an integrated Falconer-Willham model with a direct and maternal genetic effect with zero covariance and a maternal phenotypic effect (model 1 in Table 2.8). The likelihoods were deviated from this model. The estimated components were close to simulated components for model 1. Model 2, representing a Willham model with direct and maternal genetic effect with non-zero covariance and a maternal environmental component, estimated a c^2-effect of 0.03 and a significantly negative estimate for σ_{AM} resulting in a negative r_{AM} of -0.56 which was observed also by Robinson (1994). The likelihood ratio test adjudged the fit to be significantly worse than model 1 at a confidence level of 99%. The likelihood of the Falconer model, ignoring the genetic basis of the maternal effect, was greater than model 2 but significantly less than model 1 with $P < 0.05$. The 'full' Falconer-Willham model (model 4), assuming a non-zero σ_{AM}, appeared to fit better than the true model, although the difference was not significant at $P=0.05$. The 'extended' Willham model (model 5) 'picked up' most of the negative environmental covariance between dam and offspring as such. However, the effect was partially fitted as a negative σ_{AM} leading to an r_{AM} value of -0.22. The goodness-of-fit of model 5 was similar to the true model.

Field data Estimated phenotypic variances and genetic parameters for JBWT of both strains under a series of different genetic models together with their likelihoods are summarised in Tables 2.9 and 2.10. Clearly, very significant increases in log-likelihood (over model 1) demonstrate that both environmental and genetic maternal effects exist for both strains. Generally, genetic parameters were quite similar for both strains.

Fitting a maternal permanent environmental effect (with the pertaining variance component as proportion of σ_P^2 being referred to as c_{HS}^2 for maternal half sibs (HSs) and c_{FS}^2 for full sibs (FSs) in model 2 resulted in highly significant increases of the likelihood for both strains (251 and 170 over model 1 for model 2a in strain A and B, respectively). The h^2 estimates decreased to nearly 60% of their original values in model 1 for both strains and the c^2 estimates amounted to 5% and 4% for strains A and B, respectively. Estimating a c^2 for HSs and FSs simultaneously resulted in a significantly better fit with the effect of FSs being about a factor 2 greater.

The presence of a maternal heritability (m^2) in addition to h^2 (model 3) was much more likely than model 1, but fitted the data not as good as model 2. The m^2 estimate was higher for strain A (0.07) than for strain B (0.05). The fraction of the selection differential that would be realised, in direct plus maternal additive genetic merit, if selection were on phenotypic values (h^2_{A+M}) was, obviously, somewhat higher than the h^2 estimate in model 3 assuming a zero covariance between direct and maternal additive genetic variance. Allowing for a non-zero direct-maternal genetic covariance (presented as proportion of σ^2_P: c_{AM}) in model 4 just increased the likelihood significantly (over model 3) for strain A. The likelihood of model 4 for strain B was, however, not significantly different from model 3 based on a likelihood ratio test ($P > 0.05$). As a consequence, the associated direct-maternal genetic correlations (r_{AM}) were close to zero with -0.17 (strain A) and -0.11 (strain B) and, although h^2 estimates were somewhat higher, h^2_{A+M} estimates were essentially the same as in model 3.

In addition to model 3 the c^2 components were estimated in model 5. This model provided a further significant increase in log L compared to the previous models for both strains. Compared to model 3, m^2 estimates in model 5a decreased substantially for strain A (from 0.07 to 0.03) and for strain B (from 0.05 to 0.01); and thus the maternal variance seemed to be more of a (permanent) environmental than genetic origin. The overestimation of m^2, while assuming a zero c^2 (model 3), was observed in other studies also (*eg.* Meyer, 1992a). Both the estimates for h^2 and h^2_{A+M} were lower than in model 3. Estimating σ_{AM} in addition to model 5 (model 6) showed a similar pattern for both strains in terms of the reduction in m^2 compared to model 4. Most noticeable, however, was that this smaller m^2 parameter was accompanied by a much more negative c_{AM} and consequently r_{AM} relative to model 4.

Allowing for a non-zero σ_{AM} led to an increase in the h^2 estimates in model 6a of 6% for strain A and 5% for strain B relative to model 5a. However, the h^2_{A+M} estimates were lower, especially for strain A. As for model 2, the permanent environmental maternal effects for FSs in the models 5 and 6 were significantly greater than the effect for maternal HSs which is illustrated by the substantial increases in likelihood of sub-model c compared to sub-model a.

Models 7 to 12 were as models 1 to 6, but allowed for a non-zero direct-maternal environmental covariance (presented as proportion of σ^2_P: c_{EC}) in addition. Likelihoods increased considerably by adopting c_{EC}. All the c_{EC} estimates were positive and consequently the estimates of r_{AM} tended to be more negative and heritability estimates dropped somewhat. For the models 12a and 12c the m^2 estimate increased by a factor of 1.5 to 2 (from 0.04 (0.04) to 0.07 (0.06) in population A and from 0.03 (0.02) to 0.05 (0.04) in population B). Assuming a zero c_{AM} and a non-zero c_{EC} (model 11) fitted the data of population B better than the reverse assumption, a non-zero c_{AM} and a zero c_{EC} (model 6). This was not the case for population A. However, the highest likelihood for both populations was attained by assuming both these covariances to be non-zero (in model 12).

In addition to the effects fitted in the models 1 to 6 and as alternatives to the models 7 to 12, the models 13 to 18 considered the estimation of an environmental dam-offspring resemblance fitted as a regression on the dam's phenotype (Falconer parameter, F_m) in the mixed model. The models 13 and 14 are Falconer models, whereas the models 15 to 18 represent integrated Falconer-Willham models, considering both the m^2 effect and the F_m parameter. Except for model 1, all the F_m values were positive as were the c_{EC} estimates in models 7 to 12 shown before. The models without a c^2 effect (models 13, 15 and 16) fitted not as well as their counterparts fitting c_{EC} (models 7, 9 and 10, respectively). F_m estimates were generally smaller for population A and improvements in likelihood relative to the models 7 to 12 were greater than for population B. The F_m estimates for model 14b were identical to the estimates based on multiple regression of the analysis of variance components (Table 2.8). Generally, m^2 and c_{AM} estimates increased somewhat and led to more negative r_{AM} values compared to the models including c_{EC}.

Estimation of sampling variation of c_{AM} and c_{EC}

Approximate marginal likelihood profiles and (derived) sampling variances for c_{AM} (in models 6c and 12c) and c_{EC} (in model 12c) were investigated to get a better insight into the accuracy of c_{AM} in model 6c (assuming zero σ_{EC}) compared to the accuracy that could be attained when the potentially highly confounded components c_{AM} and c_{EC} (Meyer, 1992b) were estimated together (model 12c), using the present sizeable data sets.

Figure 2.1 depicts the quartic Taylor polynomial fitted to 7 points of the profile likelihood for c_{AM} (with R^2 = 100%). The resulting approximate marginal likelihood profile shows that c_{AM} is highly unlikely to be positive for both strains.

The approximate marginal likelihood profiles for c_{AM} and c_{EC} (both quartic as well with R^2 = 100%) in model 12c are shown in Figure 2.2a and 2.2b, respectively. Once again, profiles show a similar pattern for both strains and also the profiles for c_{AM} and c_{EC} act fairly similarly to the images (with opposite sign for the values) of c_{EC} and c_{AM}, respectively, which pointed towards the presence of a high negative sampling covariation between these components. The figures illustrate the low likelihood of a positive c_{AM} on the one hand and the very low likelihood of a negative c_{EC} on the other hand.

The sampling errors approximated from the above profile likelihood curves are exhibited in Table 2.11. Generally, the direct-maternal covariance components were accurately estimated for both strains, with the sampling error of c_{EC} being roughly twice as low as the approximation for c_{AM}. The accuracy of the c_{AM} estimates for models 6c and 12c were similar, hence the sampling correlation of c_{AM} with c_{EC} (in model 12c) did not hinder much the precise estimation of these components for the present data. Approximate sampling errors were also similar for both strains, which was illustrated by the similar curvatures of the marginal likelihoods for strains A and B.

DISCUSSION

Sex-linkage

The segregation of sex-linked genes affecting JBWT was found to be small which agrees with results summarised by Chambers (1990). Due to their hemizygous form these genes are likely to be driven towards fixation, especially in meat-type poultry with a long and extensive selection history for growth traits. The genetic correlation between male and female JBWT performance was just significantly different from unity, but this could easily be attributable to endocrine differences between both sexes.

Analysis of variance

The estimates of F_m, found while equating the (co)variance components to their expectations and minimising MSE, were small (0.03 and 0.07) and identical to the values found for its equivalent in a mixed model setting, model 14b. The conventional h^2 estimates were, however, substantially lower (0.21 *vs.* 0.32 and 0.19 *vs.* 0.24 for the populations A and B, respectively). The difference in estimates was larger for population A. The data on population A represented six generations (3 more than population B) and hence the numerator relationship matrix accounted for more selection in this longer time period.

Maternal effects estimation in a mixed model setting

It was shown that inclusion of a maternal permanent environmental effect provided a much better fit to the data (over model 1) and that inclusion of any more effects, although statistically significant, gave relatively a much smaller additional increase in log L (over model 2). This was reflected by the direct heritability estimates, which fluctuated within a rather narrow range for models 2 to 18 (except for model 13) compared to the heritability estimates for model 1. Consequently, the smaller additional increases in log L (over model 2) originated primarily from a 'reshuffle' of the maternal variance over environmental and genetic maternal (co)variances, although some cross-substitution of the direct additive genetic variance and hence the direct heritability with the direct-maternal genetic covariance, in particular, was likely to occur (Thompson, 1976; Meyer, 1992b).

REML combines information on various collateral relatives and various offspring-parent regressions in order to obtain one efficiently pooled estimate for h^2 with minimum variance (Thompson, 1977; Hill, 1988). The large reduction of the h^2 estimate in model 2 compared to model 1, accompanied by relatively small c^2 estimates, suggested a high weighting of the between dam family h^2 estimate, relative to the between sire family h^2 estimate. This might have been expected with such a large number of, on average, large dam families in the data (Table 2.2), leading to very accurate estimates on between dam family variance. A lower weighting of dam family information is expected for domesticated species in general and for beef cattle in particular, where dam families are much smaller (*eg.* Meyer, 1992a). The h^2 estimates in model 2 should in expectation be closer to the Henderson-III sire component h^2 estimates. Chambers (1990) pooled 53 sire component h^2 estimates from 23 studies resulting in an average value of 0.41. The present smaller h^2 estimates might be explained by the much longer and more extensive selection period the present broiler populations have undergone in comparison to the populations used in many experiments, bearing in mind that the far majority of these studies was conducted two to three decades ago. The smaller variance for strain B might, beside genetic strain differences, be due to the lesser extent of correction for reduction in variance caused by selection as only 3 generations were available for this strain compared to 6 generations for strain A. Furthermore, Chambers' (1990) summarised estimates were often based on weights at older ages (8, 9 or 10 weeks). It is not uncommon for heritabilities to increase with age of weight due to the diminishing maternal influences.

Allowing for σ_{AM}, resulted in a r_{AM} that was considerably negative in model 6. This was somewhat surprising since we expected a positive genetic correlation between JBWT and egg weight (Kinney, 1969; Chapter 6), which is believed to increase the offspring's JBWT. Fitting both σ_{AM} and σ_{EC} (model 12), to account for possible downward bias of σ_{AM} (Koch, 1972; Meyer, 1992a,b), resulted in slightly more negative r_{AM} estimates due to positive estimates of σ_{EC}. Cantet *et al.* (1988) also obtained large negative estimates of σ_{AM} accompanied by positive estimates of σ_{EC} for growth traits in beef cattle. However, Cantet *et al.* (1988) found negative estimates for F_m (in the range of -0.15 to -0.25), whereas our estimates of F_m were positive just like σ_{EC} estimates and led to even more negative r_{AM} estimates. Cantet *et al.* (1988) had a small data set and used conventional methods, equating separately estimated covariances between relatives to their expectations and solving the resulting system of linear equations. This ignores the fact that the same animal might have contributed to different types of covariances and that different observational components might have different sampling variances, *i.e.* combining information in a non-optimal way (Cantet *et al.*, 1988; Meyer, 1992b).

For our JBWT data, the genetic variance of maternal origin could, for the greater part, relate to egg (shell) quality rather than egg size, which could explain the negative sign of σ_{AM}. In Chapter 3, following suggestions by Lande and Kirkpatrick (1990), individual maternal pathways related to the egg were fitted as covariates in an offspring-parental regression model, to investigate their importance in causing maternal variation in JBWT. Those results implied a negative partial maternal effect of egg weight loss between the start and the 18th day of incubation, which would agree with Robinson *et al.* (1993) who reported a negative relationship between body weight and egg (shell) quality, an inferior quality giving rise to more loss of weight. However, this negative partial effect was offset by a positive partial maternal effect of egg weight at the 18th day of incubation, and hence the aggregate maternal effect on JBWT was found to be small (Chapter 3).

A negative σ_{AM} would decrease the efficiency of phenotypic selection for JBWT as expressed by the low h^2_{A+M} estimates for the models 12 and 18 with overall superior log L. Selection on maternal breeding values for JBWT may, however, not be very effective due to the small maternal heritability. Moreover, it might not be the preferable approach since egg (shell) quality characteristics can readily be selected for directly with higher accuracy and predictability (Chapter 3) and less delay, because the expression of the maternal effect, although occuring later in life, would not lag a generation behind the direct effect as is normally the case (Willham, 1980). Nevertheless, the presented amalgamation of Falconer and Willham models in a mixed model setting might offer attractive alternatives to Meyer's (1989) models for *eg.* beef cattle as was illustrated by results based on simulated data (Table 2.8).

Meyer (1992b) studied the sampling behaviour of REML estimates of (co)variance components due to additive genetic and environmental maternal effects. She showed that sampling correlations between estimates were high and that sizeable data sets are required to allow reasonably accurate estimates to be obtained. Results in the present study, using large data sets, illustrated the possibility of good sampling proporties for both the genetic and environmental direct-maternal covariance components. Hence, these poultry data sets might also increase the scope for the application of more detailed models, *eg.* estimating dominance variance and variance due to new mutation in addition to genetic and environmental maternal effects, yet providing sufficient contrast for the often highly correlated genetic parameters involved, to be estimated precisely.

The effect of more detailed fixed effect structures

Robinson (1994) showed that additional variation (*eg.* sire×year) unaccounted for in the model affected estimates of maternal effects. Differences in results from Mackinnon *et al.* (1991) and Meyer (1992a) for the same data suggested sensitivity of maternal effects to different fixed effects models. In our data different parental flocks of different ages and farms contributed offspring to the same hatch week. The age difference was accounted for in the model, but more specific maternal environmental flock effects were ignored. The parental flocks contributing to every hatch were identified. The effect of flock nested within hatch on the genetic parameters in models 1 and 2 was small (not presented). The effect on the genetic parameters for the more comprehensive models (5c, 6c, 11c, 12c, 17c and 18c) was investigated for both populations (see Table 2.12). The phenotypic and direct and maternal genetic variances were reduced considerably and were accompanied by r_{AM} estimates much closer to zero. The h^2 estimates were now very similar to the estimates of h^2_{A+M}. Such limited importance of maternal effects exerting a non-Mendelian influence on JBWT is in closer agreement with the results obtained in Chapter 3. The choice of the fixed effects model appears to be paramount for detailed maternal effects models, but the increase in computing time (four-fold increase per likelihood evaluation for the present data) might often restrain more refined fixed effect structures to be occupied.

SUMMARY AND CONCLUSIONS

The estimation of genetic and environmental maternal effects by restricted maximum likelihood was considered for juvenile body weight (JBWT) data on 139534 and 174668 broiler chickens of two populations. Of the biometrical models usually assumed in the estimation of maternal effects ('reduced Willham' models), a genetic model allowing for direct and maternal genetic effects with a covariance between them and a permanent environmental maternal effect provided the best fit. The maternal heritabilities (0.04 and 0.02) were low compared to the direct heritabilities (0.32 and 0.27), the direct-maternal genetic correlations (r_{AM}) were negative and identical for both strains (-0.54) and environmental maternal effects of full sibs (0.06 and 0.05) were about a factor two greater than of maternal half sibs (0.03 and 0.02). A possible environmental dam-offspring covariance was accounted for in the mixed model by 1) estimation of the covariance between the environmental maternal and the environmental residual effects (c_{EC}) and 2) a maternal phenotypic effect through regression on the mother's phenotype (F_m, 'Falconer' model). Whilst increasing the likelihoods considerably, these extended models resulted in somewhat more negative r_{AM} values due to positive estimates of c_{EC} (0.04 to 0.08 and 0.03 to 0.09) and F_m (0.03 to 0.17 and 0.07 to 0.20). A more detailed fixed effects model, accounting for environmental effects due to individual parental flocks, reduced estimates of r_{AM} (-0.18 to -0.33). Results suggested a limited importance of maternal genetic effects exerting a non-Mendelian influence on JBWT.

The present integrated 'Falconer-Willham' models allowing for both maternal genetic (co)variances and maternal action through regression on the mother's phenotype in a mixed model setting might offer attractive alternatives to the commonly used 'Willham' models for other domesticated species (*eg.* beef cattle) as was illustrated by their superior goodness-of-fit to simulated data.

TABLE 2.1

Summary statistics for juvenile body weight (kg/100) in two broiler populations with raw and corrected SDs and CVs.

strain	sex	# records	mean	$SD_{raw}{}^{\alpha}$	CV_{raw} (%)	$SD_{cor}{}^{\beta}$	CV_{cor} (%)
A	combined	139 534	224.9	29.9	13.3	19.6	8.7
	male	68 334	241.7	27.3	11.3	21.1	8.7
	female	71 200	208.8	22.6	10.8	17.9	8.6
B	combined	174 668	195.3	25.4	13.0	15.6	8.0
	male	85 325	211.4	21.8	10.3	16.9	8.0
	female	89 343	179.9	18.0	10.0	14.2	7.9

$^{\alpha}$: raw data

$^{\beta}$: data corrected for hatch and age of dam effects; combined data corrected for sex effect in addition

TABLE 2.2

Some structural aspects of the data for juvenile body weight in the two broiler populations.

	number of				
strain	records	animals	sires	dams	sire-dam combinations
A	139 534	140 983	856	5879	8337
B	174 668	177 294	698	5318	6819

TABLE 2.3

Fitted random effects and estimated (co)variance components in the six initial models of analysis[α].

model	Fitted[β]				Estimated[δ]					
No	a	m	c_{HS}	c_{FS}	σ^2_A	σ^2_M	σ_{AM}	$\sigma^2_{C_{HS}}$	$\sigma^2_{C_{FS}}$	σ^2_E
1	✓				✓					✓
2a	✓		✓		✓			✓	✓	✓
2b	✓			✓	✓				✓	✓
2c	✓		✓	✓	✓			✓	✓	✓
3	✓	✓			✓	✓				✓
4	✓	✓			✓	✓	✓			✓
5a	✓	✓	✓		✓	✓		✓	✓	✓
5b	✓	✓		✓	✓	✓			✓	✓
5c	✓	✓	✓	✓	✓	✓		✓	✓	✓
6a	✓	✓	✓		✓	✓	✓	✓	✓	✓
6b	✓	✓		✓	✓	✓	✓		✓	✓
6c	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓

[α] revised after Meyer (1989); [β] a : direct additive genetic effect; m : maternal additive genetic effect; c : maternal environmental effect on maternal half sibs (HS) and full sibs (FS); [δ] σ^2_A : direct additive genetic variance; σ^2_M : maternal additive genetic variance; σ_{AM} : direct-maternal genetic covariance; σ^2_C : maternal permanent environmental variance on maternal HSs and FSs; and σ^2_E : error variance

TABLE 2.4

Coefficients of covariances between some frequently used relatives and solutions for Falconer's (1965) model as derived by Thompson (1976).

source of (co)variation	σ^2_P	σ^2_A	$(F_m/2(2-F_m))\sigma^2_A$	σ^2_R
paternalHS	0	1/4	0	0
FS	F_m^2	1/2	4	1/4
withinFS	$1-F_m^2$	-1/2	-4	-1/4
Offspring-Dam	m	1/2	1	0
Offspring-Sire	0	1/2	1	0

TABLE 2.5

Bivariate IAM-REML phenotypic variance (in $kg^2 \times 10^{-4}$) and dispersion parameter estimates for male and female juvenile body weight considered as separate traits.

	strain A		strain B	
variance	male	female	male	female
phenotypic	475	342	296	204
sex				
male$^{\alpha}$	0.33±0.02		0.26±0.02	
female	0.95±0.01	0.36±0.02	0.92±0.03	0.30±0.02
male$^{\beta}$	0.03±0.01		0.03±0.01	
female	0.95±0.02	0.03±0.01	0.91±0.04	0.03±0.01

α : heritabilities with SE on the diagonal and genetic correlations with SE below the diagonal

β : maternal permanent environmental variances proportional to the phenotypic variances with SE on the diagonal and maternal permanent environmental correlations with SE below the diagonal

TABLE 2.6

Covariance component (in $kg^2 \times 10^{-4}$) and heritability estimates based on Henderson-III and offspring-parental regressions for both populations.

source of	strain A		strain B	
(co)variation	(co)variance	heritability	(co)variance	heritability
paternalHS	20.13	0.21	13.19	0.21
FS	57.30	0.30	34.37	0.28
withinFS	334.70		210.90	
Offspring-Dam	53.86	0.27	41.16	0.32
Offspring-Sire	41.12	0.20	24.22	0.19

TABLE 2.7

Estimated variance components (in $kg^2 \times 10^{-4}$) and resulting heritabilities for a series of values for the Falconer parameter (F_m) and their respective Mean Square Errors (MSE) with the 'optimum' results printed in bold-face for both populations.

