Genetic Analysis of Ascites-Related Traits in Broilers

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This work is dedicated to my teachers, who taught me :

How to think,

How to love ,

and How to live.

ABSTRACT Ascites is of major international concern to the broiler industry, because it has serious effect on the health, welfare and profitability of broiler flocks. The objective of this dissertation was to use traits related to ascites to quantify genetic parameters for ascites in broilers and to evaluate the opportunities to genetically change the incidence of this syndrome. The relatively high heritability estimates for ascites-related traits and the significance of maternal genetic effects for most of the traits indicated that direct and maternal genetic effects play an important role in development of the ascites syndrome. The weak but positive genetic correlation among ascites-related traits measured under cold conditions and BW measured under normal conditions indicated that there is considerable scope for simultaneous selection of birds for increased BW while controlling susceptibility to ascites. Further the weak genetic correlation (0.49) between BW measured under cold and normal conditions indicated considerable genetic by environment interaction for BW. The consequence of alternative selection strategies indicated that by ignoring ascites susceptibility in the breeding goal, although achieved gain for BW is relatively high (130 g), the genetic response for ascites susceptibility increased (0.025 unit). Including information of ascites-related traits measured under normal and cold conditions makes it possible to achieve relatively high gain for BW (111.4 g) with constant level of ascites susceptibility (zero) at lower rate of inbreeding. The QTL analysis of the present research has resulted in the identification and confirmation of five regions on two chromosomes where contain genes that may involved in susceptibility of broilers to develop ascites. The alternative selection schemes by using the Quantitative Trait Loci (QTL) information of traits related to ascites were investigated. The results indicated marker assisted selection (MAS) can be used in the breeding scheme for ascites resistance and to increase the rate of genetic improvement for BW.

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Chapter 1

General Introduction

INTRODUCTION

Poultry breeders have been selecting very successfully on growth-related traits of broilers over the last few decades. Genetic progress in broilers is delivered from pedigreed populations under selection to commercial broilers through three generations of multiplication known as great grandparents, grandparents and parents. Each of these generations takes approximately one year. Thus there is a time lag of approximately 4 years from selection decision to the effect of decisions at commercial production. The combination of short generation interval and high reproductive rate allows the poultry species to respond more quickly than other livestock species to a change in selection emphasis. The current male broiler grows from 40 gr, to 2.6 kg, in 42 days with a feed conversion ratio of 1.66 (McKay et ., 2000).

Recently, the breeding industry has taken up new challenges and efforts are being directed to produce stock adaptable to a wide range of environments and to decrease the incidence of metabolic and physiological disorders of which ascites syndrome is an example (Julian, 1998, Rauw et al., 1998). Ascites syndrome or right ventricular hypertrophy is characterized by an increase in peritoneal lymph and can lead to sudden death (Julian, 1993). Although the incidence of this disorder in well-managed flocks is very low, it causes important economic losses to the poultry breeding industry – an estimated 4.7 percent of the broilers worldwide have the disease (Maxwell and Robertson, 1997). Taking into account that around 40 billion broilers are reared per year, the magnitude of this welfare problem is clear.

ETIOLOGY OF THE ASCITES SYNDROME

Ascites syndrome is a functional hypoxia caused by the high oxygen requirement of rapid growth and the inability of the heart and lungs to deliver sufficient oxygen to the tissues. The physiology of this syndrome has been studied extensively (Julian, 1993, 2000; Scheele, 1996; Hassanzadeh, 1997; Decuypere *et al*., 2000; Wideman, 2000). A flow chart depicting the development of ascites is shown in Figure 1 (Decuypere *et al*., 2000). Fluid that accumulated in the abdomen is in fact blood plasma that has leaked from the liver, and this occurs as the end result of a cascade of events ultimately triggered by oxygen deficiency in fast growing birds. A wide range of environmental causes such as altitude, cold stress, incubator environment, infection agents, toxins and deviation from optimum nutrition will affect the incidence of ascites by increasing their metabolism and/or oxygen requirements (Balog, 2003). The need to provide more oxygen to the tissues leads to increased heart stroke volume, and ultimately to the hypertrophy of the right ventricle (Figure 2). Such heart hypertrophy, coupled with malfunction of the heart valve, leads to increased pressure in the venous supply, and so

pressure build-up in the liver, and often the characteristic fluid leakage. Further in an attempt to increase the blood's oxygen carrying capacity, red blood cell production will increase. This causes a thickening of the blood, and further resistance to blood flow, compounding the lung congestion problem. In summary, the ascites symptoms in broiler chickens include generalized edema, fluid accumulation in the pericardium, (hydropericardium, lung edema, hypertrophy and dilation of the heart, especially the right ventricle), enlarged liver and kidneys, liver cirrhosis, pale comb and higher hematocrit value of the blood. These symptoms indicate that a large number of organs (including heart, lung, liver, etc.) are involved in the disease.

Mortality due to ascites syndrome can range up to 5% in broiler flocks and up to 20% in heavier roaster flocks (Buys and Barnes, 1981; Agudelo, 1983; Julian et al., 1986; Julian et al., 1987;). Although there are several management techniques used to combat ascites syndrome in broilers, all involve reducing the bird's rapid growth rate, which has often no economic consequence for the poultry producer. One of the most common commercial treatments to reduce ascites is feed restriction (Albers et al., 1990; Arce et al., 1992; Acar et al., 1995; Balog et al., 2000). The technique that holds the most promise for the future is breeding ascites resistant broilers. To design a selection strategy to reduce the incidence of ascites while maintaining an acceptable level of gain for body weight, the genetic parameters of traits related to ascites as well as the genetic relationships among ascites-related traits and performance traits are required.

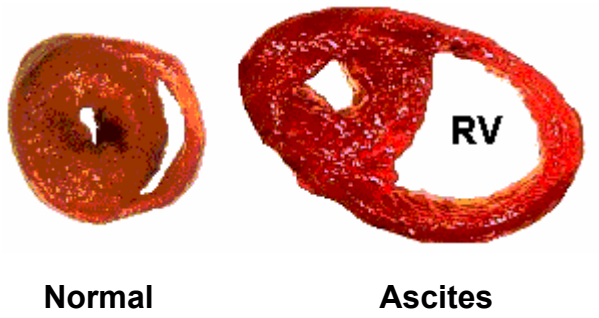

FIGURE 2. A cross sectional slice through the ventricles of two hearts. The section on the left is the heart of a healthy broiler at 42 days of age. The section on the right is the heart of a broiler with the ascites syndrome.