F_m	strain A				strain B			
	σ^2_P	σ^2_A	h^2	MSE	σ^2_P	σ^2_A	h^2	MSE
-0.20	372	172	0.46	2302.0	231	114	0.49	1181.0
-0.10	386	133	0.34	766.0	241	89	0.37	472.2
0.00	392	93	0.24	46.4	245	64	0.26	76.2
0.03	**392**	**82**	**0.21**	**0.3**	246	57	0.23	23.5
0.05	392	74	0.19	13.1	246	52	0.21	5.5
0.07	391	67	0.17	60.3	**245**	**47**	**0.19**	**1.1**
0.08	390	63	0.16	96.6	245	45	0.18	4.0
0.10	389	56	0.14	194.2	244	40	0.16	19.7
0.20	378	23	0.06	1150.0	238	19	0.08	286.5

TABLE 2.8

Estimates[α] of dispersion components and natural log-likelihoods and their significance (P) relative to model 1 for Falconer, Willham and integrated Falconer-Willham models fitted to data simulated according to model 1 assuming a direct and maternal genetic effect with zero covariance and a regression on the dam's phenotype[β] (F_m = -0.1).

model[δ]	F_m	σ^2_A	σ^2_M	σ_{AM}	σ^2_C	σ_{EC}	σ^2_E	σ^2_P	log L	P
1 integr F-W	-0.11	100	16				290	406	0.00	
2 Willham		98	35	-33	11		295	406	-7.91	<0.01
3 Falconer	-0.12	106			8		291	405	-2.91	<0.05
4 integr F-W	-0.11	109	15	-11	4		290	407	1.68	>0.05
5 extend W		109	15	-9	6	-32	322	411	0.87	>0.05
input values	-0.10	100	20	0	0	0	280	400		

[α] results represent averages of 20 replications

[β] similar to the model assumed by Robinson (1994)

[δ] models are 1) integrated Falconer-Willham model with σ_{AM}=0, 2) Willham model, 3) Falconer model, 4) integrated Falconer-Willham model with $\sigma_{AM}\neq0$, and 5) extended Willham model with $\sigma_{EC}\neq0$

TABLE 2.9

Estimates of phenotypic variances, genetic parameters and the relative (natural) log-likelihoods[α] under models 1 to 18 for juvenile body weight on population A.

model	σ_P^2	h^2	m^2	c_{AM}	r_{AM}	c_{HS}^2	c_{FS}^2	c_{EC}	F_m	h_{A+M}^2	log L
1	451	0.50								0.50	0
2a	417	0.30				0.05	0.05			0.30	251
2b	421	0.33				0.00	0.05			0.33	298
2c	414	0.28				0.03	0.06			0.28	322
3	429	0.31	0.07							0.34	232
4	429	0.33	0.08	-0.03	-0.17					0.33	236
5a	416	0.27	0.03			0.04	0.04			0.29	286
5b	416	0.28	0.03			0.00	0.03			0.29	346
5c	413	0.26	0.02			0.02	0.04			0.27	352
6a	414	0.33	0.04	-0.06	-0.54	0.05	0.05			0.26	311
6b	416	0.33	0.05	-0.05	-0.38	0.00	0.04			0.28	361
6c	412	0.32	0.04	-0.06	-0.54	0.03	0.06			0.25	376
7	414	0.27				0.06	0.06	0.06		0.27	255
8a	414	0.27				0.06	0.06	0.04		0.27	260
8b	411	0.25				0.04	0.06	0.04		0.25	333
8c	411	0.25				0.04	0.07	0.04		0.25	333
9	413	0.24	0.03			0.04	0.04	0.04		0.26	301
10	409	0.29	0.06	-0.08	-0.64	0.06	0.06	0.06		0.20	341
11a	413	0.24	0.03			0.04	0.04	0.05		0.26	301
11b	411	0.24	0.02			0.03	0.05	0.03		0.25	363
11c	410	0.22	0.03			0.02	0.05	0.05		0.24	369
12a	409	0.29	0.07	-0.09	-0.64	0.06	0.06	0.08		0.19	343
12b	407	0.29	0.05	-0.07	-0.63	0.04	0.07	0.04		0.21	399
12c	407	0.27	0.06	-0.08	-0.64	0.04	0.07	0.08		0.18	409
13	440	0.50							-0.12	0.50	38
14a	418	0.28				0.06	0.06		0.05	0.28	279
14b	421	0.32				0.00	0.05		0.03	0.32	312
14c	418	0.26				0.04	0.07		0.08	0.26	362
15	434	0.26	0.09						0.07	0.31	265
16	432	0.31	0.21	-0.19	-0.72				0.17	0.13	307
17a	419	0.25	0.03			0.04	0.04		0.07	0.27	329
17b	419	0.25	0.04			0.00	0.04		0.06	0.27	383
17c	416	0.24	0.03			0.02	0.05		0.07	0.26	401
18a	416	0.32	0.08	-0.12	-0.75	0.05	0.05		0.13	0.18	379
18b	417	0.30	0.11	-[illegible]12	-0.65	0.00	0.04		0.13	0.18	426
18c	413	0.30	0.07	-0.11	-0.72	0.03	0.06		0.12	0.17	442

[α] σ_P^2: phenotypic variance in kg^2×10^{-4}; h^2: direct heritability; m^2: maternal heritability; c_{AM}: direct-maternal genetic covariance as proportion of σ_P^2; r_{AM}: direct-maternal genetic correlation; c^2: maternal environmental variance as proportion of σ_P^2; c_{EC}: direct-maternal environmental covariance as proportion of σ_P^2; F_m: Falconer parameter representing the regression on the dam's phenotype; h_{A+M}^2: regression of direct plus maternal genotypes on the phenotype and log L: natural log-likelihood deviated from model 1

TABLE 2.10

Estimates of genetic parameters and the relative (natural) log-likelihoods[α] under models 1 to 10 for juvenile body weight on population B.

model	σ^2_P	h^2	m^2	c_{AM}	r_{AM}	c^2_{HS}	c^2_{FS}	c_{EC}	F_m	h^2_{A+M}	log L
1	271	0.42								0.42	0
2a	255	0.24				0.04	0.04			0.24	170
2b	255	0.26				0.00	0.04			0.26	256
2c	253	0.23				0.02	0.05			0.23	265
3	261	0.27	0.05							0.29	135
4	261	0.28	0.05	-0.01	-0.11					0.29	136
5a	255	0.23	0.01			0.03	0.03			0.24	180
5b	254	0.23	0.02			0.00	0.03			0.24	270
5c	253	0.22	0.01			0.01	0.04			0.23	273
6a	255	0.28	0.03	-0.05	-0.54	0.04	0.04			0.24	197
6b	255	0.28	0.03	-0.03	-0.38	0.00	0.03			0.24	280
6c	254	0.27	0.02	-0.04	-0.54	0.02	0.05			0.22	288
7	253	0.21				0.05	0.05	0.05		0.23	191
8a	253	0.21				0.05	0.05	0.06		0.22	192
8b	252	0.21				0.03	0.05	0.03		0.21	280
8c	252	0.20				0.03	0.06	0.06		0.21	291
9	253	0.21	0.01			0.04	0.04	0.04		0.22	203
10	253	0.25	0.03	-0.06	-0.65	0.05	0.05	0.05		0.19	230
11a	253	0.19	0.02			0.04	0.04	0.07		0.22	209
11b	252	0.20	0.01			0.02	0.05	0.02		0.21	285
11c	252	0.18	0.02			0.02	0.05	0.07		0.21	304
12a	252	0.24	0.05	-0.07	-0.64	0.05	0.05	0.09		0.18	239
12b	252	0.25	0.03	-0.05	-0.66	0.03	0.06	0.03		0.19	309
12c	251	0.23	0.04	-0.06	-0.63	0.03	0.06	0.09		0.17	330
13	267	0.39							-0.09	0.39	21
14a	257	0.23				0.05	0.05		0.09	0.23	193
14b	257	0.24				0.00	0.04		0.07	0.24	275
14c	256	0.22				0.02	0.05		0.10	0.22	292
15	263	0.22	0.07						0.10	0.26	145
16	265	0.33	0.20	-0.21	-0.82				0.20	0.12	150
17a	258	0.21	0.02			0.04	0.04		0.11	0.22	206
17b	257	0.21	0.03			0.00	0.03		0.11	0.23	295
17c	256	0.20	0.02			0.01	0.04		0.11	0.21	303
18a	259	0.30	0.07	-0.12	-0.81	0.04	0.04		0.17	0.16	224
18b	259	0.29	0.10	-0.13	-0.78	0.00	0.03		0.18	0.15	300
18c	258	0.29	0.07	-0.12	-0.86	0.02	0.05		0.18	0.15	311

[α] see Table 2.9 for abbreviations

TABLE 2.11

Asymptotic sampling errors for the direct-maternal genetic covariance component (c_{AM}) (in models 6c and 12c) and for the direct-maternal environmental covariance component (c_{EC}) (in model 12c) both expressed as proportion of the phenotypic variance.

strain	model	c_{AM}	c_{EC}
A	6c	0.018	-
	12c	0.019	0.009
B	6c	0.016	-
	12c	0.018	0.008

TABLE 2.12

Estimates of genetic parameters and the relative (natural) log-likelihoods under the most comprehensive models using a more detailed fixed effect structure for juvenile body weight on both populations[α].

model	σ^2_P	h^2	m^2	c_{AM}	r_{AM}	c^2_{HS}	c^2_{FS}	c_{EC}	F_m	h^2_{A+M}	log L
Strain A											
5c	373	0.20	0.02			0.02	0.05			0.21	0
6c	373	0.20	0.02	0.00	0.04	0.02	0.05			0.21	0
11c	370	0.15	0.03			0.04	0.06	0.09		0.17	47
12c	369	0.15	0.04	-0.02	-0.21	0.04	0.07	0.10		0.14	49
17c	375	0.17	0.03			0.03	0.05		0.08	0.19	70
18c	378	0.17	0.04	-0.02	-0.18	0.03	0.06		0.14	0.16	98
Strain B											
5c	237	0.21	0.01			0.02	0.04			0.22	0
6c	237	0.22	0.01	-0.01	-0.17	0.02	0.04			0.21	1
11c	235	0.15	0.01			0.03	0.06	0.10		0.16	59
12c	235	0.16	0.02	-0.02	-0.39	0.04	0.06	0.11		0.14	64
17c	233	0.15	0.02			0.02	0.05		0.20	0.16	68
18c	233	0.17	0.03	-0.02	-0.33	0.02	0.05		0.18	0.16	76

[α] see Table 2.9 for abbreviations

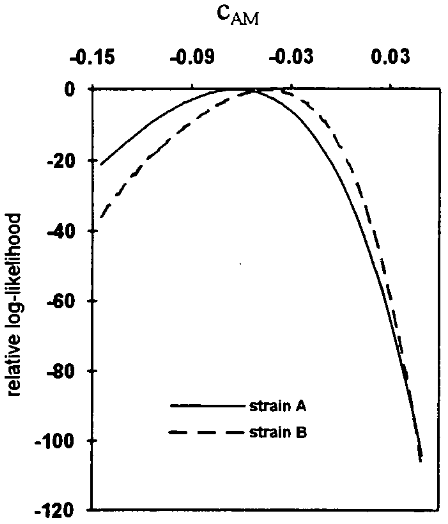


Fig. 2.1. The approximate marginal log-likelihood profile for the direct-maternal genetic covariance component expressed as proportion of the phenotypic variance (c_{AM}) in model 6c.

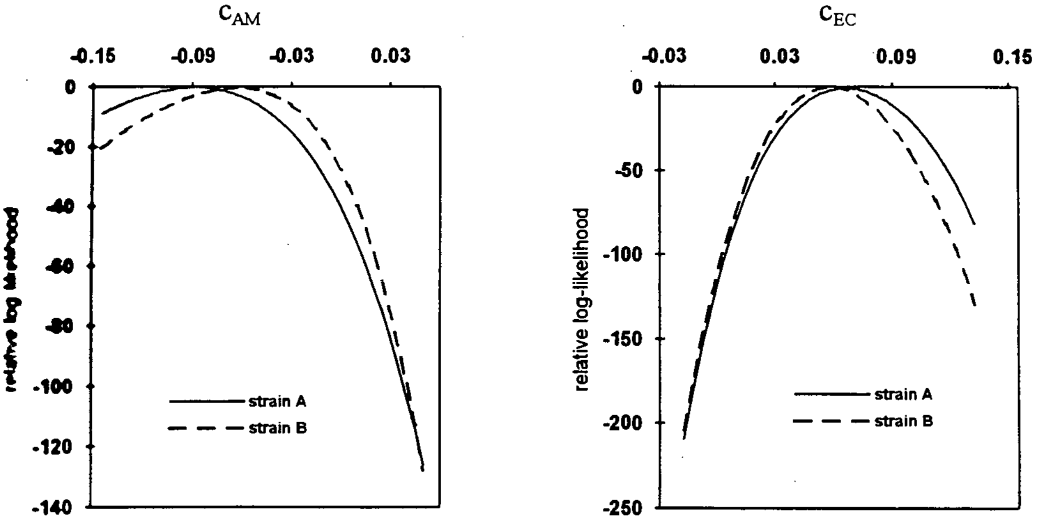


Fig. 2.2a and 2.2b. The approximate marginal log-likelihood profiles for the direct-maternal genetic covariance component (c_{AM}) and the direct-maternal environmental covariance component (c_{EC}) both expressed as proportion of the phenotypic variance in model 12c.

CHAPTER 3

A GENETIC ANALYSIS OF EGG QUALITY TRAITS AND THEIR MATERNAL INFLUENCE ON OFFSPRING-PARENTAL REGRESSIONS OF JUVENILE BODY WEIGHT PERFORMANCE IN BROILER CHICKENS

INTRODUCTION

Broiler production operations often make the assumption that 1 gram difference in egg weight (EWT) is reflected in about 10 grams difference in juvenile body weight (JBWT). This relationship was quantified by Goodwin (1961), and later confirmed by Al-Murrani (1978). The latter author identified it as a maternal effect which is only partially true. Due to the positive genetic correlation between JBWT and EWT (Kinney, 1969; Chapter 6), heavy eggs are likely to originate from dams with high JBWT. Obviously, a large portion of the offsprings' superior JBWT can be explained by their dams' high direct additive genetic merit for JBWT rather than their EWT. Consequently, Al-Murrani's (1978) estimate of the maternal effect of EWT on JBWT is much inflated.

This illustrates a general problem inherent in the estimation of maternal effects; the confounding of the maternal (indirect) effect with the contribution of the dam to the direct effect (Willham, 1980). Separation of the direct additive genetic component and the maternal genetic component of JBWT, assuming maternal performance to be unobserved (Willham, 1963; Meyer, 1989), was attempted in Chapter 2, using Restricted Maximum Likelihood (REML) methods applied to an Individual Animal Model (IAM). Significantly negative estimates were found for the genetic correlation between the direct additive and the maternal genetic effect ($r_{AM} \approx -0.6$), which was surprising since the maternal effect was expected *a priori* to represent EWT. The environmental covariance between offspring and dam, possibly biasing r_{AM} when non-zero and ignored (*eg.* Koch *et al.*, 1972), was fitted in the mixed model, but did not affect the value of r_{AM} much. It was argued, however, that the maternal genetic effect could, for a major part, relate to egg (shell) quality which would explain the negative sign of r_{AM}. Robinson *et al.* (1993) reported a negative relationship between body weight and egg (shell) quality and described the potential detrimental effects on the offspring. Nevertheless, the results in Chapter 2 add to the general scepticism with respect to the negative values of r_{AM} as frequently obtained in other species like beef cattle (Robinson, 1994).

Although these REML analyses on JBWT, presumably, give us an indication of the size of some intrinsic aggregate maternal genetic effect and its relation with the direct additive genetic component, they cannot identify specifically the maternal characteristics involved and their relative importance. Identification of such maternal traits affecting JBWT is important as additional direct selection for those traits with sufficient genetic variation could improve JBWT more effectively; and could sometimes prevent unfavourable genetic changes in response to selection for only JBWT. For instance, selection for JBWT may lead to deterioration in egg shell quality, *i.e.* eggs may be poorly calcified resulting in increased shell porosity and high weight loss during incubation, which can lead to increased embryonic mortality (Robinson *et al.*, 1993). In mammalian species in particular maternal performances are often difficult to measure, whereas maternal characteristics relating to egg quality in bird species are easily observable (for examples see below; and *eg.* Fairfull and Gowe, 1990).

Falconer (1965), studying maternal effects in litter size of mice, used the weight of the adult female as a measure of the maternal effect acting on that female through the litter size of her mother. He performed a bivariate regression analysis of daughter's litter size on mother's litter size and daughter's adult body weight. The partial regression coefficients allow a separation of the overall regression of daughters on dams into two parts, one associated with the daughter's weight and the other independent of the daughter's weight giving a more reliable estimate of the heritability. Although Falconer (1965) identified only one source of maternal variation, the method 'naturally' extends to partitioning of the overall regression of offspring on parent(s) into multiple partial maternal regressions in addition to the direct genetic transmission through both the sire and the dam (Lande and Kirkpatrick, 1990).

The objectives of this study were to investigate 1) the genetics of various egg quality characteristics of female line meat-type chickens and 2) the importance of those traits in exerting maternal influence on JBWT and their effect on (bias of) the offspring-parental regressions of JBWT.

MATERIALS AND METHODS

Data

The 6072 eggs of 221 pedigreed female line meat-type hens, descending from 39 different sires and 77 different dams, were used in this experiment. These females had undergone some selection for JBWT and egg production and were mated to 28 cockerels in a nested design. The following traits were measured on the eggs: width (WID), length (LEN), shape (SHA, defined as half the difference between WID and LEN), weight at set (EWT), specific gravity (SG, by the flotation method using seven salt solutions with SGs in the range 1.06 - 1.09 increasing in intervals of 0.005), weight at transfer from the setter to the hatcher at the 18th day of incubation (WTT), weight loss from set to transfer (WTL) and WTL as a percentage of EWT (WTL%). These traits were measured at 28, 29, 33, 34, 38 and 39 weeks of age and were recorded to individual egg within dam. The total number of eggs per hen ranged from 2 to 42 The eggs were set on a weekly basis and as a consequence the maximum age of the eggs was 7 days. The chicks were weighed to individual wingband at hatch (CHWT) and after growing to 6 weeks of age (JBWT). Every chick could be traced back to the egg it hatched from. Descriptive statistics of these traits are summarised in Table 3.1.

Estimation of genetic parameters for the maternal egg traits

Raw phenotypic correlations between dam averages of the same traits at different ages (28 *vs.* 38 and 29 *vs.* 39 weeks) were reasonably high, ranging from about 0.35 for SG to 0.55 for EWT and WTT. Also, from Fairfull and Gowe (1990) one can deduce that the genetic correlations between these traits at different ages are high. Therefore, it is probably justified to assume a repeatability model with a genetic correlation of unity between the same trait observed at these different ages. Estimation of the additive genetic, the permanent environmental and the temporary environmental residual variances was performed, using the derivative-free REML algorithm of Meyer (1989), applied to the following linear IAM with repeated records:

$$Y_{ijklm} = \mu + DAY_i + HATCH_j + AGE_k + a_l + p_l + e_{ijklm} \qquad [3.1]$$

where Y_{ijklm} is the phenotypic record on the m^th^ egg of animal l; μ is the grand mean; DAY_i is the fixed effect of the i^th^ day ($i = 1...7$), representing the effect of age of the egg in days on arrival at the hatchery; $HATCH_j$ is the fixed effect of the j^th^ hatch ($j = 1...3$), representing the effect of the hens' flock during the growing (1-6 weeks) and rearing (6-18 weeks) period; AGE_k is the fixed effect of the k^th^ age of the dam ($k = 1...6$); a_l is the random additive genetic effect of the l^th^ animal; p_l is the random permanent environmental effect of the l^th^ individual; and e_{ijklm} is the random temporary environmental residual effect associated with the egg record Y_{ijklm}. Three generations of pedigrees (the hens, their parents and grandparents) were included in the relationship matrix. The Downhill Simplex method was used to locate the maximum log-likelihood (log L). Analyses were considered converged when the variance of the function values (-2×log L) was less than 10^{-10}. Approximate sampling errors of the heritabilities were based on a Taylor series expansion about the maximum log L (Smith and Graser, 1986). Sampling errors of genetic and permanent environmental correlations were approximated according to Robertson (1959). However, the errors were shrunk when the 95% confidence interval exceeded the *a priori* known maximum range of -1 to 1, which occured for some permanent environmental correlation estimates. A series of bivariate analyses (28 combinations of the 8 traits) were performed with the univariate estimates as starting value. Average heritabilities and permanent environmental effects proportional to the phenotypic variance from the various bivariate runs were presented.

Regression on the maternal traits

Falconer (1965) suggested that a model for the phenotypic value of an individual, P, might be expressed as

$$P = A + mP' + D + C + E \qquad [3.2]$$

where A is the individual's breeding value; mP' is the maternal effect as linear function m of the mother's phenotype P'; D is the individual's dominance deviation; C is the effect of environmental factors common to full sibs that are not included in the maternal effect; and E represents all other environmental effects. This model was also considered by Thompson (1976) as an alternative model to the detailed biometrical model by Willham (1963). The coefficient m is a partial regression coefficient relating daughters' to mothers' phenotypic values in the absence of genetic variation among the mothers; and in Falconer's (1965) case represented the weight of the adult daughter acting on her own litter size through litter size of her mother. This method could be referred to as the direct method. The indirect method estimates the coefficient of the maternal effect (m) by means of the daughters' weights. The estimate for m is obtained by multiplying the regression of daughter's weight on the mother's litter size by the partial regression of daughter's litter size on daughter's weight (with mother's litter size constant, Falconer, 1965).

This indirect approach, which readily extends to multiple maternal effects, was used for our data with several potential candidates causing maternal variation in JBWT. The full model considered was

$$P_{offspring} = b_1P_{sire} + b_2P_{dam} + m_1P_{WID} + m_2P_{LEN} + m_3P_{EWT} + \\ m_4P_{SG} + m_5P_{WTT} + m_6P_{WTL\%} + C + E \qquad [3.3]$$

where $P_{offspring}$, P_{sire} and P_{dam} were the JBWT deviations from the Ordinary Least Squares (OLS) expectations based on fixed effect estimators of grand mean, hatch week, sex, and age of the dam when the egg was laid; P_{WID} and others were deviations from their OLS expectations based on the fixed effects in model 3.1; b_1 and b_2 were the partial regressions of offspring on sire and dam, respectively, representing the direct genetic transmissions through both sexes; and m_1 to m_6 were partial regressions on the maternal traits. Regressions on single parents, their average, and their interaction component to test for dominance in model 3.3, were considered in addition. The sire×dam interaction term was considered also in the polynomial approach to offspring-parent regression analysis by Gimelfarb and Willis (1994). The changes in offspring-sire and offspring-dam regression estimates due to the introduction of covariates on the maternal egg quality effects and a common environmental variance component in the model were studied. In order to describe the expectations of offspring-dam and offspring-sire covariances, we introduce a more general representation of the phenotype of an individual according to 3.3, its parents and the phenotype of the maternal traits, which are assumed to be purely direct additive genetic, ignoring the C and E terms.

$$
\begin{aligned}
Y_O &= A_{Y_O} + \mathbf{m}\,\mathbf{X}_P \\
Y_P &= A_{Y_P} + \mathbf{m}\,\mathbf{X}_{GP} \\
X_P &= A_{X_P}
\end{aligned}
$$

where Y_O and Y_P represent the offspring and parental phenotype, $\mathbf{X}_P$ and $\mathbf{X}_{GP}$ are scalars or vectors with single or multiple (grand)parental phenotypes of traits exerting maternal influence on trait Y and **m** is a scalar or a vector with the respective partial regressions of Y on X. The offspring-dam covariance is:

$$
\begin{aligned}
\mathrm{cov}(Y_O,Y_P) &= \mathrm{cov}(A_{Y_O},Y_P)+\mathbf{m}\,\mathbf{cov}(X_P,Y_P) \\
&= \mathrm{cov}(A_{Y_O},A_{Y_P})+\mathbf{m}\,\mathbf{cov}(A_{Y_O},X_{GP})+\mathbf{m}\sigma_{P_{XY}} \\
&= \tfrac{1}{2}\sigma^2_A + \mathbf{m}\,\tfrac{1}{4}\sigma_{A_{XY}} + \mathbf{m}\sigma_{P_{XY}} \qquad [3.4]
\end{aligned}
$$

where $\sigma_{A_{XY}}$ and $\sigma_{P_{XY}}$ are the genetic and phenotypic covariances of X with Y. The offspring-sire covariance is not affected by the term $\mathbf{m}\sigma_{P_{XY}}$, but is biased if the maternal characters are heritable as previously shown by Willham (1963), Eisen (1967) and Lande and Price (1989).

Prior to any multivariate regression analysis, however, ordinary regressions of JBWT on the individual maternal effects were performed to get an impression of the effect of each trait on JBWT, since the non-zero covariance structure among the multiple maternal traits makes interpretation of partial regressions more complex.

In the multivariate analyses SHA and WTL were not included as they were linear combinations of WID and LEN, and EWT and WTT, respectively. The importance of the maternal effects was tested (for CHWT and JBWT) by stepwise regression analysis minimising the Mean Square of the Error (MSE). Thereafter, REML (GENSTAT, 1993) was used to compare likelihoods of the various models and to allow for estimation of a second variance due to common environment of full sibs (C). With C in the model the significance of the maternal effects was tested by constraining them to zero one at a time and testing the changes in log L, of the resulting sub-model compared to the full model, for significance using the likelihood ratio test (Welham and Thompson, 1992). This procedure was also utilised to test the loss in likelihood for these data by considering a single maternal pathway, as Falconer (1965) did, rather than multiple maternal pathways.

In addition to these offspring-parent regression based models, analysis of variance (AOV) was performed (for both CHWT and JBWT) with sire and dam as random effects and the maternal traits as covariates using REML. AOV forms another useful way to study asymmetry of heritabilities based on sire and dam variances, especially when only one generation of data is available (as for CHWT). The expectation of the paternal half sib-covariance is $\frac{1}{4}\sigma^2_A$ and is thus not affected by maternal characters.

RESULTS

Estimation of genetic parameters for the maternal egg quality traits

Genetic parameters are presented in Table 3.2. Heritability (h^2) estimates generally had intermediate to high values (28 - 55%). Both genetic and phenotypic correlations between EWT and WTT, and between WTL and WTL% were close to unity. The genetic relationship of SG with WTL(%), both measures of the shell quality, was moderately negative.

The permanent environmental variances as percent of the phenotypic variances (p^2) had low to intermediate values (11 - 21%) and were often not significantly different from zero due to large sampling errors (see Table 3.3). Repeatabilities (h^2+p^2) were high, ranging from 44% for WTL to 70% for EWT.

Regression on sire, dam and the maternal traits

Simple regressions of CHWT and JBWT on the maternal traits are shown in Table 3.4. All the regressions, except on WTL, were significant ($P<0.001$) for CHWT and showed highly variable R^2 values (0.0% to 82.5%). An increase in SG and WTL% had a negative effect on the CHWT while increasing the others had a positive effect. The signs of the regressions were identical for JBWT, however, SHA, SG and WTL did not affect JBWT significantly. The R^2 values were low (0.0% to 2.3%).

A stepwise regression procedure of CHWT on the maternal traits, to pinpoint the effects that minimise MSE, retained (in order) WTT, SG, WTL% and WID in the model resulting in a coefficient of determination (R^2) of 85.7%. The univariate regression on WTT explained 82.5% of the variance in CHWT (Table 3.4). REML analysis of variance (AOV) was performed with these maternal effects as covariates in the model (see Table 3.5). WTT, WTL% and WID had a positive effect on CHWT, whereas SG had a negative effect. Although very significant on an ordinary basis, partial EWT was not significant at the 5% level. Introduction of the dam variance in model 2 (in Table 3.5) led to a large increase in likelihood. Further introduction of the sire variance did not significantly increase the likelihood as this variance component was not statistically different from zero. The heritability estimates of CHWT based on sire and dam variances were very close to zero and one, respectively. Incorporating dam's JBWT deviation in the model as covariate did not change the likelihood significantly; the partial regression estimate was effectively zero.

A similar stepwise regression procedure for JBWT on the maternal traits retained, in order of importance, WTT, EWT, WTL%, WID and LEN in the model. Results of regression analyses and AOV for JBWT, assuming a number of different models and using REML, are shown in Table 3.6. A straightforward regression of offspring on sire and dam showed these estimates to be different at the 5% level (see model 1 and 5 or model 13). Inclusion of the common environmental variance component (c^2) due to the dam increased the likelihood significantly in models 2, 6, 10 and 14. The regression estimate of the sire rose and the dam estimate dropped somewhat. Consequently, the estimate on the mid-parent remained unaltered. Introduction of the maternal effects in the models 11 and 15 further increased the likelihoods and the sire regression coefficient, resulting in a somewhat greater mid-parent regression estimate. For the models 3 and 7, including the maternal covariates instead of the c^2 effect reduced the relative likelihoods. The partial maternal regression coefficient was significantly negative for EWT and positive for the others. Inclusion of both the c^2 effect and the maternal effects (models 4, 8, 12 and 16) led to the highest relative likelihoods. Once again, the sire estimate increased and the dam estimate decreased, leading to similar estimates of 0.23 and 0.24, respectively, and a heritability coefficient of 0.47 based on the mid-parent. The effects of WTT, EWT and WTL% increased by taking account of the variance due to common environment, whereas the relevance of WID and LEN diminished. For the models 13 to 16 the sire×dam interaction term was tested and found insignificant ($P>0.30$).

Analysis of variance, with sire and dam as random effects (model 17), resulted in much lower heritabilities of 0.14 and 0.29 based on sire and dam components, respectively. Consideration of the maternal effects (model 18) increased the likelihood and changed the sire and dam heritability estimates to 0.16 and 0.27, respectively. The partial maternal regression coefficients were similar to the estimates for WTT, EWT and WTL% in the models 4, 8, 12 and 16 and somewhat smaller for WID and LEN.

Table 3.7 shows the significance of the maternal effects under various (regression or AOV) models with or without common environment taken into account. Changes in residual likelihood, the likelihood of the data after projection into the residual space, were considered and tested for significance by successively dropping the maternal effects from the full model. Model 15 could also be analysed directly by regression analysis as only one source of variation (the error) was present. Inclusion of the c^2 effect, in model 16, markedly increased the significance of WTT, EWT and WTL% to $P<0.01$ and made WID and LEN insignificant at the 1% and 5% level, respectively. For AOV (model 18) WID and LEN were insignificant at P=0.05. WTT, EWT and WTL% were paramount in determining maternal effect on JBWT.

The changes in the sire and dam regression estimates, the maternal regressions, the common environmental and residual variances and the likelihoods, by omitting subsequently all but one maternal pathways, were presented for the models 15 and 16 (see Table 3.6) in Table 3.8. The likelihood losses were significant in all cases. However, losses were restricted mostly with WTT or EWT in the model, which indicates that these are the most important univariate maternal pathways, ignoring any covariance structure. The fit of the model to the data was somewhat better including a regression on WTT rather than on EWT. The relevance of the remaining individual maternal effects, ignoring any covariances between them, decreased in the order of WID, LEN and WTL%, both with and without a c^2 effect in the model. The models with the best fit showed a smaller heterogeneity of sire and dam regression estimates, although differences were insignificant at P=0.05 in all cases, and smaller common environmental and residual variances. Note that these individual maternal regressions were similar to the ordinary regressions in Table 3.4. Accounting for the covariances amongst the maternal traits in the multivariate analyses (as in models 15 and 16 in Table 3.6) changed the sign of the regressions for EWT and WTL%, thereby increasing the monomial importance of WTL% as the character exerting maternal influence on JBWT.

Simple regressions of the maternal egg quality effects on maternal JBWT were performed (Table 3.9). These estimates allow us, after returning to the JBWT scale by multiplication with the partial regression coefficients of the offspring's JBWT on the respective maternal traits (Falconer, 1965), to determine both the partial and the summed effects of these traits on the total offspring-dam regression estimates and to compare the relative importance of the egg traits on an identical scale. These indirect partial regression estimates on the egg traits, describing the biological maternal effects, were presented for the models 8 and 16 in Table 3.10. WTT, EWT and WTL% (in model 8) had significant regression estimates only, which was largely in agreement with the tests in Table 3.7. WTT and EWT appeared to be most influential, a higher WTT increasing and a higher EWT decreasing the offspring's JBWT performance. The effect of WTL% reduced to zero in model 18. The aggregate maternal effect was positive (0.01) and explained the differences between the offspring-dam regression estimates in models 8 and 6 and 16 and 14, respectively.

DISCUSSION

The genetics of the egg quality traits

Selection on JBWT and egg production might have affected egg quality dispersion parameters somewhat. For instance, in Chapter 6 a heritability of 0.55 was estimated for EWT in a univariate REML analysis, which is similar to the present estimate of 0.52. Consideration of all the JBWT data in a bivariate analysis, however, increased the heritability to 0.64. Nevertheless, the present heritability estimates are generally substantial and the other traits are probably not as strongly correlated to JBWT as EWT (Kinney, 1969). The prolonged extensive selection might have driven gene frequencies in a particular direction, and thus making parameters unique to this individual population.

Discrepancies in heritability coefficients based on sire or dam regression or variance component estimates have frequently been observed. Often, these differences can be attributed to characters exerting maternal influence on the trait of direct interest (see *eg.* Lande and Kirkpatrick (1990) for references). As a consequence, the dam estimate, or both the sire and dam estimate, as well as their average may be biased (Willham, 1963; Falconer, 1965; Eisen, 1967; Lande and Price, 1989). In the present study, a number of maternal pathways relating to the egg, possibly exerting non-Mendelian influence on JBWT performance in the offspring, were evaluated for their relevance and their (aggregate) effect on the offspring-sire, the offspring-dam and their average regressions. It was shown that the existence of multi-dimensional antagonistic maternal pathways explained the significant difference between the ordinary offspring-sire and offspring-dam regression coefficients. The traits WTT and

EWT had large positive and negative partial maternal effects, respectively, on the offspring's JBWT. The WTL% of the egg had a smaller positive effect on the offspring's performance. The relative importances of these factors agreed with the analysis of principal components (GENSTAT, 1993), showing, after a factor rotation, that the original variability contained within all the maternal traits could largely be displayed in two linear combinations, the first consisting of mainly WTT and EWT explaining 95.8% of the variance and a second including WTL%, WTT and EWT accounting for a further 4.1% of the variance. Although the antagonistic partial effects of these traits on the dam regressions were appreciable (see Table 3.8), the aggregate bias was only small (0.01). The offspring-sire regression estimates were also affected by the covariates on the maternal phenotypes ($m\sigma_{P_{XY}}$) in the present data (with a summed effect of -0.02), which is not expected theoretically since the expectation of the offspring-sire covariance is $\frac{1}{4}\sigma_A^2 + \frac{1}{4}m\sigma_{A_{XY}}$ (compare model 3.4). However, the effect was not statistically significant and probably represented sampling. The term $\frac{1}{4}m\sigma_{A_{XY}}$ must on aggregate be very close to zero, and hence negligible, in this case because i) the partial regressions on WTT and EWT are of similar size with opposite sign, and ii) the genetic covariances of those traits with JBWT are similar due to their genetic correlation of 0.96 (see Table 3.2) and their similar variances. The effect on the mid-parent regression was minimal, changing from 0.46 to 0.47.

By testing the sire×dam interaction component, the importance of dominance variation in causing differential heritabilities was found to be negligible. Another possible cause of asymmetry is sex-linkage, which was ignored in the analyses performed here. The similarity of the sire and dam regression after accounting for maternal effects and common environment, however, suggests that sex-linked variation in JBWT is not of great importance, which is in agreement with Chapter 2 where similar heritabilities for male and female JBWT and genetic correlations close to unity (0.92 to 0.95) were found.

Analysis of variance resulted in similar maternal effect coefficients, but much lower heritability estimates that were still notably different for sire and dam (0.16 and 0.27, respectively) after accounting for these maternal traits. The much lower heritabilities were due to the parental variance component estimates being affected considerably by the selection of the parents for JBWT-index, whereas offspring-parent regressions are unaltered by such selection (Robertson, 1977). The remaining asymmetry of sire and dam heritabilities was caused by the common environmental variance component being confounded with the dam variance component resulting in an overestimation of the dam heritability. In the regression model, however, this common environmental variance component and the direct genetic transmission through the dam were separated. Analysis of variance on CHWT also showed substantial variation due to the dam, independent of the maternal traits included. The negligible variation among sires demonstrated that the direct heritability of CHWT is close to zero, and hence the dam variance component must have been of a maternal environmental or a maternal genetic rather than a direct genetic type. The majority of variation in CHWT was already accounted for by maternal variation in egg weight (see Table 3.4). The presence of a common maternal environmental component is easily comprehended when one considers the hatching environment, with full siblings sharing the same micro-environment of one hatching basket. Further evidence of the substantial effect of the (pre- and post-) hatching environment was provided by an insignificant partial regression ($P>0.90$) of JBWT on CHWT, which is perhaps surprising from a developmental viewpoint. Nevertheless, the maternal traits were affecting CHWT and JBWT in similar directions. However, in contrast with CHWT, the maternal variation in JBWT was only minor relative to the direct variation.

Scope for improvement of progress in traits of direct and maternal importance

In recent years an exhaustive amount of research effort has gone into the estimation of maternal effects for beef cattle in particular (see *eg.* Mohiuddin, 1993). The majority of these studies has been based on the models of Willham (1963), in which maternal performance is assumed to be unobserved. The application of such models has been greatly facilitated and hence encouraged by derivative-free REML programs of Meyer (1989), in which estimation of genetic maternal effects according to Willham (1963) forms a standard feature. There is an abundance of evidence, however, showing that separation of these highly confounded components is difficult without direct observation of the maternal traits (Eisen, 1967; Thompson, 1976; Willham, 1980; Meyer, 1992a,b). Although the simplification of Willham's (1963) model by assuming *a priori* a zero environmental dam-offspring covariance in Meyer's (1989) programs is likely to result in improvement of precision of the estimated components (Thompson, 1976), it may not always be warranted and can lead to biased estimates of the correlation between the direct and maternal genetic effect (r_{AM}) in particular (Koch *et al.* ,1972; Thompson, 1976; Meyer, 1992a,b). Also, Lande and Kirkpatrick (1990) showed that cycles of maternal effects as in Falconer's (1965) model cannot be accounted for by Willham's models. Maybe, a striking example of this was given by Robinson (1994), who demonstrated by simulation that a negative dam-offspring covariance, as in Falconer's (1965) model with a maternal coefficient (m) of -0.2, was fitted by Willham's model partially as a negative r_{AM} and as a permanent environmental maternal effect using Meyer's (1989) REML programs. Consequently, Robinson (1994) argued that maternal action according to these, Falconer-type, models might explain the often disputed negative r_{AM} estimates.

Instead, single or multiple observed maternal effects, like the egg quality traits in this study, can readily be accounted for using a Falconer-type model. Application of this model in IAM-REML programs is straightforward by fitting the (deviations of OLS expectations of) maternal observations as covariates and assuming, for instance, a direct additive genetic and a common permanent environmental variance component due to the dam. Inefficiencies in selection due to the presence of maternal variation in the direct trait of interest can thus largely be avoided, if the relevant maternal pathways have been identified and included. The identification and inclusion of individual networks of maternal effects, rather than combining all non-Mendelian inheritance into a single maternal effect, has been advocated before by Lande and Kirkpatrick (1990). For the present JBWT trait in broilers, however, the antagonistic effects of the maternal traits, largely offsetting each other and hence only biasing the heritabilities slightly, makes inclusion less urgent (the Pearson correlation coefficient of uncorrected and corrected JBWT deviations was 0.98).

The present maternal effects were very significantly heritable (see Table 3.2) and might be expected to have moderate to high correlations with JBWT. For instance, in Chapter 6 a genetic correlation of 0.63 between JBWT and EWT was found. In dam lines, in particular, the inevitable correlated responses to selection for JBWT are not always desirable and therefore specific selection pressure on the egg quality traits may be required. This can be established, as for any other trait of economic relevance, by including it in the selection index or BLUP analyses and selecting for the direct breeding value (often based on maternal performance) of the individual maternal egg quality effects. This enables precise prediction of the expected as well as estimation of the realised responses per individual trait, whereas the biological meaning of the response to selection for a single combined maternal breeding value can really only be speculated upon. Therefore, the maternal traits can have two explicitly different appearances, i) as nuisance parameter, *i.e.* a covariate to correct for maternal variation in a trait of direct interest (*eg.* JBWT), and ii) as another direct trait of economic interest (*eg.* EWT or WTL%) being part of a combined index to improve the aggregate genotype of female lines. Presumably, one might want to consider solely i) for male lines.

These procedures might, of course, have less scope for traits with crucial maternal effects being difficult and/or costly to measure. Dam's milk production, mothering ability and uterine environment (Meyer, 1992a), in mammalian species in general and beef cattle in particular, might be appropriate examples. When economic values of such traits are high, however, and genetic correlations with other traits of high economic interest are unfavourable, the measurement costs might be far outweighed by a higher economic output especially when genetic selection is centralised in small nucleus-type populations as opposed to large scale (national) selection programmes. More straightforward indirect Falconer-model analyses, like JBWT in broilers with only EWT as maternal component (see Table 3.8) or (birth) weights of beef calves with the dam's mature body weight as the maternal component or the sow's litter size with her mature body weight as the maternal component could also be of interest to breeders.

SUMMARY AND CONCLUSIONS

The maternal egg characteristics, length, width, weight at set (EWT), specific gravity (SG), weight at transfer (WTT) and weight loss from set to transfer (WTL) were measured for female line meat-type chickens to investigate 1) the genetics of these egg quality characteristics and 2) the effect of these maternal traits on (bias of) the offspring-parental regressions for JBWT performance and the significance of their regressions. Animal model REML heritability estimates of the egg traits had intermediate to high values, ranging from 28% for SG to 55% for WTT. Simple regression coefficients of offspring on sire and dam for JBWT were significantly different (0.20 and 0.26, respectively). Extension of this single regression model with covariates on all the maternal egg quality phenotypes as well as a second variance component due to common permanent environment of full siblings alleviated the asymmetry in offspring-sire and offspring-dam regressions (0.23 and 0.24, respectively). EWT and WTT had significant antagonistic partial effects on the dam regression (-0.06 and 0.07, respectively). The antagonistic effects of these maternal pathways largely offset each other, and hence biased the offspring-dam regression only slightly (0.01). The scope for application of these types of models, assuming observed maternal performances, in animal breeding to improve the progress in traits of direct and maternal importance was discussed.

TABLE 3.1

Descriptive statistics of the traits measured on the eggs originating from 221 hens (with units in parentheses), width (WID), length (LEN), shape (half the difference of LEN and WID, SHA), weight at set (EWT), specific gravity (SG), weight at transfer (WTT), weight loss from set to transfer (WTL), WTL as percentage of EWT (WTL%) and weights of the chick at hatch (CHWT) and at 6 weeks (JBWT).

trait	# records	mean	min	max	SD	CV (%)
WID (mm)	6072	43.1	38.0	48.0	1.38	3.21
LEN (mm)	6072	55.7	48.0	65.0	2.37	4.26
SHA	6072	6.3	3.0	12.0	1.12	17.82
EWT (g)	6072	58.3	42.0	76.6	4.91	8.43
SG	6040	5.7	1	8	1.14	19.77
WTT (g)	4353	51.7	30.0	70.4	4.62	8.95
WTL (g)	4348	6.5	1.6	25.1	1.41	21.82
WTL%	4348	11.2	3.2	45.4	2.44	21.83
CHWT (g)	3720	38.7	25.7	52.1	3.67	9.47
JBWT (kg/10)	2930	22.9	12.0	29.7	2.46	10.75

TABLE 3.2

Estimates of the heritabilities (on the diagonal ± SE), the phenotypic correlations (above the diagonal) and the genetic correlations (below the diagonal ± SE) in percent for the maternal egg quality traits.

	WID	LEN	SHA	EWT	SG	WTT	WTL	WTL%
WID	48 ± 14	15	-37	81	-11	72	11	-13
LEN	28 ± 20	38 ± 13	86	67	01	64	03	-17
SHA	-33 ± 20	81 ± 08	34 ± 11	23	06	23	-02	-09
EWT	83 ± 06	75 ± 09	24 ± 20	52 ± 14	-00	94	07	-23
SG	-15 ± 23	44 ± 20	47 ± 19	20 ± 21	28 ± 10	10	-39	-37
WTT	81 ± 07	73 ± 10	24 ± 20	96 ± 01	30 ± 20	55 ± 14	-27	-55
WTL	-06 ± 22	-01 ± 24	06 ± 24	-09 ± 21	-51 ± 19	-31 ± 19	32 ± 11	95
WTL%	-37 ± 19	-26 ± 22	-02 ± 23	-43 ± 17	-54 ± 17	-63 ± 12	93 ± 03	35 ± 11

see Table 3.1 for abbreviations

TABLE 3.3

Estimates of the permanent environmental variances as percentage of the phenotypic variances (on the diagonal ± SE) and the correlations in percent between these permanent environmental components (below the diagonal ± SE) for the maternal egg quality traits.

	WID	LEN	SHA	EWT	SG	WTT	WTL	WTL%
WID	16 ± 11							
LEN	17 ± 42	21 ± 11						
SHA	-30 ± 35	89 ± 06	21 ± 10					
EWT	88 ± 11	64 ± 18	20 ± 38	18 ± 12				
SG	-16 ± 37	-60 ± 20	-49 ± 24	-40 ± 30	21 ± 09			
WTT	74 ± 27	63 ± 19	23 ± 39	96 ± 05	-33 ± 34	13 ± 13		
WTL	78 ± 20	10 ± 43	-30 ± 35	57 ± 22	-37 ± 32	24 ± 38	12 ± 09	
WTL%	42 ± 29	-19 ± 41	-40 ± 30	12 ± 44	-22 ± 39	-22 ± 39	89 ± 11	11 ± 09

see Table 3.1 for abbreviations

TABLE 3.4

Univariate regressions and their SE, significance (P) and coefficient of determination (R^2 in %) of CHWT and JBWT on the maternal egg quality traits.

	CHWT			JBWT		
egg trait	b ± SE (/10)	P	R^2	b ± SE	P	R^2
WID	19.45 ± 0.35	<0.001	52.1	20.69 ± 2.81	<0.001	1.8
LEN	8.82 ± 0.22	<0.001	35.6	8.59 ± 1.54	<0.001	1.0
SHA	5.27 ± 0.51	<0.001	3.6	4.21 ± 2.92	0.150	0.0
EWT	7.29 ± 0.07	<0.001	80.7	7.08 ± 0.84	<0.001	2.3
SG	-4.42 ± 0.55	<0.001	2.1	-2.30 ± 3.15	0.465	0.0
WTT	7.52 ± 0.06	<0.001	82.5	7.16 ± 0.86	<0.001	2.3
WTL	0.89 ± 0.26	0.103	0.1	3.25 ± 3.11	0.296	0.0
WTL%	-5.61 ± 0.30	<0.001	11.0	-4.08 ± 1.78	0.022	0.1

see Table 3.1 for abbreviations

TABLE 3.5

Analysis of variance on CHWT with the maternal egg traits (and maternal JBWT, m_{DAM}) as covariates, with the respective log-likelihoods (log L) relative to model 1.

model	σ_{SIRE}^2	σ_{DAM}^2	$^*m_{WTT}$	m_{SG}	$m_{WTL\%}$	m_{WID}	m_{DAM}	σ_E^2	log L
1			7.55±0.10	-4.61±0.22	0.77±0.15	0.78±0.31		129.8±3.4	0
2		37.42±4.50	7.58±0.13	-4.33±0.25	0.87±0.18	0.72±0.35		94.5±2.6	278
3	2.33±2.23	35.31±4.51	7.57±0.13	-4.33±0.25	0.86±0.18	0.71±0.35		94.4±2.6	279
4	2.08±2.17	35.50±4.54	7.58±0.13	-4.33±0.25	0.87±0.18	0.70±0.35	-0.006±0.005	94.4±2.6	280

see Table 3.1 for abbreviations; $^*m_i$ is the partial regression on trait i

TABLE 3.6

Regression analyses (model 1-16) of offspring JBWT on parental JBWT and on the maternal egg traits, with or without common maternal environment (C) as second variance; and analysis of variance (AOV, model 17-18) on JBWT with sire and dam as random effects and the maternal egg traits as covariates, with their respective log-likelihoods (log L) relative to models 1 (for 1 to 4), 5 (for 5 to 8), 9 (for 9 to 12), 13 (for 13 to 16) and 17 (for 17 and 18).

regression	b_{SIRE}	b_{DAM}	b_{S+D}	m_{WTT}	m_{EWT}	$m_{WTL\%}$	m_{WID}	m_{LEN}	σ_C^2	σ_E^2	log L
model 1	0.20±0.03									28751±751	0
2	0.21±0.05								2796±474	25981±703	57
3	0.22±0.03			44.5±15.7	-38.1±14.2	23.4±9.1	16.1±7.5	5.38±3.46		27863±730	45
4	0.23±0.04			55.7±16.1	-46.6±14.6	29.3±9.4	15.9±7.7	4.15±3.65	2574±450	25369±688	96
5		0.26±0.03								28600±747	0
6		0.25±0.05							2632±457	25995±703	52
7		0.25±0.03		40.0±15.7	-36.0±14.2	21.1±9.1	19.3±7.6	7.16±3.47		27830±729	40
8		0.24±0.05		54.5±16.1	-46.4±14.6	28.4±9.4	16.8±7.7	4.77±3.65	2532±446	25387±688	88
9			0.46±0.04							28141±735	0
10			0.46±0.06						2160±408	26003±703	39
11			0.47±0.04	37.5±15.5	-33.4±14.1	19.1±9.1	19.3±7.5	6.75±3.43		27298±715	44
12			0.47±0.06	50.9±16.0	-43.4±14.5	26.2±9.3	17.4±7.7	5.00±3.61	1964±387	25400±688	78
13	0.20±0.03	0.26±0.03								28134±735	0
14	0.21±0.04	0.25±0.05							2165±409	26005±703	39
15	0.22±0.03	0.25±0.03		37.2±15.5	-33.2±14.1	18.9±9.1	19.5±7.5	6.88±3.43		27302±715	44
16	0.23±0.04	0.24±0.05		50.9±16.0	-43.4±14.5	26.2±9.4	17.4±7.7	5.02±3.61	1980±390	25401±688	77

AOV	σ_{SIRE}^2	σ_{DAM}^2	m_{WTT}	m_{EWT}	$m_{WTL\%}$	m_{WID}	m_{LEN}	σ_E^2	log L
model 17	1032±444	2138±431						25998±704	0
18	1114±467	1944±409	53.1±16.2	-43.7±14.7	27.5±9.5	14.4±7.7	2.72±3.63	25377±688	38

see Table 3.1 for abbreviations

TABLE 3.7

The change in likelihood (Δ log L) and its significance (P) based on the likelihood ratio test, constraining the maternal traits to zero one at a time.

maternal egg trait	model 15		model 16		model 18	
constrained to zero	Δ log L	P	Δ log L	P	Δ log L	P
WTT	-2.86	<0.05	-5.03	<0.01	-5.30	<0.01
EWT	-2.78	<0.05	-4.47	<0.01	-4.36	<0.01
WTL%	-2.17	<0.05	-3.90	<0.01	-4.15	<0.01
WID	-3.39	<0.01	-2.56	<0.05	-1.73	>0.05
LEN	-2.01	<0.05	-0.97	>0.05	-0.28	>0.05

see Table 3.1 for abbreviations

TABLE 3.8

Regression analyses of offspring JBWT on parental JBWT and on the individual maternal egg traits, with or without common maternal environment (C) as second variance with their respective log-likelihoods (log L) and their significance (P) relative to models 15 (for 15a to 15e) and 16 (for 16a to 16e) in Table 3.6 with all relevant maternal pathways included.

model	b_{SIRE}	b_{DAM}	m_{WTT}	m_{EWT}	$m_{WTL\%}$	m_{WID}	m_{LEN}	σ_C^2	σ_E^2	log L	P
15a	0.22±0.03	0.25±0.03	7.3±0.8						27426±717	-6	<0.05
15b	0.22±0.03	0.25±0.03		7.2±0.8					27407±717	-7	<0.01
15c	0.21±0.03	0.26±0.03			-4.8±1.7				28023±733	-40	<0.01
15d	0.21+0.03	0.25±0.03				21.3±2.8			27543±721	-14	<0.01
15e	0.21±0.03	0.26±0.03					8.7±1.5		27799±727	-28	<0.01
16a	0.22±0.04	0.25±0.05	8.2±1.0					1925±383	25558±691	-7	<0.01
16b	0.22±0.04	0.24±0.05		8.0±1.0				1897±380	25566±692	-9	<0.01
16c	0.21±0.04	0.25±0.05			-5.8±2.0			2157±409	25912±702	-34	<0.01
16d	0.22±0.04	0.25±0.05				23.2±3.3		1943±385	25644±694	-14	<0.01
16e	0.21±0.04	0.25±0.05					8.5±1.8	1957±388	25882±701	-28	<0.01

see Table 3.1 for abbreviations

TABLE 3.9

Univariate regressions and their SE ($\times 10^{-4}$) and significance (P) of the maternal egg quality traits on maternal JBWT.

maternal egg trait	$b_{DAM} \pm SE$	P
WID	2.13 ± 2.14	0.321
LEN	2.20 ± 3.91	0.574
EWT	14.19 ± 7.12	0.046
WTT	12.82 ± 6.98	0.066
WTL%	1.76 ± 3.42	0.607

see Table 3.1 for abbreviations

TABLE 3.10

The partial and aggregate (m_{TOT}) maternal effects of the egg characteristics acting on the progeny's JBWT through JBWT of their mothers and the resulting total regression of offspring on dam ($b_{TOT} = b_{dam} + m_{TOT}$) for the models 8 and 16.

model	m_{WTT}	m_{EWT}	$m_{WTL\%}$	m_{WID}	m_{LEN}	m_{TOT}	b_{TOT}
8	0.07±0.01	-0.07±0.01	0.01±0.00	0.00±0.00	0.00±0.00	0.01	0.25
16	0.07±0.01	-0.06±0.01	0.00±0.00	0.00±0.00	0.00±0.00	0.01	0.25

see Table 3.1 for abbreviations and Table 3.5 for b_{dam} estimates and other details on models

CHAPTER 4

PREDICTED REPONSE IN FOOD CONVERSION RATIO FOR GROWTH BY SELECTION ON THE RATIO OR ON LINEAR COMPONENT TRAITS, IN A (SEQUENTIAL) SELECTION PROGRAMME

INTRODUCTION

Conversion of consumed food into weight gain (FCR) is a trait of high economic importance. For this reason, numerous researchers have studied the implications of selection for a ratio trait in general and FCR in particular (*eg.* Turner, 1959; Sutherland, 1965; Pym and Nicholls, 1979; Lin, 1980; Gunsett, 1984; Essl, 1989). Linear approximations to avoid problems of selection for FCR appear to have risen in popularity since Lin's (1980) selection index approach. Often, however, linear approximations of a ratio of two component traits are applied without having knowledge of the (size of) ratio-related problems that might occur.

Anticipated problems with direct selection for a ratio are two-fold. (1) Traits are combined in a fixed nonlinear fashion, independent of the variance-covariance structure of the component traits. The ratio can be seen as a linear index of the logarithms of the component traits with fixed index coefficients of 1 for the numerator and -1 for the denominator. Implied relative economic values (Gibson and Kennedy, 1990) for the (logarithmic) component traits, and therefore selection responses, depend on their variance-covariance structure. (2) Nonlinear combination of two normally distributed traits results in deviation from normality. The size of this non-normality is dependent on the coefficients of variation of the component traits.

Quantification of these problems is important in deciding how to select for a ratio trait, because they might counterbalance the higher costs associated with dispersion parameter and breeding value estimation when using a linear combination of traits. For example, direct selection for FCR by Best Linear Unbiased Predicted (BLUP) breeding values requires univariate analysis, whereas indirect selection for a linear combination of component traits would require bivariate analysis (or alternatively, but less efficiently, two univariate analyses followed by the combination of information on single traits by means of selection index methodology) for food consumption (FC) and weight gain (WG).

Selection for ratio traits only in single step selection structures has been considered in the literature. In broilers, however, selection for FCR is typically performed after some selection for juvenile body weight (JBWT). This may complicate the quantification of ratio-related problems as JBWT is correlated to the ratio and its component traits. Furthermore, it also complicates (co)variance component estimation since selection on JBWT can not be ignored when bias on ratio (component) traits is to be prevented. Under such a sequential selection programme, unbiased covariance estimates between ratio component traits in particular, necessary when combining those traits in an index, are difficult to obtain. Once again, considering whether the extra effort in estimating dispersion parameters and breeding values outweighs the anticipated loss in selection response due to direct selection on the ratio seems to be appropriate.

The first objective of this study was to compare direct selection for a ratio with indirect selection for a linear combination of component traits for a (broiler) population under both single- and two-step selection for JBWT and FCR. For this purpose selection index methodology was used. Secondly, the effects of non-normality of FCR on (co)variance component estimation were investigated.

MATERIALS AND METHODS

The population

A population of 600 animals under sequential selection was assumed. The infinitesimal model was assumed, *i.e.* the limiting case of a genetic model with a very large number of unlinked loci, each having a very small additive effect on the traits of interest, *i.e.* JBWT, FC, WG and FCR. After selection for JBWT, 60 males and 120 females were retained for FCR-testing. From these individuals the best 3 males and 30 females were selected as parents based on direct or indirect phenotypic performance for FCR. As a comparison, a single-step selection programme was also studied, with all animals having observations on all traits.

Approaches to selection for FCR

Three approaches to selection for FCR were considered. They were all based on manipulation to linear selection for either the ratio trait or its components in order to use standard selection index theory (Hazel, 1943).

Lin's (1980) approach. By following the definition of genetic change in a ratio trait Lin (1980) derived the weighting factors for FC and WG to maximise genetic response in the ratio. The weighting factors for FC and WG proved to equal the population mean for WG and minus the population mean for FC. These weighting factors do not necessarily lead to maximisation of economic efficiency, for they are not the relative economic values of the traits, but rather to maximisation of the gross efficiency (*i.e.* minimisation of FCR) (Pym, 1985).

Turner's (1959) approach. Turner (1959) used the fact that a fraction can be linearised by taking its logarithm. For FCR this can be formulated as:

$$\log(\mathrm{FCR}) = \log(\mathrm{FC/WG}) = \log(\mathrm{FC}) - \log(\mathrm{WG})$$

A similar transformation was applied to product traits by Simm *et al.* (1987). The standard deviations of the transformed traits equal the coefficients of variation (CVs) of the untransformed traits if natural logarithms are used, which follows from first order statistical differentiation. The (co)variance components Turner (1959) derived for the ratio trait and its components using this linearisation were identical to the approximations given by Pearson (1897) (Sutherland, 1965). Assuming that the more cumbersome estimation of dispersion parameters and breeding values of component traits can be circumvented by direct selection for the ratio, the log transformation method was not further used.

Pearson's (1897) approach. Pearson (1897) derived a formula to approximate correlations between two ratio traits, say x_1/x_2 and x_3/x_4 with means μ_1 to μ_4. The formula follows from the first order Taylor's approximation

$$\text{cov}(x_1/x_2, x_3/x_4) \cong \frac{\mu_1\mu_2}{\mu_3\mu_4}\left(\frac{\text{cov}(x_1,x_2)}{\mu_1\mu_2} + \frac{\text{cov}(x_3,x_4)}{\mu_3\mu_4} - \frac{\text{cov}(x_1,x_4)}{\mu_1\mu_4} - \frac{\text{cov}(x_2,x_3)}{\mu_2\mu_3}\right)$$

This formula is a good approximation if CVs are small, is very flexible and can also be used for approximating genetic and phenotypic correlations between ratio component traits (*eg.* FC and WG), a ratio component trait and the ratio (*eg.* WG and FCR), ratio component trait and another trait (*eg.* FC and JBWT) or the ratio and another trait (*eg.* FCR and JBWT). Selection can now be performed on FCR treated as a linear trait and correlated responses in component traits can be predicted either assuming FCR or component traits FC and WG (with weighting factors according to Lin (1980)) to form the aggregate genotype.

Studied selection indexes and aggregate genotypes

Response in the component traits can readily be compared using selection index theory when only FCR (or a linear function thereof) is in the selection index and aggregate genotype. In a sequential selection programme, however, JBWT is part of the selection index and/or the aggregate genotype. Table 4.1 shows the combinations of selection indexes and aggregate genotypes studied. The same combinations were investigated for 1-step and 2-step selection. Selection in the first step of the sequential structure was always for JBWT, whereas selection in the second step (and the only step in the 1-step alternative) was for one of these indexes. The combinations of selection indexes and aggregate genotypes can be partitioned into three stages when based on the use of Lin's (1980) or Pearson's (1897) methods. These stages, with the first stage containing component traits in both the aggregate genotype and the index, represent the possible increase in loss of genetic response due to using FCR as a linear trait, firstly only in the index (stage 2) and thereafter both in the index and aggregate genotype (stage 3). It is the latter stage that is of main interest because of the possible savings in estimation of (co)variance components and breeding values, particularly for the sequential selection structure.

Defining the relative weighting factor for JBWT

Addition of JBWT to the aggregate genotype depends on its economic weight relative to FCR or components. To do this the specific sequential structure of the breeding programme (60/120, 60 males and 120 females retained after the first selection step) was utilised and assumed implicitly to maximise response in the aggregate genotype. Weighting factors for the ratio trait components were assigned according to Lin (1980) and were kept constant. The weighting factor for FCR as a linear trait was put to -1 since only proportionality matters. Over a range of relative weighting factors for JBWT, response in the aggregate genotypes, comprising either JBWT, FC and WG or JBWT and FCR, was investigated for the current breeding programme (60/120) as well as for structures with more selection pressure on JBWT (50/100) or more selection pressure on FCR or its components (70/140). The assumed optimum weighting factor for JBWT was chosen on the basis of the maximum conditional sum of ($\Delta H_{60/120}$ - $\Delta H_{50/100}$) and ($\Delta H_{60/120}$ - $\Delta H_{70/140}$), the conditions being both ($\Delta H_{60/120} > \Delta H_{50/100}$) and ($\Delta H_{60/120} > \Delta H_{70/140}$) in order to satisfy the implicit assumption of maximisation of ΔH under the present sequential structure (60/120) where ΔH is the change in the aggregate genotype due to direct and correlated responses of the contributing traits.

Genetic parameters

Genetic parameter values (see Table 4.2) were based largely on Pym's selection experiment (Pym and Nicholls, 1979; Pym, 1983). Heritabilities of the ratio component traits WG and FC were similar. A second and third set of parameters were used to investigate whether or not the presumed superiority of selection for components over direct selection on the ratio when heritabilities of the component traits are different (Gunsett, 1984) holds under the present sequential selection programme. In these cases, genetic and phenotypic correlations were identical to alternative 1, whereas heritabilities of WG and FC were assumed to be 0.5 and 0.2 respectively for alternative 2 and *vice versa* for alternative 3.

The sensitivity of differences in response between direct selection for the ratio and indirect selection for its components to differences between the genetic and environmental correlation was investigated by successively changing the environmental correlation to 0.25, 0.0 and -0.5, while holding the other parameters at their base values. Typically, the information given by the second trait depends on the difference between the phenotypic and genetic regressions of one trait on the other and thus, if assuming equal heritabilities, on the difference in correlations rather than on the absolute values (Sales and Hill, 1976).

Asymptotic responses

Genetic parameters and expected responses to selection are reduced as a consequence of gametic phase disequilibrium, induced by selection, until an equilibrium is approached after a few generations (Bulmer, 1971). Comparisons among different selection strategies should therefore be made by using asymptotic rather than single generation responses. Wray and Hill (1989) presented selection index methodology based algorithms to predict asymptotic response rates using a BLUP animal model and Villanueva *et al.* (1993) focused on the prediction of asymptotic rates of response from selection on multiple traits. These methods were used to predict asymptotic responses for multivariate (sequential) phenotypic selection on JBWT and FCR or its components.

Non-normality of FCR

The extent and effects of skewness and kurtosis of the distribution of phenotypic FCR and of (natural) logarithm transformed FCR were studied by Monte Carlo simulation of 50 data sets of 20,000 randomly drawn phenotypes for FCR assuming a range of coefficients of variation of the normally distributed component traits FC and WG. Consequences for estimation of (co)variance components were studied by comparing estimates for FCR and transformed FCR. For this purpose a multivariate method based on the derivative-free REML algorithm, which assumes normality of the data in the calculation of the likelihood, was used (Thompson and Hill, 1990).

RESULTS

Relative weighting factors for JBWT

Derived relative weighting factors for JBWT with FC and WG in the aggregate genotype were 0.46, 0.40 and 1.18 for intermediate, high and low heritability for FC, respectively. These values were 1.10, 0.96 and 2.55, respectively, with FCR in the aggregate genotype. The weighting factor for JBWT dropped somewhat going from intermediate to high heritability for FC. The same response for JBWT was achieved in the first step but less in the second step because of the higher (negative) response in FC, which is positively correlated with JBWT. Therefore, the importance of JBWT is somewhat lower under the presently assumed sequential selection scheme (60/120). Response in JBWT was, however, high in both the first and the second step and its weighting factor increased substantially when the heritability for WG was high. Subsequently, standard selection index theory was applied to aggregate genotypes consisting of FC, WG and JBWT or FCR and JBWT.

Varying the heritabilities of the ratio component traits

Selection index results for various alternatives both under 1-step and 2-step selection are shown in Table 4.3. Alternatives were partitioned into two components; the first representing the addition of JBWT to the index (i-) or both the index and aggregate genotype (ia) and the second representing the transition in selection on the ratio components FC and WG (--) to selection on FCR directly (ia). The alternatives JBWT--/FCRia and JBWTi-/FCRia were identical to JBWT--/FCRi- and JBWTi-/FCRi-, respectively. Response in the aggregate genotype (H) was expressed in terms of FC and WG (as well as JBWT if part of H).

Adding JBWT to the index (alternative -- to i-) generally had very little effect, although under alternative FCRi- (FC and WG in the aggregate genotype and FCR in the index) it added somewhat more information than under alternative FCR-- (FC and

WG both in the aggregate genotype and index). JBWT compensated for some loss in information due to selection for FCR.

Differences in response in H between selection for FC and WG or FCR (going from alternative FCR-- to FCRi- to FCRia) were negligible when heritabilities for component traits were similar, whereas responses in the components were different. These results were in agreement with Gunsett (1984). Differences between direct selection for FCR and the linear combination of component traits appeared when heritabilities differed. The reduction in response was greater when FC had a high heritability than when WG had a high heritability as a result of a much higher correlation between FCR and WG than between FCR and FC (based on statistical differentiation as in Pearson's (1897) formulae). Loss of response in H due to direct selection for FCR was reduced when JBWT was part of H, and the relative importance of FCR (and components) then decreased.

Relative responses in H were similar for 1-step and 2-step selection. The actual responses were higher in 1-step selection as all information on FC and WG, and thus on FCR, was available. When the heritability for FC was high and JBWT was not part of H, JBWT decreased in the first selection step (not presented).

The aggregate genotype H linearly approximates the genetic value of FCR. Differences between rH and rFCR for alternatives JBWT-- and JBWTi- are likely to be due to a mere arithmetic phenomenon that reducing the numerator by x% is more effective in reducing a ratio than increasing the denominator by an identical percentage. The linear approximation H does not account for this property that is inherent to selection for a reduced ratio. This is, for example, illustrated by alternative JBWT--/FCR-- under intermediate and high heritability for FC. With a heritability of 0.5 response in H was lower whereas FCR was higher (5.240 and 0.131, respectively) compared to a heritability of 0.3 (5.496 and 0.127, respectively).

Relative asymptotic responses were similar to relative first generation responses and thus were not presented. The unchanged ranking of various selection strategies was observed also by Wray and Hill (1989) and shown by Dekkers (1992). The absolute asymptotic response rates were, however, significantly lower (approximately 27%) as the high selection intensities induced considerable gametic phase disequilibrium.

The effect of the difference between genetic and environmental correlations

Table 4.4 shows 2-step selection responses for various indexes based on the ratio or its components with or without JBWT in index and H under small and large differences between the genetic and environmental correlation. The loss of information under direct selection for the ratio is negligible when the genetic and environmental correlation are somewhat different. Considerably lower responses are expected when these correlations are wide apart.

Non-normality of FCR

Monte Carlo simulation results of variable CVs for FC and WG are given in Table 4.5. It can clearly be seen that deviation from normality is reduced when the CVs of the components are closer to each other and smaller. The (natural) logarithm transformed FCR is more nearly normal. Of main interest were the consequences of non-normality for the estimation of (co)variance components on FCR and related traits (JBWT, FC and WG). Simulated data were based on random mating without missing values, CVs for FC and WG were 8.66% and 13.15% respectively, and heritabilities were 0.3 for all traits. The expected skewness and kurtosis for FCR in these data were 0.690 and 1.152, respectively (see Table 4.5). Logarithm transformed FCR, which was much closer to normality, was also evaluated to check robustness of REML for deviations from normality. All parameter estimates (Table 4.6) for FCR and logarithm transformed FCR were very similar. REML appears to be robust for non-normalities of this kind. Furthermore, the effect of ignoring higher moments in the formulae of Pearson (1897) could be tested empirically. Table 4.6 shows that results are generally very close to REML estimates, which illustrates the minor significance of the higher moments in this situation.

DISCUSSION

It was shown that, in some cases, selection for a linear representation of FCR, with weights for FC and WG based on statistical differentiation (as in Lin, 1980), can lead to additional progress in FCR. However, it is not these weights as such that result in this extra response, but rather the linear independent form of FC and WG, which allows us to take into consideration their covariation resulting in extra accuracy, especially when differences in heritabilities and/or correlations of FC and WG are large. When heritabilities and correlations are identical no extra information becomes available (Sales and Hill, 1976) by this linearisation and therefore direct and indirect selection give equal response in FCR. The large differences between heritabilities of FC and WG simulated in the present study (0.2 *vs.* 0.5) may be unrealistic (*eg.* Pym, 1990), and a difference of 0.1 in heritabilities gave only 1-3% extra response.

In practice, selection index weights are based on estimates of (co)variances in place of the true population parameters used in the present study, and there is an inevitable loss in selection response when using an index with weights obtained from estimates of genetic and phenotypic parameters rather than the population parameters (Hayes and Hill, 1980). Under the present sequential selection structure it is difficult to estimate covariances between FC and WG, which are needed when selection is on a linear index rather than the ratio. The use of inaccurate estimates of these genetic and phenotypic covariances is likely to overestimate the presumed superiority of selection on the index. As published estimates of the heritability of FC and WG tend to be similar, one may be worse off by applying indirect selection based on inaccurate covariances than by selection on FCR.

The usual assumption of normality is likely to be violated for FCR, which is a nonlinear function of FC and WG, and which was assumed to be controlled indirectly by many genes affecting its component traits directly. However, REML, based on a BLUP animal model, was shown to be robust to such deviations from normality. Hence, transformation of FCR does not seem necessary to enable accurate selection and estimation of response based on BLUP breeding values. In addition, although it might seem intuitively correct to assume indirect control of FCR through genes affecting its components, we have no exact knowledge of this. FCR, a gross measure of efficiency, may be partially driven by genes coding for products which regulate efficiency directly. As such, non-normality of FCR could be even less a problem.

In conclusion, direct selection for FCR is very likely most effective and practical for a broiler breeding operation, in terms of the expected genetic response and the simplicity of the genetic evaluation of selection candidates.

SUMMARY AND CONCLUSIONS

Direct *versus* indirect selection for food conversion ratio of growth (FCR) after selection for juvenile body weight (JBWT), a sequential scheme often applied in broilers, was considered. In the present study loss of response in either FCR or aggregate genotype (H) when JBWT was included was investigated under selection on a linear index of ratio component traits (and JBWT) or FCR (and JBWT) by selection index methodology. Relative responses in FCR and H were generally very similar under single-step and sequential selection. Without JBWT in H, selection for linear index or ratio gave similar responses in FCR when heritabilities of components were equal. With large differences in heritabilities (0.2 *vs.* 0.5) or genetic and environmental correlation (>0.6) significant differences in response (5-12%) in FCR emerged. Therefore, whether additional costs are justified for parameter and breeding value estimation when using a linear index in place of selection for the ratio depends on the difference in heritabilities and correlations of the ratio component traits. With JBWT in H, loss of response in FCR was partially or entirely offset by response in JBWT. The non-normality of FCR and consequences for (co)variance component estimation were studied in terms of the coefficients of variation of the component traits of FCR. Restricted Maximum Likelihood (REML) estimation of (co)variance components for both FCR and logarithm transformed FCR (closer to normality) showed the robustness of REML to such deviations from normality.

TABLE 4.1

Studied combinations (marked by ×) of selection indexes and aggregate genotypes both under single and two-step selection for juvenile body weight (JBWT) and food conversion ratio (FCR) or alternatively the component traits food consumption (FC) and weight gain (WG).

selection index elements	aggregate genotypes			
	FCR	JBWT, FCR	FC, WG	JBWT, FC,WG
FCR	×		×	
JBWT, FCR	×	×	×	×
FC, WG			×	
JBWT, FC, WG			×	×

TABLE 4.2

Assumed values of the parameters for JBWT, WG and FC.

	trait		
	JBWT	WG	FC
JBWT	.3[1] (.0375)	.3[2]	.3
WG	.5[3]	.3 (.0140)	.5
FC	.5	.64	.3 (.0300)

---

[1] heritabilities, with phenotypic variances (kg^2) in parentheses, on the diagonal
[2] environmental correlations above the diagonal
[3] genetic correlations below the diagonal

TABLE 4.3

Comparison of genetic response in JBWT (BWT), computed only when part of the aggregate genotype), FC, WG, H and FCR after one round of selection under various heritabilities (h^2), indexes and aggregate genotypes with FCR defined as a ratio or as a linear combination of component traits, using selection index theory and assuming single or two-step selection.

alternative		genetic response									
		single-step selection					two-step selection				
BWT	FCR	BWT(kg)	FC(kg)	WG(kg)	$rH^{1,3}$	$rFCR^{2,3}$	BWT(kg)	FC(kg)	WG(kg)	$rH^{1,3}$	$rFCR^{2,3}$
						h^2_{FC} = 0.3	h^2_{WG} = 0.3				
--[4]	--[5]	-	.010	.060	1.00	1.00	-	.031	.062	1.00	1.00
--	i-	-	-.003	.054	0.99	1.00	-	.024	.059	1.00	1.00
i-	--	-	.011	.060	1.00	1.00	-	.032	.062	1.00	1.00
i-	i-	-	.003	.056	1.00	1.00	-	.025	.059	1.00	1.00
ia	--	.108	.053	.068	1.00	1.00	.103	.051	.067	1.00	1.00
ia	i-	.106	.039	.061	0.99	1.00	.101	.036	.060	0.99	1.01
ia	ia	.105	.038	.061	0.99	1.01	.100	.036	.060	0.99	1.01
						h^2_{FC} = 0.5	h^2_{WG} = 0.2				
--	--	-	-.141	-.011	1.00	1.00	-	-.145	-.025	1.00	1.00
--	i-	-	-.056	.020	0.87	0.84	-	-.087	-.004	0.87	0.85
i-	--	-	-.140	-.010	1.00	1.00	-	-.144	-.025	1.00	1.00
i-	i-	-	-.068	.016	0.88	0.85	-	-.089	-.005	0.87	0.85
ia	--	.083	-.012	.026	1.00	1.00	.078	-.015	.025	1.00	1.00
ia	i-	.091	.019	.035	0.98	0.85	.085	.015	.034	0.98	0.87
ia	ia	.089	.017	.035	0.98	0.88	.084	.014	.034	0.98	0.88
						h^2_{FC} = 0.2	h^2_{WG} = 0.5				
--	--	-	.057	.128	1.00	1.00	-	.062	.119	1.00	1.00
--	i-	-	.031	.111	0.94	0.96	-	.045	.107	0.95	0.96
i-	--	-	.057	.128	1.00	1.00	-	.062	.119	1.00	1.00
i-	i-	-	.037	.114	0.95	0.96	-	.046	.108	0.96	0.97
ia	--	.125	.067	.114	1.00	1.00	.121	.066	.114	1.00	1.00
ia	i-	.124	.052	.103	0.97	0.95	.119	.050	.103	0.97	0.96
ia	ia	.122	.052	.104	0.97	0.97	.118	.050	.104	0.97	0.97

[1] : response in H was expressed as weighted response in FC and WG (and JBWT if part of H)

[2] : response in FCR expressed as $\frac{\mu_{FC}+\Delta G_{FC}}{\mu_{WG}+\Delta G_{WG}} - \frac{\mu_{FC}}{\mu_{WG}}$ where μ is the initial mean and ΔG is the genetic response

[3] : relative responses in H and FCR to that of the first alternative for every subgroup

[4] : -- = BWT not in index or aggregate genotype	[5] : -- = FCR not in index or aggregate genotype
i- = BWT in index but not in aggregate genotype	i- = FCR in index, FC and WG in aggregate genotype
ia = BWT in both index and aggregate genotype	ia = FCR in both index and aggregate genotype

TABLE 4.4

Comparison of relative genetic response in H, to that of the first alternative for each subgroup, under various differences between the (fixed) genetic (r_g=0.64) and (variable) environmental correlation (r_e) assuming equal heritabilities of 0.3 for all traits.

alternative[1]		r_e (difference between r_g and r_e in parentheses)			
JBWT	FCR	.50 (.14)	.25 (.39)	.00 (.64)	-.50 (1.14)
--	--	1.00	1.00	1.00	1.00
--	i-	1.00	0.97	0.94	0.83
i-	--	1.00	1.00	1.00	1.00
i-	i-	1.00	0.98	0.94	0.84
ia	--	1.00	1.00	1.00	1.00
ia	i-	0.99	0.97	0.94	0.87
ia	ia	0.99	0.97	0.94	0.87

[1] see Table 4.3 for indexes and aggregate genotypes

TABLE 4.5

Skewness[1] and kurtosis[2] of FCR and logFCR under various simulated population means and coefficients of variation (CV) for FC and WG, which were normally distributed.

mean (kg)		CV (%)		skewness		kurtosis	
FC	WG	FC	WG	FCR	logFCR	FCR	logFCR
2.00	.90	8.66	13.15	.69 (.08)[3]	.29 (.05)	1.15 (.37)	.30 (.13)
2.00	1.20	8.66	9.86	.37 (.06)	.08 (.05)	.37 (.16)	.11 (.09)
1.75	1.20	9.90	9.86	.30 (.05)	-.00 (.05)	.29 (.14)	.11 (.09)
2.40	.90	7.22	13.15	.76 (.08)	.36 (.06)	1.34 (.41)	.35 (.14)
2.40	1.20	7.22	9.86	.44 (.06)	.17 (.05)	.48 (.19)	.13 (.10)
2.40	1.65	7.22	7.17	.21 (.05)	-.00 (.04)	.14 (.11)	.05 (.08)

[1] $(E(x-\mu)^3/\sigma^3)$; [2] $(E(x-\mu)^4/\sigma^4 - 3)$

[3] empirical SDs of 50 replicates in parentheses

TABLE 4.6

Estimates of the heritabilities of FCR and logFCR and correlations with other traits using REML, and approximations from Pearson's (1897) formulae for simulated data[1].

parameter	correlated trait	REML		Pearson's formulae
		FCR	logFCR	FCR
genetic correlation	JBWT	-.20 (.13)	-.20 (.13)	-.22
	FC	.04 (.10)	.05 (.09)	.02
	WG	-.72 (.07)	-.71 (.07)	-.75
phenotypic correlation	JBWT	-.14 (.02)	-.14 (.02)	-.14
	FC	.12 (.02)	.13 (.02)	.14
	WG	-.75 (.01)	-.75 (.01)	-.76
heritability		.22 (.03)	.22 (.03)	.25

[1] empirical SDs of 20 replicates in parentheses

CHAPTER 5

NON-NORMALITY OF EGG PRODUCTION DISTRIBUTIONS IN POULTRY AND THE EFFECTS OF OUTLIER ELIMINATION AND TRANSFORMATION ON SIZE AND CURVILINEARITY OF HERITABILITY

INTRODUCTION

In standard analyses of variance the model specifies that the effects of the different factors are additive and the residuals from the model are normally and independently distributed with constant variance (Snedecor and Cochran, 1989). In a quantitative genetic context, the requirements of additivity and normality of random family or group effects and linearity of heritability are usually to be satisfied in addition when using selection index or BLUP methods (Abplanalp, 1961; Nishida and Abe, 1974; Robertson, 1977; Ibe and Hill, 1988). Tests of linearity of heritability can, for instance, be performed by regression of offspring on (mid) parent (Kempthorne and Tandon, 1953). Strictly speaking, however, no assumption needs to be made of linearity of the offspring on parent regression, for a curvilinear model can be fitted or the regression computed on only a selected set of parents (Hill, 1978). For instance, in a genetic selection programme, where parents are directionally selected and thus often within a narrow phenotypic range, the genotypic value of offspring might be linearly estimated from the phenotypic value of the parent without being biased by concavity of the heritability of the trait of interest. Nishida and Abe (1974) give a practical way to use the curvilinear heritability by dividing the data into an appropriate number of groups and fitting a linear heritability in each group separately. They provide a worked example for a sigmoid-shaped heritability.

Nowadays, decision-making on selection candidates is mostly based on estimates of genotypic value combining parental and collateral information using selection index or BLUP methods. These methods become less efficient when normality, linearity of heritability and homogeneity of variance are not satisfied (Ibe and Hill, 1988). The idea of Nishida and Abe (1974) might be extended to selection index or even BLUP methods, weighting relatives differently dependent on their phenotypic value and the amount of genetic information they are likely to contain. This makes the methods more robust against non-linearity of heritability but does not tackle overestimation of individuals from groups with extreme variance (Ibe and Hill, 1988) or overestimation of predicted genetic response (Clayton, 1975; Rao and Jain, 1981).

Ibe and Hill (1988) and Besbes *et al.* (1993) have studied the scope of Box-Cox power transformations (Box and Cox, 1964) to reduce deviations of the usual assumptions for egg production data on laying hens. These transformations simultaneously handle heterogeneity of variance, non-additivity and non-normality to some degree (Snedecor and Cochran, 1989) and as a result improve linearity of heritability (Robertson, 1977). Ibe and Hill (1988) and Besbes *et al.* (1993) use the multi-step approximate transformation model suggested by Hinkley (1985). The initial transformation was based on maximisation of the likelihood of the error variance treating sire and dam as fixed (Ibe and Hill, 1988), whereas further transformation was considered when either normality or homogeneity of error variance was not established initially. In addition, coefficients of determination of the regression of half sib average on individual, a method introduced by Abplanalp (1961) and revisited and clarified by Hill (1978), were monitored in both studies to measure the goodness-of-fit of the data to linearity of this genotypic regression. Offspring-parent regression could not be used by Ibe and Hill (1988) as data were available on only one generation. Besbes *et al.* (1993), although having multiple generations of data available, did not perform offspring-parent regressions. Intense selection of parents for egg number leading to decreased statistical power to detect curvilinearity could have been a reason. In a recent study Gimelfarb and Willis (1994) did find significant curvilinearity of offspring-parent regression for a number of quantitative traits in an experimental *Drosophila melanogaster* population; and further references on various species are given by Hill (1978).

Prior to analyses, Ibe and Hill (1988) made an arbitrary decision to omit all records less than 10 eggs, whereas Besbes *et al.* (1993) checked for outliers without reporting the statistical reasoning behind their identification or the limit at which records were eliminated. Formally, as pointed out by Barnett and Lewis (1994), potential outliers need to be statistically tested for discordance based on a working hypothesis expressing some basic probability model for the generation of all the data with no contemplation of outliers and an alternative hypothesis expressing a way in which the model may be modified to incorporate or explain the outliers as a reflection of contamination. If any outlier is adjudged to be discordant the working hypothesis is implicitly rejected and replaced by some alternative hypothesis, including *i.a.* (Barnett and Lewis, 1994), (i) the inherent alternative where outliers have appeared in the data merely as a reflection of a greater degree of inherent variability than initially anticipated (*eg.* upper outliers may reflect, say, that an initial assumption of a gamma distribution is best replaced with a log-normal distribution), (ii) the mixture alternative where the outliers reflect low-level contamination from a (foreign) population other than that represented by the basic model and (iii) the slippage alternative, by far the most common, which states that all observations apart from some prescribed small number k (1 or 2, say) arise independently from an initial model (say F) defined by location and dispersion parameters, μ and σ^2, whilst the remaining k are independent observations from a modified version of F in which μ or σ^2 have been shifted in value. In much published work F is a normal distribution (*eg.* Grubbs, 1950; Dixon, 1950; Anscombe, 1960; Grubbs, 1969 and Stefansky, 1972) and numerous tables have been constructed to guide the investigator as to how rare an extreme observation, not a product of slippage, would be if the data were normal and followed the assumed model (Snedecor and Cochran, 1989). Barnett and Lewis (1994) emphasise that we must know what alternative hypothesis is being adopted, for any assessment of the power of the prevailing discordancy test depends on the form of the alternative hypothesis. Hence, investigation of possible underlying probability distributions for egg production characters can be useful to assist in the choice of a suitable alternative hypothesis.

The objectives of this study were to investigate 1) the goodness-of-fit of some 'standard' probability distributions to the phenotypic reproduction data of female line meat-type chickens by maximum likelihood in order to identify outliers on a phenotypic level using the distribution with the best fit, and 2) the effect of outlier identification and subsequent elimination and/or Box-Cox power-transformation of the data on non-normality and curvilinearity and on the size of the heritability.

MATERIALS AND METHODS

Data

Data were available on approximately eight overlapping generations of a broiler-type female line. Traits included: the age at the first egg in days (AFE) indicative of the point of sexual maturity; the number of eggs until 48 weeks of age, hen housed production (HHP); and the rate of lay in the period from AFE to 48 weeks, hen day percentage (HD%). Descriptive statistics of these traits are summarised in Table 5.1. The skewness provides a measure of the degree of asymmetry of a distribution around its mean and the kurtosis measures the relative thickness of the tails of a distribution. Both measures are zero for a normal distribution. The traits show deviation from normality as observed in many studies. Both HHP and HD% are negatively skewed, whereas AFE is positively skewed. All three traits are leptokurtic, *i.e.* peaked. Frequency histograms (Fig. 5.1) display the various features of the observations.

Probability distributions fitted to reproduction data

The distribution directive in GENSTAT (1993) was used to test the goodness-of-fit of various 'standard' probability distribution functions to the raw phenotypic data on reproduction traits. An iterative Gauss-Newton optimisation method is used to estimate the parameters of the distribution and convergence was assumed when the change in log-likelihood was less than 10^{-8}. The data were grouped in evenly spaced intervals of 5 eggs, 5% and 5 days for HHP, HD% and AFE, respectively. This grouping strategy takes into consideration the importance of the tail cells, often with small expected frequencies, and is likely to be more powerful in detecting non-normality, compared to GENSTAT's default method with groups of equal frequency and thus based on unevenly spaced intervals. The choice of the density functions to be tested was facilitated by the descriptive statistics in Table 5.1 and the frequency histograms in Fig. 5.1. For all traits the (single) normal distribution, the double-normal distribution (a mixture model of two normal distributions $N_1(\mu_1,\sigma_1)$ and $N_2(\mu_2, \sigma_2)$ with different variances and locations and with compound density function $f(x) = p \times \Phi(x;\mu_1;\sigma_1) + (1-p) \times \Phi(x;\mu_2;\sigma_2)$ where p is the proportion of observations in N_1) and the binomial distribution were tested. Due to the proportional character of the trait, HD% was also exposed to logit and angular transformation before fitting a Gaussian density function. For the positively skewed AFE the log-normal distribution (with or without a change of **a** in location) was tested additionally. The double-normal was exposed to an additional grid-search in the 5-dimensional parameter space (μ_1, σ_1, p, μ_2 and σ_2) to ensure localisation of the global maximum of the likelihood function, since clear bimodality was absent (see Fig. 5.1). See GENSTAT (1993) for more details and further references on the method. Strictly speaking, the log-likelihoods might not always be directly comparable across all these distributions, therefore a further indication of goodness-of-fit was provided by the coefficient of determination of the regression (without intercept) of observed on expected frequency of observations.

Genetic model

The genetic model used throughout was the additive individual animal model (IAM):

$$y_{ijk} = \mu + h_i + a_j + e_{ijk} \qquad [5.1]$$

where y_{ijk} is an untransformed or transformed, continuous or discrete observation; μ is the grand mean; h_i is the fixed effect of hatchweek i; a_j is the breeding value of animal j and e_{ijk} is the random error term.

Estimation of variance components and heritabilities was performed by the derivative-free REML programs of Meyer (1989).

Outlier identification

Investigation for outlying observations was based on egg number (HHP). One way of identifying potential outliers was based on a discordancy test applicable to the distribution with the best fit to the raw phenotypic data following from the previously described maximum likelihood estimation method.

An alternative quantitative genetic approach based on partitioning of the total phenotypic data distribution into one part with heritability equal to zero, and another part with heritability greater than zero was considered. All-or-none genetic analysis was performed by dividing the data into two parts (0 and 1) representing rejected (possibly outlying) records and accepted records. This analysis was repeated at various zero-one thresholds in order to localise the point of separation between some 'foreign nuisance' data population (with $h^2 \approx 0$) and the main population of observations (with $h^2 > 0$). The transformation of Robertson and Lerner (1949), which is $p(1-p)/z^2$, where p is the population incidence and z is the height of the ordinate of a standardised normal at the threshold point corresponding to p, was used to convert heritability estimates onto a hypothetical underlying continuous scale. Mercer and Hill (1984) showed by simulation, with incidences in the range of 0.5% to 5%, that this transformation is accurate when true heritabilities on the continuous scale are low.

Transforming the data

Maximising the likelihood

The approximate transformation model suggested by Hinkley (1985) and applied by Ibe and Hill (1988) and Besbes *et al.* (1993) was used to determine an optimum transformation producing near linearity, normality of errors and homogeneity of error variance. The power transformation method due to Box and Cox (1964) produced standardised transformed variates, z(t):

$$z(t) = \frac{y^t - 1}{tG_y^{t-1}} \qquad [5.2]$$

where y is an original untransformed observation; G_y is the geometric mean of the original observations and t is the power of transformation with $t \neq 0$. A power of zero (t=0) represents a log transformation. A series of REML runs with different values for t were performed to produce the profile log-likelihood for t and pinpoint the first-stage optimum t, where the natural log-likelihood function for an additive IAM (see Meyer, 1989) was maximised. This is a more classical approach than the Bayesian approach suggested by Gianola *et al.* (1990) with joint estimation of t and the dispersion parameters of interest. Hereafter, if necessary, the likelihood was compromised somewhat (<10%) to attain a more homogeneous error variance and normality of the errors.

Considering curvilinearity and non-normality

The linearity of the genotypic regressions of hatch-corrected mean offspring performance on corrected dam performance (Kempthorne and Tandon, 1953) and of hatch-corrected average performance of half sibs of an individual, itself and full sibs excluded, on the corrected performance of the individual (Hill, 1978) were both checked on the original and the t-transformed scale. Quadratic and cubic terms were tested for significance and the increase in the coefficient of determination of non-linear regression compared to linear regression was investigated. Plots were drawn to enable visual assessment of non-linearity.

Normality of the residuals was studied on the untransformed and t-transformed scales by looking at skewness. Markedly skewed errors illustrate the non-normality and imply heterogeneity of error variance. The heterogeneity of error variance amongst environmental groups (hatches) was not investigated explicitly. Two types of residuals were considered, the residuals from both linear genotypic regressions and the residuals from the mixed model BLUP analyses calculated as the observations minus the fixed effect estimators (BLUEs) and the breeding value predictors (BLUPs).

RESULTS

Likelihood of some probability distribution functions

For all traits the (single) normal distribution could be rejected as a function explaining the raw phenotypic data (see Table 5.2). HHP was best represented by a double-normal density function. Logit and angular transformation of HD% led to significant increases in the log-likelihood and R^2. The highest likelihood was, however, achieved by fitting a double-normal density function. Although the double-normal showed a very good fit to AFE, it was outperformed by the log-normal distribution after a change of **a** in location. The log-likelihood values were closely followed by the coefficients of determination and were very high for all 'best' fits.

Outlier identification and elimination

Based on the previous analyses, the mixture model consisting of two normal distributions differing in both location and scale was chosen as the alternative hypothesis to explain the data of the trait HHP. This model is depicted in Fig. 5.2 and the relevant parameter estimates are in Table 5.3. The proportion of data in the left-hand normal distribution was similar for HHP and HD% (29.2% and 27.8%, respectively). Consider now the extreme, perhaps unrealistic, assumption that the contaminated outlying observations are not of interest. The applied test for identification of these outliers consisted of the observations beyond three times the SD of the mean of the main distribution (normal 2 in Fig. 5.2). Records of sixty eggs or less were eliminated on this basis, representing about 11% of the data.

The alternative quantitative genetic approach based on partitioning of the total phenotypic data distribution into one part with heritability equal to zero and another part with heritability greater than zero resulted in the much lower limit of outlying records at 25 eggs HHP, representing 2.5% of the data. Up to the HHP level of 25 eggs the adjusted all-or-none heritability equals zero to two decimal points. Rejecting records up to 30 eggs HHP led to a substantial increase in heritability compared to the 25 eggs HHP level of rejection. Higher levels of rejection result in higher converted all-or-none heritabilities as might be expected. Heritabilities on the continuous scale kept increasing throughout the exhibited rejection limits for HHP of eggs (see Table 5.4).

The effect of outlier elimination and Box-Cox transformation of the data on size and linearity of heritability and normality of errors

Linear estimation of heritability of all untransformed data by offspring on dam and half sib average on individual regression was performed and compared to IAM-REML estimates (see Table 5.5). Estimates of offspring-dam regression were highest, those for half sib average-individual regression were low and IAM-REML estimates had intermediate values. Skewness of the errors of regression was considerable for the reproduction traits HHP, HD% and AFE. Deviation of normality of errors based on BLUP-analyses were similar to the deviations shown by the residuals of regression.

Goodness-of-fit of the data to the quadratic regression model was better (see Table 5.6), in particular for the traits HD% and HHP. Generally, increases in R^2 were substantially greater for regression of half sib average on individual. All quadratic regression coefficients were significant at the 5% level. The cubic relationships (not in table) did not significantly improve the R^2 of the quadratic regression model.

The following plots (Fig. 5.3) illustrate the superior goodness-of-fit of the curvilinear regression models to the data. To give the reader some impression about the data, they were depicted in a compressed format by ranking them on merit of dam and individual, respectively, and splitting them into 5 equal groups. The (non-) linear regression plots were, however, based at all times on all the individual data points as presented in the tables. Non-linearity of heritability was most obvious under regression of half sib average on individual for HD% and HHP, which was expected since increases in the R^2 were greatest (see Table 5.6). Both these heritabilities were concave upwards. For AFE the heritability was slightly concave downwards. It can be observed in the graphs that dams must have been exposed to some directional selection for HHP and HD% as their phenotypic range is much narrower and shifted compared to the scale of individuals.

Results of estimation of the heritability by linear regression and IAM-REML analysis after omission of potential outliers identified by the all-or-none quantitative genetic approach or according to outlier theory ignoring any underlying genetic variability are given in Table 5.7. Both the R^2 and the heritability increased considerably, particularly for regression of half sib average on individual for which heritabilities were most concave (see Fig. 5.3). The IAM-REML estimates for HHP and HD% increased significantly as could also be seen in Table 5.4. Properties of the errors improved for HHP and HD% in particular; less skewness indicates more normal errors and implies more homogeneous error variance. Further changes in R^2 and heritability by increasing the limit of rejection from 25 to 60 eggs were relatively small. The skewness of errors decreased further, however.

Quadratic regression analysis (Table 5.8) showed the increases in R^2 compared to linear regression to be modest, especially when compared to the regression of half sib on individual for the total untransformed data set (see Table 5.6) . Increases were very similar for rejection of records up to 25 or 60 eggs and quadratic regression coefficients were no less significant for the latter. The plots in Fig. 5.4 assist in visual assessment of the consequences of elimination of outliers (records with 25 eggs or less) for the non-linearity of the heritability based on half sib average-individual regression.

Consequences of Box-Cox transformation of HHP and HD% and log transformation (after a shift in location) of AFE for the goodness-of-fit of the transformed data to linear estimation of the heritability and the skewness of the error terms were considered (see Table 5.9). Increases in the percentage of variance explained by both linear regression methods for all transformed data were large compared to the explained percentages by these methods fitted to all the untransformed data. In comparison to exclusion of records up to 25 eggs without transformation (see Table

5.7), the goodness-of-fit appeared to be better for the offspring-dam regression and for the trait AFE. Noteworthy are the increases in heritability resulting from half sib average-individual regression and the relatively small changes in heritability from offspring-dam regression compared to values in Table 5.5. IAM-REML heritability estimates also increased relative to analyses of all untransformed data and were now more similar to estimates from offspring-dam regression. The residual terms from the regression methods and the BLUP analyses were close to normality.

Transformation of the data as well as exclusion of outlying records up to 25 eggs HHP led to further increases in R^2 and heritabilities of HHP and HD% in particular. The properties of the error terms were very similar to the errors of all transformed data. The heritability estimates of AFE did not increase after exclusion of outliers based on the number of eggs HHP.

Fitting a quadratic regression model to the transformed data with or without elimination of outliers generally gave only small increases in the coefficient of determination (see Table 5.10), despite the quadratic regression coefficients still being significant at the 5% level for half sib average-individual regression.

The plots (Fig. 5.5) exhibit that the relationship between HD% of half sib average and individual is clearly still somewhat non-linear and tended towards a sigmoid curvature ($P<0.05$), but the rounded R^2 was not higher for the cubic than for the quadratic regression analysis. The near perfectly linear relationships of both regression methods for AFE is conspicuous and supports the close fit of a log-normal density function to the data after a shift in location of AFE.

DISCUSSION

Probability distributions to explain the data

The goodness-of-fit of the double-normal density function to the HHP and HD% data was very high. The double-normal probability distribution has been assumed before by Gavora *et al.* (1980; 1982; 1983) to describe egg production data in populations affected by disease, with special reference to lymphoid leukosis virus (LLV) infection. They distinguished between test-positive and -negative birds and could therefore identify the shift in location and variance of egg production due to this disease and furthermore describe the consequences for the egg production distribution of the total population. In most cases such specific information is not available and also the population egg production performance might be hampered by other, sometimes multiple, clinical or subclinical diseases or other (*eg.* leg or nutritional) problems affecting mortality and morbidity. This discrepancy in analysis of the data, *i.e.* evaluation of means and variances within specifically identified subsets of the data *versus* fitting a probability distribution to the total phenotypic data without prior knowledge of the 'affected' or 'non-affected' status of birds, is likely to account for some of the difference in the estimated proportion of 'affected' birds, which was 3.9% for the first (Gavora *et al.*, 1980) and 29.2% for the latter (see Table 5.3), respectively. In addition, the proportion found by Gavora *et al.* (1980) was in a Leghorn population under specific selection for eggs, whereas the present analysis was based on meat-type chickens subject to less genetic improvement for reproduction. Intensive selection for egg production generally results in a lower incidence of congenitally transmitted diseases and possibly in a lower susceptibility to genetically transmitted diseases or more general problems when challenged before selection. Gavora *et al.* (1980) illustrated this with a control strain having a much higher proportion of the congenitally transmitted disease (LLV 'affected' birds 18.5%).

The trait AFE had a much smaller percentage of 'affected' birds (12.8%, not presented) when fitting a double-normal probability distribution. This might be expected since the majority of diseases or problems may occur after the start of the egg production. Also the preceding selection step on juvenile body weight prevents a high incidence of late sexually maturing very light (possibly ill-conditioned) birds. One might expect the trait AFE, describing the response time, to follow an exponential distribution, where response rate can be assumed constant, or a Weibull distribution with a response rate varying monotonically with time (Johnson and Kotz, 1970). However, likelihoods of these distributions (not presented) were low. The log transformation after a shift in location produced near normality and reflected the greater degree of inherent variability than anticipated from a normal distribution.

Identifying potential outliers

According to Grubbs (1969), an outlying observation, or 'outlier', is one that appears to deviate markedly from other members of the sample in which it occurs. Strictly applying this definition, one could argue whether there were any outlying observations at all in these data, since the data seem to be more or less continuous without a member or block of members deviating markedly from the other members (there was no clear bimodality, see Fig. 5.1). However, if a normal probability model is assumed, a large number of 'outliers' can be demonstrated and an alternative model (*eg.* a double-normal) needs to be adopted to take account of their existence. The association of these 'outliers' with environmental factors (such as disease), as suggested by Clayton (1975), could justify the elimination of all outlying contaminated observations (60 eggs or less), since these records would be genetically non-informative but could seriously distort (genetic) inferences. Several researchers, however, estimated non-zero heritabilities for diseases affecting egg production or for egg production in the left-hand tail of the distribution (*eg.* Shalev, 1977; Gavora, 1990). Separation of the data into one (foreign) population with heritability equal to zero and another (main) population with heritability greater than zero by all-or-none genetic analysis at several zero-one thresholds largely alleviated this problem and considered only 2.5% of the data (instead of 11%) to be non-informative. Still, the problem of segregating recessive deleterious genes at low or moderate frequencies contributing significantly to the genetic variance (*eg.* Falconer, 1971; Robertson, 1977; Al-Murrani and Roberts, 1974) remains since such an effect is not easily 'picked up' by the preceding heritability analyses. Moreover, this problem might be more predominant in meat-type poultry because of the combined selection for, often antagonistic, reproductive and broiler characteristics. Therefore, systematic exclusion of any 'outliers' from selection decisions could involve the risk of drift towards a more negatively skewed egg production distribution with possibly a higher proportion of the birds representing the distribution accounting for the left-hand tail (see Fig. 5.3) due either to increased deleterious recessive gene frequency or higher susceptibility to some diseases.

Differences in heritability estimates

Differences in heritability estimates by the different methods before transformation of the data were very substantial. Offspring-parent estimates were high; firstly these estimates were likely to be affected by environmental and or genetic dam-offspring covariances and secondly this regression was less affected by non-linearity due to directional selection of the dams as was expected *a priori*. Hence, the offspring-dam regression was relatively little changed by transformation or outlier elimination. The regressions of half sib average on individual were low for untransformed HHP and HD% data due both to the substantial curvilinearity (see Fig. 5.4) and the fact that this component was not augmented by maternal effects as was the offspring-parent regression. The heritabilities resulting from this regression nearly doubled by transformation and outlier elimination (compare Table 5.5 and Table 5.9). Finally, REML estimates were intermediate, which might be expected because both offspring-parent and collateral information are pooled into one estimate. However, after manipulation of the data, these estimates were effectively as high as the estimates originating from offspring-parent regressions. Estimates were high as a result of the much alleviated curvilinearity, the loss of variance due to selection (over about 8 generations) being accounted for by the numerator relationship matrix and the full-sib correlation, which is most likely to be augmented by environmental and dominance effects, forming an important part of the REML heritability.

Despite the increases in coefficients of determination of a quadratic model compared to a linear model being small or even zero after transformation and outlier elimination, quadratic regression coefficients were still notably different from zero. Although relationships between performances might realistically not be expected to be purely linear, a further look into the matter was thought useful. Robertson (1977) proposed a separate analysis for the top and bottom halves of the population to compare effective heritabilities for selection upwards and downwards. Hill (1978) illustrated this idea by using the regression method of half sib average on individual, Abplanalp's (1961) 'linear heritability estimate', where the data were ranked on individual performance and divided into top and bottom half. Basically, this procedure was repeated for the present data on HHP of eggs and HD%, comparing changes in heritabilities in the up and down direction after the various data manipulations as well as the heritability estimate for the total data (shown before without SE in the various tables). Results are exhibited in Table 5.11. Clearly, the heritability based on raw data was extremely curvilinear, with the heritabilities in the up direction being much greater than the heritabilities downwards. Transformation reduced non-linearity substantially by increasing the heritability in the down direction and decreasing the heritability in the up direction somewhat. Omission of outliers had a very considerable effect on the effective heritability of HD% in the down direction, increasing from 0.002 to 0.064. Transformation after outlier elimination reduced curvilinearity somewhat more. In spite of these manipulations the heritabilities in the up and down direction were still significantly different.

There were conspicuous differences in sampling errors in the up and down direction for the raw untransformed data, which illustrates the heterogeneity of variance in the up and down direction. More (environmental) variation, in this case in the down direction (compare Fig. 5.3), results in a lower sampling error of the regression coefficient. Furthermore, it can be seen how transformation alleviated much of this heterogeneity by 'pulling' the low observations back into a Gaussian-shaped distribution; consequently sampling errors were now similar for top and bottom heritabilities.

Scope for improvement of genetic progress in the number of eggs

Ibe and Hill (1988) clearly pointed out how transformation of egg production could increase efficacy of (BLUP or index) selection through a higher heritability of the transformed data and consequently higher accuracy of selection decisions, a more linear heritability estimating more precisely responses in the up and down direction and a more homogeneous variance making it less likely for an excessive number of animals to be selected from the extreme groups. As concluded from Table 5.11 considerable curvilinearity was present after transformation of the data. The use of the average heritability would thus still lead to biased breeding values (EBVs), with high EBVs regressed too little and low EBVs regressed too much from the mean. The method of Nishida and Abe (1974) is again relevant. They divided the data into an appropriate number of groups and fitted a linear heritability in each group separately. If it is assumed that the top and bottom trait have a correlation of unity and identical economic importance, it is simple to weight relatives differently in a curvilinear index dependent on their phenotypic value. This method can make selection more robust against curvilinearity of the heritability. Subdivision of the data into more than two parts might further increase response, probably involving a function of accuracy or R^2 of the fit to the curvature and the sampling errors of the partial heritability estimates. However, the additional benefit is likely to be smaller.

Koerhuis (1995) looked at the possibility of within-hatch power transformation followed by scaling. Simulation of selection from environmental groups with a variable degree of skewness and variation demonstrated the potential usefulness of this alternative transformation. However, more work would be needed as to the statistical correctness of the method, for example to allow for sampling error of the within-hatch estimates of skewness it might be necessary to use a best weighted combination of the *a priori* (population) estimate and the sample estimate. Furthermore, the underlying genetic variability in the double-normal mixture model should be the subject of further study. Individuals could be assigned to one or the other data populations based on a probability, and bivariate analysis performed to investigate genetic (co)variation of both populations.

SUMMARY AND CONCLUSIONS

Egg production data on approximately eight overlapping generations of a female meat-type chicken population were available for investigation of 1) possible underlying probability distributions of the data, 2) size and non-linearity of heritability, and 3) non-normality of errors. A mixture model of two Gaussian probability functions with different location and dispersion parameters gave the best fit to the phenotypic data for number of eggs or hen housed production (HHP) and rate of lay or hen day percentage (HD%). The age at first egg, *i.e.* sexual maturity, closely followed a log-normal distribution after a shift in location. Identification of outliers of HHP was on the basis of i) outlier theory on the phenotypic mixture model or ii) the underlying genetic variability as derived from a series of all-or-none genetic analyses, which led to different thresholds for the number of eggs regarded as outlying. Elimination of these identified outliers generally improved the properties of the data. Consequences of systematic elimination of outliers from selection decisions were discussed. Box-Cox power-transformation of the data substantially improved normality and (linearity of) heritability, estimated by offspring-parent regression, half-sib average on individual regression and REML. Additional improvements through omission of potential outliers prior to transformation were generally small. In spite of appreciable decreases, curvilinearity of heritabilities of HHP and HD% was still significant after transformation by comparison of effective heritabilities in the up and down direction of selection. The use of differential heritabilities was discussed as a means to make selection decisions more robust against the remaining curvilinearity of heritability.

TABLE 5.1

Descriptive statistics for hen housed production (HHP), hen day percentage (HD%) and age at first egg in days (AFE).

trait	# records	mean	median	min	max	SD	CV	skewness	kurtosis
HHP	15038	100.0	106.0	3	167	28.6	28.6	-1.02	.99
HD%	15038	65.0	68.2	2	94	14.8	22.8	-1.34	2.27
AFE	15038	182.1	180.0	150	327	14.7	8.1	1.59	8.35

TABLE 5.2

Some 'standard' probability distributions fitted to the data on reproduction characters with their log-likelihoods (log L) and coefficients of determination (R^2).

trait	distribution	log L	R^2 (%)
HHP	normal	0.0	80.6
	double-normal	2984.6	99.3
	binomial	-406.9	78.6
HD%	normal	0.0	79.7
	double-normal	3920.7	98.1
	binomial	-584.7	78.2
	logit-normal	744.8	90.2
	angular-normal	704.1	85.8
AFE	normal	0.0	92.6
	double-normal	2953.2	98.2
	binomial	633.6	93.1
	log-normal (X)	1415.8	94.1
	log-normal (X-a)	3082.3	99.1

TABLE 5.3

Maximum likelihood estimates of the parameters in the double normal density function as depicted in figure 5.2.

distribution	proportion	± SE	mean	± SE	SD	± SE
normal 1	0.292	0.014	70.55	1.46	30.10	0.56
normal 2	0.708	0.014	112.13	0.29	16.53	0.22
double normal*	1.0		99.97		28.57	

* mean is $p\mu_1 + (1-p)\mu_2$ and SD is $\sqrt{[p\sigma_1^2 + (1-p)\sigma_2^2 + p(1-p)(\mu_1 - \mu_2)^2]}$ where p is the proportion of the data in normal 1

TABLE 5.4

Converted all-or-none heritability estimates (h_1^2) at various zero-one thresholds and continuous heritability estimates (h_2^2) excluding the records below the threshold from the analysis.

	HHP of eggs as threshold for rejection					
	-	10	20	25	30	40
% rejected	0.0	1.0	2.1	2.5	3.1	4.7
h_1^2	-	0.000	0.000	0.002	0.068	0.123
h_2^2	0.194	0.231	0.250	0.259	0.268	0.276

h_1^2. all-or-none heritability estimate adjusted for discontinuity according to Robertson and Lerner (1949)

TABLE 5.5

Linear regression (and derived heritability) estimates of offspring on dam and half sib average on individual compared to IAM-REML heritability estimates for all untransformed data.

estimation method	trait	# data points	b	h^2	R^2 (%)	skewness of *e*
regression of offspring average on dam	HHP	2968	0.157	0.314	1.7	-1.20
	HD%	2968	0.104	0.208	0.6	-1.47
	AFE	2968	0.216	0.432	4.5	1.62
regression of half sib average on individual	HHP	13729	0.032	0.128	0.5	-1.17
	HD%	13729	0.027	0.108	0.4	-1.43
	AFE	13729	0.065	0.260	1.8	1.68
IAM-REML	HHP	15038		0.194		-1.23
	HD%	15038		0.151		-1.44
	AFE	15038		0.371		1.98

b, linear genetic coefficient of regression; h^2, linear heritability estimate; R^2, coefficient of determination; skewness of *e*, the random error term; HHP, hen housed production of eggs; HD%, hen day percentage or rate of lay and AFE, age at first egg

TABLE 5.6

Curvilinear regression estimates of offspring on dam and half sib average on individual for all untransformed data.

		quadratic regression			increase
estimation method	trait	b_2	t-Prob.	R^2 (%)	in R^2
regression of offspring average on dam	HHP	0.0014	0.041	1.8	6
	HD%	0.0039	0.029	1.0	43
	AFE	-0.0029	0.002	4.8	7
regression of half sib average on individual	HHP	0.0006	<0.001	0.8	60
	HD%	0.0011	<0.001	0.8	100
	AFE	-0.0008	<0.001	2.2	22

see Table 5.5 for abbreviations; increase in R^2 compared to the linear regression model in the preceding table

TABLE 5.7

Linear regression (and derived heritability) estimates of offspring on dam and half sib average on individual compared to IAM-REML heritability estimates for the untransformed data after elimination of outlying observations.

estimation method	trait	# data points	b	h^2	R^2 (%)	skewness of *e*
	A. analyses excluding records with 25 eggs or less					
regression of offspring average on dam	HHP	2939	0.159	0.318	2.2	-0.83
	HD%	2939	0.116	0.232	0.9	-1.16
	AFE	2939	0.211	0.422	4.6	1.48
regression of half sib average on individual	HHP	13360	0.046	0.184	1.0	-0.64
	HD%	13360	0.041	0.164	0.8	-1.00
	AFE	13360	0.071	0.284	2.1	1.69
IAM-REML	HHP	14656		0.259		-0.84
	HD%	14656		0.211		-1.05
	AFE	14656		0.375		1.65
	B. analyses excluding records with 60 eggs or less					
regression of offspring average on dam	HHP	2845	0.146	0.292	2.5	-0.35
	HD%	2845	0.108	0.216	1.2	-0.61
	AFE	2845	0.196	0.392	4.6	1.20
regression of half sib average on individual	HHP	12257	0.048	0.182	1.0	-0.16
	HD%	12257	0.040	0.160	0.8	-0.36
	AFE	12257	0.081	0.324	2.7	1.10
IAM-REML	HHP	13509		0.273		-0.36
	HD%	13509		0.221		-0.59
	AFE	13509		0.373		1.19

see Table 5.5 for abbreviations

TABLE 5.8

Curvilinear regression estimates of offspring on dam and half sib average on individual for the untransformed data after omission of outlying observations identified in two different ways.

		quadratic regression			
estimation method	trait	b_2	t-Prob.	R^2 (%)	increase in R^2
	A. analyses excluding records with 25 eggs or less				
regression of offspring average on dam	HHP	0.0012	0.055	2.3	5
	HD%	0.0046	0.005	1.2	33
	AFE	-0.0027	0.003	4.8	4
regression of half sib average on individual	HHP	0.0006	<0.001	1.2	20
	HD%	0.0010	<0.001	1.0	25
	AFE	-0.0009	<0.001	2.4	14
	B. analyses excluding records with 60 eggs or less				
regression of offspring average on dam	HHP	0.0016	0.027	2.6	4
	HD%	0.0051	<0.001	1.6	33
	AFE	-0.0024	0.008	4.8	4
regression of half sib average on individual	HHP	0.0006	<0.001	1.1	10
	HD%	0.0015	<0.001	1.0	25
	AFE	-0.0007	<0.001	2.8	4

see Table 5.6 for abbreviations

TABLE 5.9

Linear regression (and derived heritability) estimates of offspring on dam and half sib average on individual compared to IAM-REML heritability estimates for the t-transformed (HHP and HD%) or the log-transformed (AFE) data with and without elimination of outlying observations.

estimation method	trait	# data points	b	h^2	R^2 (%)	skewness of *e*
	A. analyses including all records					
regression of offspring average on dam	HHP	2968	0.142	0.284	2.5	-0.06
	HD%	2968	0.101	0.202	1.3	0.01
	AFE	2968	0.211	0.422	5.5	0.38
regression of half sib average on individual	HHP	13729	0.046	0.184	1.0	0.23
	HD%	13729	0.043	0.172	0.9	0.33
	AFE	13729	0.077	0.308	2.5	0.45
IAM-REML	HHP	15038		0.261		-0.08
	HD%	15038		0.231		0.07
	AFE	15038		0.415		0.46
	B. analyses excluding records with 25 eggs or less					
regression of offspring average on dam	HHP	2939	0.147	0.294	2.7	-0.09
	HD%	2939	0.108	0.216	1.6	0.04
	AFE	2939	0.208	0.416	5.4	0.37
regression of half sib average on individual	HHP	13360	0.053	0.212	1.2	0.19
	HD%	13360	0.049	0.196	1.1	0.36
	AFE	13360	0.080	0.320	2.6	0.44
IAM-REML	HHP	14656		0.283		-0.01
	HD%	14656		0.253		0.01
	AFE	14656		0.413		0.42

see Table 5.5 for abbreviations; for all data $t_{HHP} = 2.5$ and $t_{HD\%} = 3.5$ and for data omitting outliers $t_{HHP} = 2.3$ and $t_{HD\%} = 3.5$; the shift in location before log-transformation of AFE was 140 in both cases [log(AFE-140)]

TABLE 5.10

Curvilinear regression estimates of offspring on dam and half sib average on individual for the t-transformed (HHP and HD%) or the log-transformed (AFE) data with and without elimination of outlying observations.

		quadratic regression			increase
estimation method	trait	b_2	t-Prob.	R^2 (%)	in R^2
	A. analyses including all records				
regression of offspring average on dam	HHP	0.0005	0.376	2.5	0
	HD%	0.0024	0.068	1.4	8
	AFE	-0.0630	0.129	5.5	0
regression of half sib average on individual	HHP	0.0005	0.001	1.0	0
	HD%	0.0012	<0.001	1.0	11
	AFE	-0.0223	0.006	2.5	0
	B. analyses excluding records with 25 eggs or less				
regression of offspring average on dam	HHP	0.0006	0.365	2.7	0
	HD%	0.0028	0.031	1.7	6
	AFE	-0.0760	0.080	5.5	2
regression of half sib average on individual	HHP	0.0004	0.004	1.3	8
	HD%	0.0009	0.002	1.2	9
	AFE	-0.0180	0.047	2.6	0

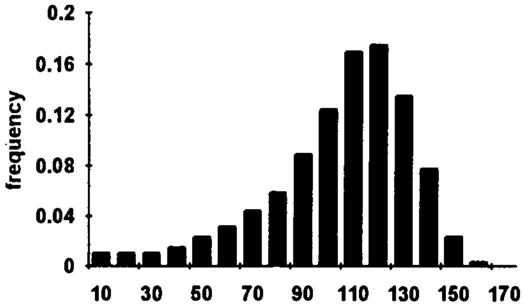
see Table 5.6 for abbreviations and Table 5.9 for information on the transformations

TABLE 5.11

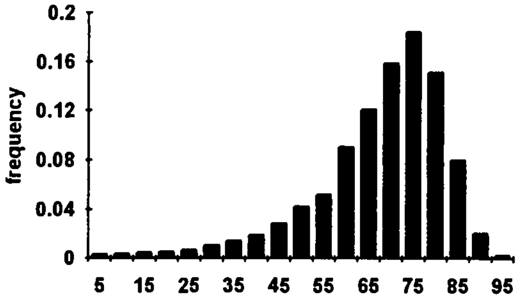
Linear heritability estimates (with SE in parentheses) based on half sib average-individual regression for bottom and top half of the HHP and HD% data ranked on individual performance and the total data, untransformed or t-transformed and with or without elimination of outliers.

trait	status of data	bottom half	top half	total
		A. analyses including all records		
HHP	untransformed	0.028 (0.024)	0.285 (0.058)	0.128 (0.015)
	t-transformed	0.084 (0.037)	0.246 (0.038)	0.185 (0.016)
HD%	untransformed	0.002 (0.023)	0.284 (0.058)	0.109 (0.015)
	t-transformed	0.019 (0.039)	0.223 (0.036)	0.172 (0.015)
		B. analyses excluding records with 25 eggs or less		
HHP	untransformed	0.084 (0.029)	0.343 (0.052)	0.185 (0.016)
	t-transformed	0.126 (0.038)	0.276 (0.040)	0.211 (0.016)
HD%	untransformed	0.064 (0.026)	0.279 (0.056)	0.164 (0.016)
	t-transformed	0.084 (0.041)	0.236 (0.037)	0.198 (0.016)

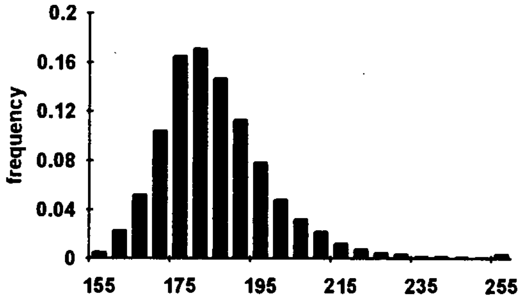
see Table 5.9 for information on transformations



A. hen housed production



B. hen day percentage



C. age at first egg in days

Fig. 5.1. Frequency histograms for the reproduction characters.

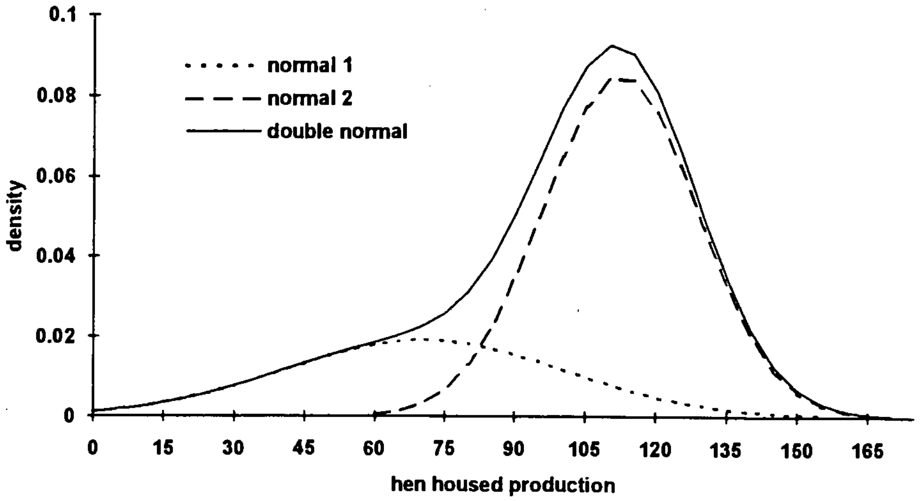


Fig. 5.2. The single (and aggregate double) normal density functions as underlying distributions of hen housed production.

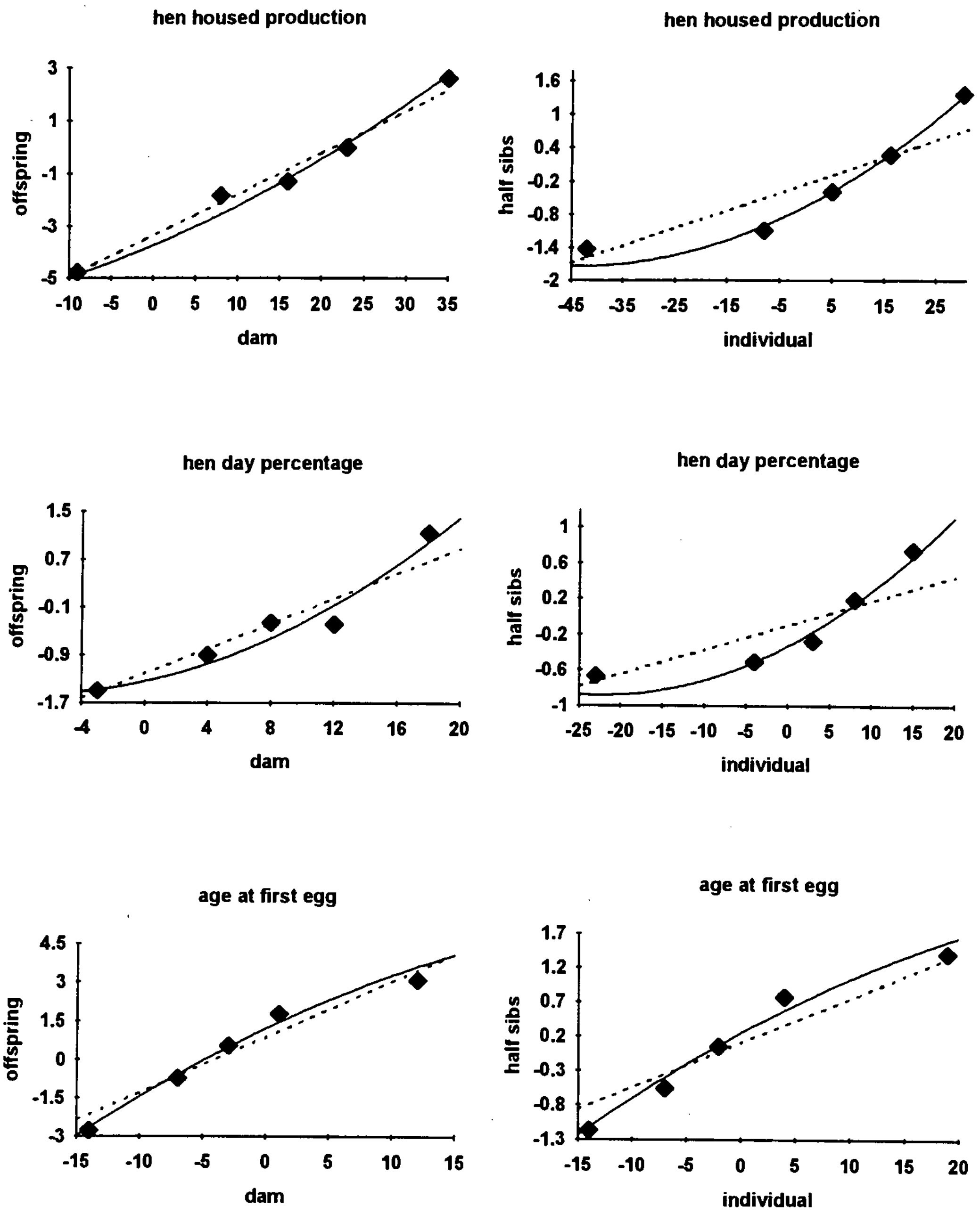


Fig. 5.3. Plots of the linear and curvilinear offspring-dam and half sib average-individual regression models and all the untransformed data ranked into five groups.

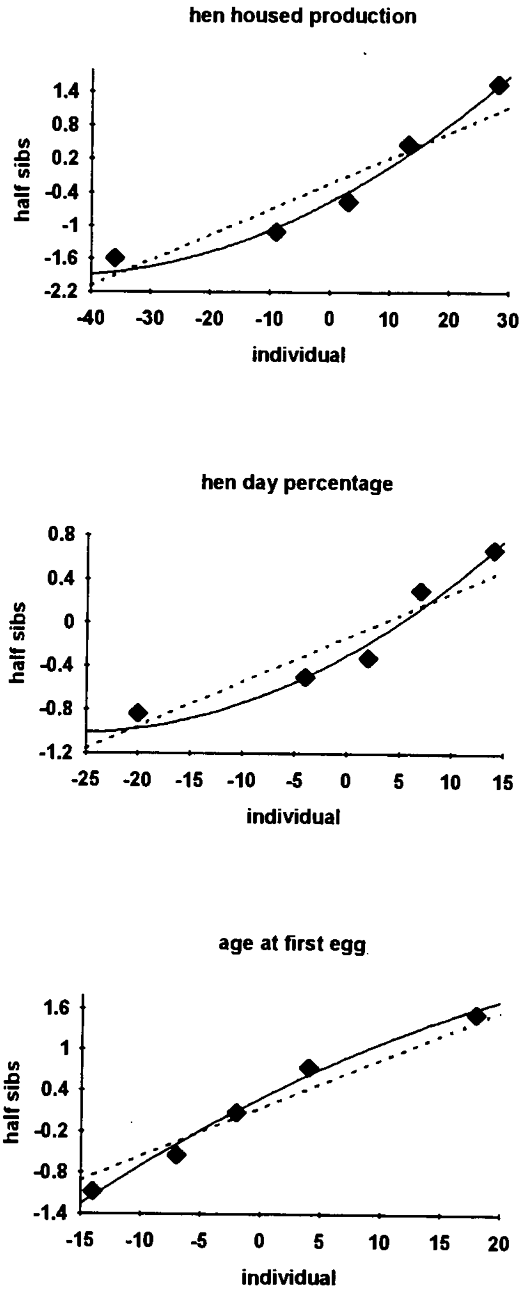


Fig. 5.4. Plots of the linear and curvilinear half sib average-individual regression models and the untransformed data ranked into five groups after exclusion of outlying observations with 25 eggs or less.

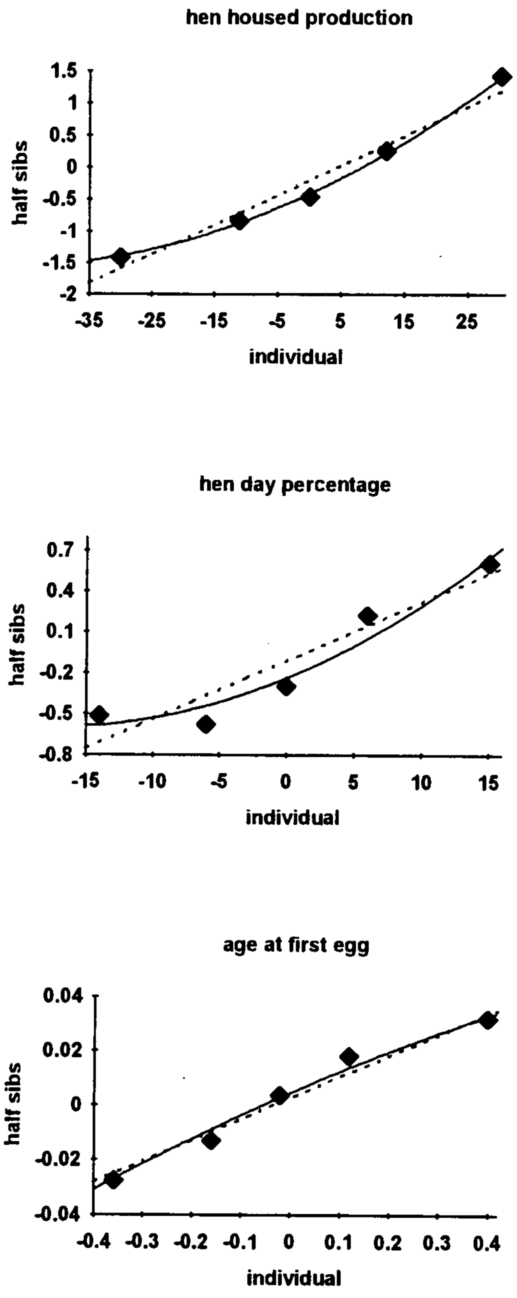


Fig. 5.5. Plots of the linear and curvilinear half sib average-individual regression models and all the t-transformed (HHP with t_{HHP} = 2.5 and HD% with $t_{HD\%}$ = 3.5) or the log-transformed (log(AFE-140)) data ranked into five groups.

CHAPTER 6

RESTRICTED MAXIMUM LIKELIHOOD ESTIMATION OF GENETIC PARAMETERS FOR EGG PRODUCTION TRAITS IN RELATION TO JUVENILE BODY WEIGHT IN BROILER CHICKENS

INTRODUCTION

Chambers (1990), in a comprehensive survey on the genetics of growth and meat production in chickens, reported that genetic relationships between growth and reproduction traits were reviewed by Marks (1985) and Siegel and Dunnington (1985). He added that little additional information appeared since their reports, which at present still holds true. In fact, the genetic correlations presented by Marks (1985) and Siegel and Dunnington (1985) were largely derived from studies performed two to three decades earlier (*eg.* Ideta and Siegel, 1966; Kinney, 1969). Consequently, the question arises how population parameters have been affected by prolonged selection for performance traits.

Up to date population specific estimates are of great relevance as many generations of extensive selection might well have changed the genetic correlations between juvenile body weight and egg production characters due to i) differential selection objectives driving gene frequencies in different directions, and thus making parameters unique to individual populations (Falconer, 1989) and ii) combined selection for broiler and egg production traits (in dam lines), which increases the likelihood of fixation of pleiotropic or closely linked genes causing changes in genetic covariation among the genes left segregating (Lush, 1948; Lerner, 1950). Environmental changes during this time span may also have had an impact on the magnitude of genetic correlations. For example, nowadays feed restriction programs for broiler parents are routine husbandry practices (Katanbaf *et al.*, 1989), whereas in the studies by Ideta and Siegel (1966) and Kinney (1969) parents were fed *ad libitum*. Strong evidence of differential genetic correlations between two traits measured in an *ad libitum versus* feed-restricted environment was found in pigs (Crump, 1992; Cameron *et al.*, 1995).

Current broiler breeding programs generally have a sequential selection structure in which selection for reproduction is typically performed after some selection for growth. Multiple trait genetic evaluation may be required to overcome selection bias, and possibly depression of genetic progress in such populations (Pollak *et al.*, 1983; Koerhuis and van der Werf, 1994). In these cases, estimation of the (co)variance matrices, needed for the genetic evaluation, by ANOVA-type methods may yield strongly biased results (Rothschild *et al.*, 1979; Meyer and Thompson, 1984). Restricted Maximum Likelihood (REML, Patterson and Thompson, 1971), applied to an Individual Animal Model (IAM) (*eg.* Henderson; 1988), can alleviate this selection bias when all the data that selection decisions were based upon are included in the analysis, which makes it statistically superior but at the same time computationally cumbersome. However, the rapid growth in power of computers accompanied by recent improvements of computing algorithms (Thompson and Hill, 1990; Thompson *et al.*, 1995) have made IAM-REML feasible for solving some of the problems described here, involving large numbers of animals.

In Chapter 5 it was shown that some of the egg production characteristics in the present data were very non-normal and that properties could be improved upon by either outlier elimination or data transformation of some kind. The resulting heritabilities based on the transformed data increased substantially, particularly for HHP and HD%. The changes in correlations among egg production traits and in relation to juvenile body weight due to transformation of the data were not investigated, but are of interest.

Objectives of the present study were 1) to estimate genetic (co)variances and parameters for egg production characteristics in relation to juvenile body weight and genetic (co)variances and parameters among egg production characteristics by REML using bi- and multivariate individual animal models in female line meat-type chickens and 2) to investigate the effect of transformation of the egg production data on the magnitude of heritability and correlations between the egg production traits and juvenile body weight and among the egg production traits.

MATERIALS AND METHODS

Data

Data were available on approximately 8 overlapping generations of a broiler-type female line. The traits considered were juvenile body weight (JBWT), recorded at 6 weeks of age; the age at first egg in days (AFE) indicative of the point of sexual maturity; the number of eggs until 48 weeks of age, hen housed production (HHP); the rate of lay in the period from AFE to 48 weeks, hen day percentage (HD%); and the average egg weight (EWT), recorded at 28 weeks of age. Descriptive statistics of all traits are summarised in Table 6.1. Details on the non-normality of the egg production traits in these data were given in Chapter 5. The total number of animals in the JBWT data was 573 127, from which 2 113 were sires and 16 260 were dams. The population was subjected to some selection for secondary traits *(eg.* conformation and leg-defects), however, the vast majority of the selection pressure was put on both JBWT and the reproduction characteristics.

Transformation of data

HHP and HD% were exposed to a Box-Cox power transformation (Box and Cox, 1964) to reduce non-normality and curvilinearity of heritability. Transformation parameters (t) of 2.5 for HHP and 3.5 for HD% were used as suggested for these data in Chapter 5. AFE was log-transformed after a shift of 140 days in location: log([AFE-140]) (Chapter 5). EWT was not transformed since it was normally distributed and linear in heritability (tests not presented).

Genetic models

The following linear IAM was fitted to the data on JBWT:

$$Y_{ijklm} = \mu + SEX_i + HW_j + AGE_k + a_l + p_m + e_{ijklm} \qquad [6.1]$$

where Y_{ijklm} is the phenotypic record of animal l on JBWT; μ is the grand mean; SEX_i is the fixed effect of the ith sex (i = 1,2); HW_j is the fixed effect of the jth hatch week (j = 1...304); AGE_k is the fixed effect of the kth class of age of dam (k = 1...7), representing the effect due to size of the egg; a_l is the random additive genetic effect of the l^{th} animal; p_m is the random permanent environmental effect of the m^{th} dam; and e_{ijklm} is the random environmental effect associated with record Y_{ijklm}.

With the exception of the sex effect, the linear model applied to the reproduction traits was identical to 6.1. The number of hatch weeks was slightly smaller ($j_{max} = 284$).

Methods of analysis

Bivariate estimation. Consider model 6.1 applied to the bivariate (body weight and egg production) traits in a more general matrix notation:

$$\begin{bmatrix} \mathbf{y}_1 \\ \mathbf{y}_2 \end{bmatrix} = \begin{bmatrix} \mathbf{X}_1 & 0 \\ 0 & \mathbf{X}_2 \end{bmatrix} \begin{bmatrix} \mathbf{b}_1 \\ \mathbf{b}_2 \end{bmatrix} + \begin{bmatrix} \mathbf{Z}_{a1} & 0 & \mathbf{Z}_{p1} & 0 \\ 0 & \mathbf{Z}_{a2} & 0 & \mathbf{Z}_{p2} \end{bmatrix} \begin{bmatrix} \mathbf{a}_1 \\ \mathbf{a}_2 \\ \mathbf{p}_1 \\ \mathbf{p}_2 \end{bmatrix} + \begin{bmatrix} \mathbf{e}_1 \\ \mathbf{e}_2 \end{bmatrix} \qquad [6.2]$$

where, for trait i (i =1,2), $\mathbf{y}_i$ is a vector of observations; $\mathbf{b}_i$ is a vector of fixed effects; $\mathbf{a}_i$ is a vector with random additive genetic animal effects; $\mathbf{p}_i$ is a vector with random maternal permanent environmental effects; $\mathbf{e}_i$ is a vector with random residual effects; and $\mathbf{X}_i$, $\mathbf{Z}_{ai}$ and $\mathbf{Z}_{pi}$ are incidence matrices relating the observations to the respective fixed and random effects. The assumed variance-covariance structure is:

$$V\begin{bmatrix} \mathbf{u} \\ \mathbf{e} \end{bmatrix} \equiv V\begin{bmatrix} \mathbf{a}_1 \\ \mathbf{a}_2 \\ \mathbf{p}_1 \\ \mathbf{p}_2 \\ \mathbf{e}_1 \\ \mathbf{e}_2 \end{bmatrix} = \left[\begin{array}{cccc|cc} \mathbf{A}\sigma^2_{a1} & \mathbf{A}\sigma_{a12} & 0 & 0 & 0 & 0 \\ \mathbf{A}\sigma_{a12} & \mathbf{A}\sigma^2_{a2} & 0 & 0 & 0 & 0 \\ 0 & 0 & \mathbf{I}_1\sigma^2_{p1} & \mathbf{B}\sigma_{p12} & 0 & 0 \\ 0 & 0 & \mathbf{B}\sigma_{p12} & \mathbf{I}_2\sigma^2_{p2} & 0 & 0 \\ \hline 0 & 0 & 0 & 0 & \mathbf{I}_1\sigma^2_{e1} & \mathbf{C}\sigma_{e12} \\ 0 & 0 & 0 & 0 & \mathbf{C}\sigma_{e12} & \mathbf{I}_2\sigma^2_{e2} \end{array}\right] \equiv \left[\begin{array}{cc|c} \mathbf{A}\otimes\mathbf{G} & 0 & 0 \\ 0 & \mathbf{P} & 0 \\ \hline 0 & 0 & \mathbf{R} \end{array}\right] \equiv \begin{bmatrix} \mathbf{T} & 0 \\ 0 & \mathbf{R} \end{bmatrix}$$

$$V\left(\mathbf{y} = \begin{bmatrix} \mathbf{y}_1 \\ \mathbf{y}_2 \end{bmatrix}\right) = \begin{bmatrix} \mathbf{Z}_{a1} & 0 & \mathbf{Z}_{p1} & 0 \\ 0 & \mathbf{Z}_{a2} & 0 & \mathbf{Z}_{p2} \end{bmatrix} \mathbf{T} \begin{bmatrix} \mathbf{Z}_{a1} & 0 & \mathbf{Z}_{p1} & 0 \\ 0 & \mathbf{Z}_{a2} & 0 & \mathbf{Z}_{p2} \end{bmatrix}' + \mathbf{R} \equiv \mathbf{ZTZ}' + \mathbf{R}$$

where σ^2_{ai}, σ^2_{ci} and σ^2_{ei} are the additive genetic, the maternal permanent environmental and the residual environmental variances for trait i; σ_{a12}, σ_{p12} and σ_{e12}

are the corresponding covariances between the traits 1 and 2; **A** is the relationship matrix; $\mathbf{I}_i$ is an identity matrix; **B** is an incidence matrix linking progeny records of body weight and egg production to the dam; **C** is an incidence matrix relating body weights to egg production records; and $\otimes$ denotes direct product.

REML estimation of these (co)variances would yield a 9-dimensional maximisation problem. Thompson *et al.* (1995) proposed scaling and transformation models by which the computation can be reduced. The two correlated residual effects in **R** were reparameterised into independent effects (σ^{*2}_{e1} and σ^{*2}_{e2}) by introducing an extra uncorrelated effect (σ^2_b) common to both traits after appropriate scaling:

$$\begin{aligned}\sigma^2_{e1} &= \sigma^{*2}_{e1} + a^2\sigma^2_b \\ \sigma_{e12} &= ab\sigma^2_b \\ \sigma^2_{e2} &= \sigma^{*2}_{e2} + b^2\sigma^2_b\end{aligned}$$

where a ($=\sigma^*_{e1}$) and b ($=\sigma^*_{e2}$) are scaling factors. Meyer's (1989) univariate algorithm could then be used to evaluate the likelihoods. Further scaling of **G** and **P** into $\mathbf{G}_s$ and $\mathbf{P}_s$, respectively, with $\mathbf{G}_s = \mathbf{sGs}$, $\mathbf{P}_s = \mathbf{sPs}$ and $\mathbf{s} = \begin{bmatrix} 1/\sigma^*_{e1} & 0 \\ 0 & 1/\sigma^*_{e2} \end{bmatrix}$, allowed estimation of σ^{*2}_{e1} and σ^{*2}_{e2} from the respective partial derivatives of the log-likelihood (log L) function, given $\mathbf{G}_s$, $\mathbf{P}_s$ and σ^2_b, and thereby reducing the dimension of search from 9 to 7. See Thompson *et al.* (1995) for more details. For the present data this algorithm resulted in 1 753 171 equations in the mixed model. The log L values were found directly by a derivative-free approach (Meyer, 1989). Equations in the mixed model matrix (MMM), the coefficient matrix and the RHS's augmented, were reordered using a multiple minimum degree reordering (George and Liu, 1980) to minimise fill-in, before Gaussian elimination was performed on MMM. This resulted in 9 386 915 non-zero elements in the reordered MMM. The maximum log L was localised by the Downhill Simplex method. Initial runs were performed including a threshold-factor (Thompson *et al.*, 1994) with size 10^{-3}, being the operational zero for off-diagonal elements in MMM, and convergence was assumed when the variance of log L values in the simplex was less than 10^{-2}. In this way, the multi-dimensional likelihood surface was roughly 'scanned' for the maximum with time savings per likelihood evaluation being over 60%. The parameters obtained from the maximum of the approximate run were used as priors in the final run, where the operational zero was set to 10^{-8} for both diagonal and off-diagonal elements and a convergence criterion of 10^{-5} was assumed. This two-step procedure proved to be robust and very time efficient for these sizeable data sets, particularly when the initial choice of priors was poor. Approximate sampling errors of the heritabilities and the permanent environmental variances proportional to the phenotypic variances were based on a Taylor series expansion about the maximum log L (Smith and Graser, 1986). Sampling errors of genetic and permanent environmental correlations were approximated according to Robertson (1959). The bivariate analyses evaluating JBWT and the individual reproduction traits (HHP, HD%, AFE and EWT) resulted in four estimates of variance components and parameters for JBWT which were presented as an arithmetic average.

Multivariate estimation. In illustration of the applied method consider model 6.2 and its variance-covariance structure again, assuming equal design matrices (*i.e.* $\mathbf{X}_1=\mathbf{X}_2$, $\mathbf{Z}_{a1}=\mathbf{Z}_{a2}$ and $\mathbf{Z}_{p1}=\mathbf{Z}_{p2}$) for the traits y_1 and y_2. In order to reduce computations involved in multivariate equal design estimation of variance components, Thompson and Hill (1990) suggested a sequence of univariate analyses based on analysing the transformed traits in $\mathbf{z}=\mathbf{H}_0\mathbf{y}=\begin{bmatrix}1 & 0\\ 0 & 1\\ 1 & 1\end{bmatrix}\begin{bmatrix}\mathbf{y}_1\\ \mathbf{y}_2\end{bmatrix}=\begin{bmatrix}\mathbf{y}_1\\ \mathbf{y}_2\\ \mathbf{y}_1+\mathbf{y}_2\end{bmatrix}$ to determine **G**, **P** (see above) and **E** (the environmental variance-covariance matrix). Covariance terms in **G**, **P** and **E** were estimated using the formula: $\text{cov}(y_1, y_2) = \frac{1}{2}[\text{var}(y_1+y_2)-\text{var}(y_1)-\text{var}(y_2)]$. A canonical transformation **T** reducing **G** and **E**+**P** to diagonal and identity form, respectively, was identified. Univariate analyses were repeated using the less correlated canonical variates $\mathbf{z}=\mathbf{H}_0\mathbf{T}\mathbf{y}$. Back transformation of the canonical variances to the original scale allows the procedure to be repeated, until **T** gives approximately uncorrelated canonical variates. This algorithm was only applied to the reproduction data, including the traits HHP, HD%, AFE and EWT simultaneously in a quadrivariate analysis which involved 10 separate univariate analyses. Each univariate analysis had 21 362 equations and 121 688 non-zero elements in the reordered MMM. A convergence criterion of 10^{-6} was assumed for the univariate analyses on both the original and the canonical scale, locating the maximum log L as described above. The iteration procedure was ceased when the mean absolute values of correlations on the canonical scale were less than 10^{-4} or after 15 iteration rounds. Test runs showed that changes in (co)variance estimates were minimal when the procedure was allowed to go beyond this point.

Univariate variance estimation for JBWT and the reproductive traits was considered also, as a comparison to the bivariate and multivariate estimates. The maximum log L was obtained in the same manner, assuming convergence at 10^{-8}.

RESULTS

Estimates of the variances and parameters from the analyses of untransformed data are shown in Table 6.2. The bivariate analyses resulted in a somewhat increased accuracy for JBWT through correlations with the reproductive traits. There was a slight increase in σ_a^2, primarily originating from the inclusion of EWT, and as a consequence the h^2 increased from 0.28 to 0.29 which was not significant (SE of h^2 was 0.008). Considering all the JBWT records in the bivariate analyses of HHP, HD% and AFE did not significantly affect the h^2 estimates, which were low for HHP and HD% and intermediate for AFE. The estimates of σ_p^2 for HHP and HD% increased somewhat (from 712 to 730 and from 204 to 209, respectively), however this was due to increases in the σ_e^2 estimates (from 592 to 612 and from 179 to 183, respectively). The c^2 estimates remained unaltered. The differences between the r_g and r_p estimates were not large for HHP, HD% and AFE, and r_g and r_p estimates were generally similar to estimates of r_c and r_e respectively. The heritability of EWT, on the other hand, was significantly underestimated ($P<0.05$) when ignoring selection on JBWT in the univariate analysis (0.55 *vs.* 0.64). The bivariate analysis increased the σ_a^2 variance component by 31% relative to the univariate estimate. The genetic correlation between JBWT and EWT was high (0.63) and the difference with r_e (-0.14) substantial.

A multivariate (4-trait) analysis was performed among the reproductive characters. The genetic and phenotypic correlation of HHP with HD% were close to unity (0.92 and 0.89 respectively). The difference in genetic correlation of AFE with HHP and HD% was considerable (-0.76 *vs.* -0.45). The σ_a^2 estimates of HHP and HD%, in particular, were greater relative to either the uni- or the bivariate analyses resulting in somewhat greater heritabilities although not significant. The additional additive genetic variation observed in HHP and HD% can be attributed to AFE, which was highly genetically correlated with HHP (-0.76) especially, and less phenotypically correlated (-0.44). The σ_c^2 estimates and the derived c^2 parameter were not affected. The r_g and r_p estimates of EWT with HHP, HD% and AFE were close to zero, and hence the multivariate variance component estimates of EWT were identical to the univariate components.

Results of the analyses on the transformed reproduction data are presented in Table 6.3. The bi- and multivariate variance component estimates and the corresponding dispersion parameters of the original JBWT and EWT data, respectively, were not affected by the transformation of the other reproductive traits. Compared to the variances of the untransformed traits, the transformation of HHP and HD% brought about a much smaller environmental variance proportional to the estimate of σ_a^2. Consequently, the h^2 estimates of HHP and HD% increased considerably ($P<0.01$) from 0.14 to 0.21 and from 0.10 to 0.18, respectively. The increase in h^2 of log-transformed AFE was much smaller (0.34 to 0.38), yet significant at $P=0.05$. As for the reproductive traits on the original scale, the bivariate analyses on the transformed scale did not affect the dispersion parameter estimates of these traits significantly. The genetic correlations between JBWT and the transformed reproductive traits were only a little more unfavourable and hence changes were statistically insignificant. The estimates of r_c for HHP and HD% were somewhat closer to zero. The relative changes in variance component and genetic parameter estimates of multivariate compared to univariate analyses were similar for reproductive data on the original and the transformed scale. Noteworthy are the more negative r_g estimates between EWT and HHP and HD%, respectively changing from -0.08 to -0.21 and -0.07 to -0.22 with significance at P=0.05.

DISCUSSION

Heritability estimates of reproductive traits

The present IAM-REML heritabilities for the untransformed reproductive traits HHP and HD%, accounting for variation due to maternal permanent environment, were very similar to estimates for the same data derived from the regression of half sib average on individual (0.13 and 0.11 for HHP and HD%, respectively) in Chapter 5. The regression estimates were a little lower for the reproductive traits on a transformed scale (0.18 and 0.17 for HHP and HD%, respectively). For AFE the differences between this genetic regression and the present IAM-REML estimates on the original (0.26 *vs.* 0.34) and the log scale (0.31 *vs.* 0.38) were somewhat greater. Some difference between these methods is, of course, anticipated as the regression of half sib average on individual is equivalent to the analysis of variance of half sibs (Hill, 1978), whereas REML considers all genetic relationships and offspring-parental and collateral information, which is likely to yield a higher pooled estimate of the heritability.

A comparison of the present heritability estimates of reproductive traits was made to some frequently cited results in the literature on meat-type poultry (see Table 6.4). The estimates of Ideta and Siegel (1966) were based on the realised response in the seven initial generations of Siegel's bidirectional selection experiment on juvenile body weight. Kinney (1969) summarised the literature estimates on meat-type poultry. The estimates of Ideta and Siegel (1966) were atypical for HD% and AFE. The authors mentioned that their population had no selection history for egg production, which according to them could explain the much higher additive genetic variation. However, in that situation one might also then have expected a higher estimate for AFE. Consideration of the standard errors in their study (0.13 and 0.06

for HD% and AFE, respectively) points towards those estimates being considerably affected by chance. Kinney's (1969) summary, in which extreme sampling cases are likely to average out, gave h^2 estimates much more similar to the present study. In spite of the inclusion of eight generations of data and genetic relationships, the present h^2 estimates are still expected to be somewhat reduced by selection applied for many more generations. The distributions of HHP and HD% are best described by a double normal mixture model with different dispersion and location parameters (Chapter 5). Alternatively, one could argue that in modern meat-type poultry dam line populations linear estimates of heritability of egg production are more underestimated due to greater non-normality and curvilinearity. This results from the 'pulling apart' of the true underlying normal distributions due to selection for egg production in these lines, with the right-hand distribution showing a greater (genetic) shift in location compared to the left-hand distribution. The distribution accounting for the left-hand tail is more affected by environmental variability (Chapter 5) resulting in a lower genetic response.

Recently, Besbes *et al.* (1993) and Wei and van der Werf (1993) estimated genetic parameters for reproductive traits in layers using IAM-REML methods. The former study solely considered an additive genetic effect, whereas the latter included a dominance component. Presumably, the c^2 effect included in the present study accounted for both maternal permanent environmental variation as well as most of the dominance variation, since this component largely represented covariances between full sibs (the majority of dams was nested within sire) and therefore is likely to be highly correlated with dominance. The h^2 estimates of Wei and van der Werf (1993) were clearly higher and the effect of transformation was smaller (for HHP in 26-65 wks the average heritability of 3 populations was 0.23 and 0.26 on the original and transformed scales, respectively). The estimates of Besbes *et al.* (1993), ignoring any c^2 effect, and the sensitivity of the h^2 to transformation were somewhat lower relative to the present study (for HHP in 26-54 wks the average heritability of 2 populations was 0.12 and 0.17 on the original and transformed scales, respectively). Our definition of HHP is, however, affected by variation in AFE, and therefore the comparison with HD% might be more appropriate. The h^2 of HD% rose by 80% (from 0.10 to 0.18) due to transformation. The combined selection for broiler and reproductive characteristics in these populations might increase the incidence of recessive genes with a deleterious effect on reproduction (Chapter 5) and of several reproductive complications associated with broiler growth (Siegel and Dunnington, 1985). As a result transformation might generally have more effect in such meat-type populations with possibly a higher proportion of the birds representing the distribution accounting for the left-hand tail.

Correlation estimates between body weight and reproduction

The r_g between JBWT and percent egg production (HD%) was similar for Ideta and Siegel (1966) and Kinney (1969) and notably more antagonistic in this study (see Table 6.5). In the former studies selection pressure was on JBWT, whereas the present population was subjected to improvement of both JBWT and egg production. As a result, this more negative correlation might be explained by the fixation of some pleiotropic and/or closely linked genes with a favourable effect on both JBWT and HD%. Also, genes with independent desirable effects on either trait are likely to be directed towards fixation, while allelic genes with undesirable effects might be lost (Lush, 1948; Lerner, 1950). However, in a two-trait selection experiment of 22 generations on *Drosophila melanogaster*, changes in genetic correlations were variable and unpredictable (Sheridan and Barker, 1974). The differences in correlations with AFE and EWT were more profound, the present study showing a change of sign for AFE compared to the former ones.

The possible effect on the genetic correlations of feed restriction applied to the present population during the rearing and laying periods, to preclude obesity and its negative effects on reproduction (Katanbaf *et al.*, 1989), cannot be ignored. In pigs, for instance, feed restriction is known to change the sign of the genetic correlation between daily gain and backfat depth. Lean growth requires less energy than fat deposition and so at higher levels of restriction the animals which grow faster will be those which are depositing muscle rather than fat, while at *ad libitum* feeding levels energy is not limiting and so the faster growing animals will be producing both lean and fat (Crump, 1992; Cameron *et al.*, 1995). Our case, however, is slightly different in that JBWT is not affected by restriction of feed but egg production is, since body weight is controlled after *ad libitum* growth to 6 weeks of age. Studies have shown that sexual maturity can be achieved only if thresholds of chronological age, body weight, and body composition are reached (for references see Katanbaf *et al.*, 1989). The lower limit for genetic potential of minimum age of lay should be expressed under *ad libitum* feeding, whereas a restricted feeding regime should allow for expression of minimum body weight and body composition requirements (Katanbaf *et al.*, 1989). Body weight *per se* was probably relevant to the start of egg production in the populations studied by Ideta and Siegel (1966) and Kinney (1969), resulting in a negative correlation with AFE. In the present genetically much heavier and leaner, restricted-fed population, body weight *per se* is not expected to have an effect on AFE, except perhaps in the unlikely event where JBWT is considerably negatively correlated to body weight at onset of lay (which was unavailable). Hence, the relationship of JBWT with body composition is very likely an important determinant of the positive r_g between JBWT and AFE. Birds which are genetically superior for JBWT are generally more efficient (r_g between weight gain and FCR is -0.50; Pym, 1990), and might in a feed-restricted environment preferentially partition energy towards protein deposition rather than towards fat deposition. As a consequence, the heavier juvenile birds probably take a longer time to surpass the threshold for fat reserves. This positive effect on AFE is likely to drive the genetic correlation of JBWT with HHP and HD% down, because of the genetic relationship between those traits and AFE.

As stated previously, body weight *per se* can in some cases accelerate onset of egg production through effects on endocrine tissue growth and target organ sensitivity (Siegel and Dunnington, 1985). This increased potential to respond in heavier birds can only have an effect on age at first egg if the photoreceptors respond to photostimulation. The 'photoperiodic drive', describing the response of the bird to photostimulation, can be quantified as the number of days to first egg after relaxing dietary restriction (Eitan and Soller, 1994). Eitan and Soller (1994) found a negative effect of body weight on the photoperiodic drive, which could contribute to the positive sign of the genetic correlation between JBWT and AFE.

The effects of transformation on the correlation parameters were generally small. Besbes *et al.* (1993) also observed only slight changes in genetic correlations after transformation. The estimates of the genetic correlations of HHP and HD% with EWT, however, became considerably more antagonistic. The resulting correlations were in fact similar to estimates summarised by Kinney (1969). The multivariate correlation estimates related to EWT might be somewhat biased due to ignoring any selection on the highly correlated JBWT. The correlation parameters involving the other reproductive characters are not expected to be affected much due to the generally low genetic relationships with JBWT. Consequently, the genetic evaluation of reproductive merit in the present population could probably ignore any relationship with JBWT, which could lead to substantial savings in computing when applying multivariate BLUP. Consideration of selection for JBWT in the genetic evaluation of EWT is recommended to preclude large bias in the latter trait. A better understanding of the genetic and physiological relationships between these traits can optimise selection strategy and management within the selection programme.

SUMMARY AND CONCLUSIONS

Juvenile body weight (JBWT) and the reproductive traits, hen housed egg production (HHP), rate of lay expressed as hen day percent (HD%), age at first egg (AFE) and egg weight (EWT) on approximately 8 overlapping generations of a broiler-type female line were available to study 1) their genetic (co)variances and dispersion parameters, and 2) the effect of transformation of the egg production data on the magnitude of heritability and the genetic correlation structure. Bi- and multivariate animal model REML estimations were feasible for the present sizeable data sets (including 573 127 animals) by reducing the models to univariate forms using scaling and transformation.

Heritabilities were low for HHP (0.14) and HD% (0.10), intermediate for AFE (0.34) and high for EWT (0.55). Genetic correlations between JBWT and HHP (-0.18), HD% (-0.20) and AFE (0.15) were low, whereas EWT was highly correlated to JBWT (0.63) and only the bivariate heritability estimate of EWT was increased by including all the JBWT data (0.55 increased to 0.64). Genetic correlations of HHP with HD% and AFE were large (0.92 and -0.76, respectively), while HD% and AFE were less correlated (-0.45). EWT was little correlated to the other reproductive characters. Box-Cox transformation of HHP and HD% and logarithmic transformation of AFE increased the heritability estimates (0.21, 0.18 and 0.38 for HHP, HD% and AFE, respectively), but had generally little effect on the genetic correlation estimates. Comparison to earlier literature estimates revealed substantial differences in the genetic correlation structure. Possible reasons were discussed. A better understanding of the genetic and physiological relationships between these traits can optimise selection strategy and management within the selection programme.

TABLE 6.1

Descriptive statistics for juvenile body weight in kg×10^{-2} (JBWT), hen housed production (HHP), hen day percentage (HD%), age at first egg in days (AFE) and egg weight in g (EWT).

trait	# records	mean	SD	CV (%)
JBWT	570 508	185.5	30.1	16.2
HHP	15 038	100.0	28.6	28.6
HD%	15 038	65.0	14.8	22.8
AFE	15 038	182.1	14.7	8.1
EWT	13 801	55.4	3.9	7.0

TABLE 6.2

Uni-, bi- and multivariate IAM-REML variance and dispersion parameter estimates for JBWT ($kg^2 \times 10^{-4}$) and the reproductive traits HHP, HD%, AFE and EWT ($g^2/10$).

	Univariate analyses (UNI)					Bivariate analyses (BI)					Multivariate analysis (MULTI)			
variance	JBWT	HHP	HD%	AFE	EWT	JBWT[δ]	HHP	HD%	AFE	EWT	HHP	HD%	AFE	EWT
additive genetic	74	100	20	58	77	76	97	19	58	101	112	22	59	77
mat. perm.environmental	11	20	6	3	3	7	21	7	2	1	19	6	3	3
residual	179	592	179	110	60	183	612	183	106	55	585	177	109	60
phenotypic	264	712	204	171	140	266	730	209	167	157	716	205	171	140
trait														
JBWT[α]	0.28					0.29	-0.11	-0.09	0.09	0.21				
HHP		0.14				-0.18	0.13				0.16	0.89	-0.44	-0.03
HD%			0.10			-0.20		0.09			0.92	0.11	-0.18	-0.02
AFE				0.34		0.15			0.35		-0.76	-0.45	0.35	0.02
EWT					0.55	0.63				0.64	-0.08	-0.07	0.07	0.55
JBWT[β]	0.04					0.03	-0.10	-0.08	0.07	-0.14				
HHP		0.03				-0.21	0.03				0.03	0.88	-0.35	0.01
HD%			0.03			-0.18		0.03			0.95	0.03	-0.11	0.02
AFE				0.02		0.05			0.01		-0.56	-0.42	0.02	-0.02
EWT					0.02	-0.15				0.01	-0.47	-0.47	0.22	0.02

[α] : heritabilities (h^2) on the diagonal, phenotypic correlations above and genetic correlations (r_g) below the diagonal; UNI: SE of h^2 of JBWT and the average SE of the h^2s of the reproductive traits were 8×10^{-3} and 0.02, respectively; BI: average SE of the r_gs between JBWT and the reproductive traits was 0.03; MULTI: average SE of the r_gs among the reproductive traits was 0.04.

[β] : maternal permanent environmental variances proportional to the phenotypic variances (c^2) on the diagonal, environmental correlations above and maternal permanent environmental correlations (r_c) below the diagonal; UNI: SE of c^2 of JBWT and average SE of the c^2s of the reproductive traits were 1×10^{-3} and 0.01, respectively; BI: average SE of the r_cs between JBWT and the reproductive traits was 0.06; MULTI: average SE of the r_cs among the reproductive traits was 0.12.

[δ] : variances and parameters of the four bivariate analyses were averaged for JBWT

TABLE 6.3

Uni-, bi- and multivariate IAM-REML variance and dispersion parameter estimates for JBWT and the Box-Cox transformed HHP (t=2.5) and HD% (t=3.5), the log-transformed AFE (log[AFE-140]) and the original EWT.

	Univariate analyses			Bivariate analyses				Multivariate analysis			
variance	HHP	HD%	AFE$^{\alpha}$	JBWT	HHP	HD%	AFE$^{\alpha}$	HHP	HD%	AFE$^{\alpha}$	EWT
additive genetic	95	19	31	76	96	20	30	106	21	31	77
mat. perm. environmental	12	3	2	7	11	3	1	12	3	2	3
residual	345	86	48	183	358	89	46	339	85	48	60
phenotypic	452	108	82	266	465	112	77	457	109	81	140
trait											
JBWT				0.29	-0.13	-0.11	0.10				
HHP	0.21			-0.21	0.21			0.23	0.88	-0.47	-0.06
HD%		0.18		-0.22		0.18		0.90	0.19	-0.17	-0.06
AFE			0.38	0.18			0.39	-0.73	-0.37	0.38	0.04
EWT								-0.21	-0.22	0.09	0.55
JBWT				0.03	-0.10	-0.08	0.10				
HHP	0.03			-0.14	0.02			0.03	0.88	-0.37	0.04
HD%		0.03		-0.13		0.03		0.90	0.03	-0.09	0.04
AFE			0.02	0.04			0.01	-0.55	-0.21	0.02	-0.00
EWT								-0.36	-0.21	0.28	0.02

See Table 6.2 for definitions and layout of the genetic parameters and sizes of SEs.

$^{\alpha}$: variances of log (AFE-140) multiplied by 10^3

TABLE 6.4

Some literature heritability estimates of reproductive traits in meat-type poultry compared to the univariate estimates on the original data in the present study.

	heritability estimates		
trait	Ideta and Siegel (1966)	Kinney (1969)	present study
HHP	-	-	0.14
HD%	0.48	0.15	0.10
AFE	0.19	0.39	0.34
EWT	0.53	0.57	0.55

TABLE 6.5

Some literature estimates of genetic correlations between JBWT and the reproductive traits in meat-type poultry compared to the bivariate estimates on the original scale in the present study.

	Genetic correlation estimates with JBWT		
trait	Ideta and Siegel (1966)	Kinney (1969)	present study
HHP	-	-	-0.18
HD%	-0.14	-0.12	-0.20
AFE	-0.24	-0.10	0.15
EWT	0.23	0.26	0.63

CHAPTER 7

GENERAL DISCUSSION

Methodology and computing

Traditionally, the need to use REML (co)variance component estimation (Patterson and Thompson, 1971) has been less for poultry than for other domestic species (Hartmann, 1992). However, broiler breeding schemes have become increasingly complex with the introduction of additional traits like FCR and reproduction. Their sequential selection structure inevitably causes ANOVA-type methods to produce biased dispersion parameters (Rothschild *et al.*, 1979; Meyer and Thompson, 1984). REML can alleviate this selection bias when the data that selection decisions were based upon are included in the analysis. Therefore, REML applied to individual animal models has been used throughout in this thesis.

To allow REML analysis of poultry data including large numbers of animals, subsetting of the data has been applied in the literature (*eg.* Besbes *et al.*, 1992). Population estimates can be found by pooling the results of the subsets of data. Empirical sampling errors ($\sigma/\sqrt{n}$, where n is the number of subsets) can be derived simultaneously. Disadvantages of this method are (1) the simple arithmetic mean of the subset estimates do not necessarily maximise the likelihood of the total data, (2) for multivariate analysis combined matrices might not be positive semi-definite and (3) estimates might be more affected by large sampling (co)variation. Although (2) can be circumvented by forcing matrices to be within the bounds of the parameter space (*eg.* by a procedure termed 'bending' (Hayes and Hill, 1981)) it does not guarantee maximum likelihood of the total data given the pooled ('bent') subset estimates. Hence, from a statistical viewpoint, REML on total data, as performed in the present studies, must be preferred.

Despite the large number of animals, comprehensive analyses including several random effects (particularly in Chapters 2 and 6) were facilitated by the specific data structure of poultry populations with a high ratio of non-parents to parents resulting in a relatively low number of additional non-zero off-diagonal elements (fill-in) after Gaussian elimination of the reordered equations in the mixed model matrix. Koerhuis (1994) showed that, for a purely direct additive genetic animal model, the reordering of equations based on the number of off-diagonals (Meyer, 1989) reduced the CPU time per likelihood evaluation by a factor of 12 for the JBWT data in Chapter 2 compared to a factor of 2 to 3 for data that were more typical for other domestic species (Meyer, 1991).

Practical implications and suggestions for further research

The finding of a negative genetic relationship between the direct additive and the maternal additive genetic components (r_{AM}) of JBWT using standard models for the genetic evaluation of maternal effects due to Meyer (1989) was not expected *a priori*. Various estimates and thoughts presented in the literature, although often at a phenotypic level, suggest otherwise (Al-Murrani, 1979; Marks, 1985; Chambers, 1990). These unexpected results prompted two directions of research (1) the investigation of more appropriate and detailed statistical models taking into account the possible environmental dam-offspring covariance (Chapter 2) and (2) the identification of individual maternal pathways related to the egg and investigation of their effect on offspring-parental regressions and their genetics (Chapter 3).

The models investigated in Chapter 2 might not be the most effective for poultry where several maternal performances related to the egg are readily directly observed (see Chapter 3). However, for other species (*eg.* beef cattle) studies on these new models for the estimation of maternal effects as alternative to the existing models by Meyer (1989) would be of interest.

In Chapter 2 it is suggested that increased weight loss during incubation can have a negative maternal effect on JBWT. The loss in egg weight is often the consequence of poor calcification, high shell porosity and hence inferior specific gravity, which impair embryonic survival (Robinson *et al.*, 1993). Weight loss from set to transfer and specific gravity are inherently related to egg shell quality. Therefore, direct selection for those traits (with intermediate heritabilities of around 0.3, as estimated in Chapter 3) in female lines must be seriously considered, primarily to restrict the negative trend of embryonic survival, often expressed as hatchability of fertile eggs (HOF), in response to selection for JBWT (Robinson *et al.*, 1993), but perhaps also to improve JBWT somewhat more efficiently by alleviating the maternal variation due to various egg quality related traits although extra gains are unlikely to be great (Chapter 3). This might offer an efficient means for indirect improvement of HOF since direct selection has often been shown to be insufficient due to extremely low heritabilities (*eg.* 0.03 estimated by Catterall and Pollott, 1995).

It is likely that weight loss during incubation and specific gravity are curvilinear in their relationships with the percentage HOF and thus optimum levels of these traits might have to be strived for. The energy for embryonic development is provided by metabolism of egg yolk and like all other metabolic processes, requires the supply of oxygen and the expulsion of carbon dioxide. Since the weight of the chick is about 60-65% of the original egg weight, a considerable amount of water is lost during embryonic development. The shell, therefore, may be considered to be the respiratory organ of the embryo. In the initial stages of embryonic development, it alone is responsible for the transfer of gaseous water and carbon dioxide from the embryo and oxygen to the embryo by diffusion (Etches, 1993). Extreme shell structure and quality in either direction might handicap the egg's respiratory ability and hence the embryo's survival rate. Also, it is possible that egg shell quality problems occur only later in life. A detailed study on the curvilinearity of the correlations of egg quality traits with HOF, and the genetic relationships between egg quality traits over a wider age range would be useful. Continual monitoring of the changes in relationships between these traits and HOF should prevent overshooting of the possible optima from a point of view of maximisation of HOF.

Loss of accuracy by selection for a trait defined as a ratio can be especially high when differences in heritabilities and/or correlations of component traits are large (Chapter 4), which is not the case for FCR (Pym, 1990). A potentially more relevant candidate for indirect selection on the components is the rate of lay or hen day percentage (HD%) of broiler dams. The component traits of HD%, *i.e.* the number of eggs (numerator) and the age at first egg (explanatory of the variation in the denominator), differ considerably in heritability even when non-normality of these traits is accounted for (Chapters 5 and 6).

A mixture model of two Gaussian probability functions with different location and dispersion parameters gave the best fit to the phenotypic data for number of eggs (HHP) and rate of lay or hen day percent (HD%) (Chapter 5). Some individuals might be affected by disease which hampers their performance and creates a negative skewness. Statistically, these individuals' phenotypes are sampled from a 'foreign nuisance' population with shifted location and scale. However, in an environment with high risk of exposure to pathogens, what is a 'foreign nuisance' population in the present data could actually represent the basic model, so that the majority of individuals would be sampled from such an 'affected' distribution.

Breeders are evidently faced with the problem of genotype×environment (G×E) interaction. In considering this problem, Bell (1970) suggested that there were four alternatives, not necessarily mutually exclusive: 1) to select under a uniform and optimum environment, 2) to select under environmental conditions other than optimum, 3) to develop specialised strains or genotypes uniquely adapted to specific environmental conditions, and 4) to select for general adaptability to a wide range of environments. The route to take depends upon the economic importance of the trait of interest and the nature of the particular G×E interaction. The further study of the underlying genetic variability in the double-normal mixture model (as suggested in Chapter 5) can support such decisions. By assigning individuals to one or the other data populations, bivariate analysis can be performed to investigate the heritabilities and the genetic correlation of egg production performance in a low *versus* high 'health risk' environment which should help to model the possible solutions. Most nucleus poultry selection lines are held under isolated quarantine conditions in conjunction with disease eradication/limitation programs, which are often atypical of practical commercial environments with higher incidences and greater risk of exposure to pathogens (Sheridan, 1990). Such approaches might have to be reconsidered if the genetic correlation between performances in both environments proves to be low or even antagonistic. According to Sheridan (1990) some breeders already consider that exposure to pathogens assists in selection for viability in the field and are less stringent regarding disease preventative measures.

The effect of feed restriction applied during the rearing and laying periods, to preclude obesity and its negative effects on reproduction, was discussed in Chapter 6 as a possible reason for changes in genetic relationships between reproduction and growth performance in comparison to earlier literature. Commercial broiler parents are usually restricted in their growth during the first six weeks also. Hence, *ad libitum* growth of female line hens to six weeks of age, to obtain their JBWT for selection purposes, might introduce another important source of G×E interaction which could reduce the efficiency of selection for reproductive performance. Furthermore, the great length and intensity of the lighting intervals during this *ad libitum* growing period, reducing later responsiveness to photostimulation, could play a role. Studies on the genetic relationships between performances under these different circumstances are required. Female line hens raised in a restricted feed and lighting environment could be selected for *ad libitum* growth family performances. The loss of progress in broiler traits, due to 10-15% lower accuracy of these indices, could be counterbalanced by a considerably higher response in reproductive performance in commercially relevant environments. Depending on the genetic relationship between *ad libitum* and restricted growth, this loss could be diminished by incorporating the restricted growth performances into the selection decisions. An additional benefit might arise from a higher selection intensity as a result of better reproductive performance after restricted feed and lighting in the juvenile stage.

Use of poultry data to test quantitative genetic theory

Commercial broiler populations have been selected extensively over the past decades, particularly for JBWT. Havenstein *et al.* (1994) assessed the relative contributions of genetic selection and dietary regimen on the performance of broilers. Body weights were measured in a 1957 randombred control strain of broilers and in 1991 commercial broilers when fed "typical" 1957 and 1991 diets. The 1991 broilers on the 1957 and the 1991 diets were 4.1 and 3.4 times larger than the 1957 broilers at six weeks of age, which illustrates the extraordinary impact of genetic selection. As a result the additive genetic variation has decreased, the present studies showing appreciably lower heritabilities in comparison to earlier literature (0.33 and 0.26 in Chapter 2 *vs.* an average literature value of 0.41 (Chambers, 1990) although these are often based on weights at older ages). Nevertheless, sufficient variation has remained making further genetic improvement possible.

Mutation Frankham (1980) showed that mutations of major effect arising in selection lines can have a substantial contribution to genetic variation and hence can influence long term selection response. An important parameter determining the expected response from fixation of the new mutations is the new mutational variance arising per generation, V_M , which is usually expressed as a proportion of the environmental variance, V_M/V_E (Falconer, 1989; Keightley and Hill, 1992; Caballero *et al.*, 1995). Keightley and Hill (1992) estimated V_M/V_E for growth rate in the mouse using REML based on an individual animal model. The estimate of V_M/V_E maximising the likelihood was localised by approximation of the marginal log-likelihood surface of V_M/V_E. The analyses were based on 3142 records of an initially inbred line which had been selected divergently for 25 generations. Caballero *et al.* (1995) obtained an independent estimate of mutation rate for body weight in the mouse from that obtained by Keightley and Hill (1992).

For growth in broiler chickens similar exercises would be of interest and could, presumably, be performed with more statistical power despite data not being available on experimental divergently selected sublines. Generally, growth data and full pedigree structures are available for 10 to 15 generations of chickens. Data on

200 000 to 400 000 individuals over such a time range are not exceptional. Even for detailed statistical models (*eg.* Chapter 2) highly peaked likelihood curvatures are observed, locating maximum likelihood estimates with narrow confidence intervals. Keightley and Hill (1992) attempted to distinguish response and variance caused by initially segregating alleles ($V_{g,0}$, in the base population) from that due to new mutation. For such an investigation poultry data might make more powerful statistical inference possible, although $V_{g,0}$ is expected to be much larger in chickens as they are not highly inbred as were the mice used by Keightley and Hill. Also, extension to bivariate (or even multivariate) cases could be interesting and conceptually straightforward, if not computationally, with a mutational dispersion (variance-covariance) matrix rather than a dispersion scalar. The possibility of pleiotropic effects of new mutations affecting genetic relationships between metric characters has not been studied. The substantial differences in genetic relationships among JBWT and reproductive traits in comparison to earlier literature estimates (Chapter 6) might, at least in part, be attributable to mutational covariation differing from the existing covariation between those characters in the base population ($C_{g,0}$).

Selection limit Without the creation of (appreciable) new variation by mutation, the response to selection cannot be expected to continue indefinitely. Sooner or later the genes segregating in the base population will be brought to fixation (or equilibrium if there is overdominance) by the selection or the accompanying inbreeding (Falconer, 1989). The response will therefore slowly diminish and finally cease. Although, seemingly, plenty of additive genetic variation has remained in JBWT, investigation of the magnitudes of heritabilities in the up and down direction of selection is of interest. Some fixation of genes improving the response in the prolonged previous upward direction of selection is likely to have reduced this specific directional heritability. Also, it is not clear whether downward heritabilities would be negatively affected by bad growth performance of stunted birds (compare Chapter 5). If so, the heritability of JBWT could actually have a sigmoid shape with the intermediate phenotypes exhibiting the greatest heritability. However, if one or more recessives with large effect are segregating at the low end of the distribution, the downward heritability and hence the curvature are difficult to predict. Such studies can contribute to the general validation of predictions made on the basis of the usual "normal" model of genetic and environmental variation for economic performance traits in farm animals subjected to prolonged extensive selection.

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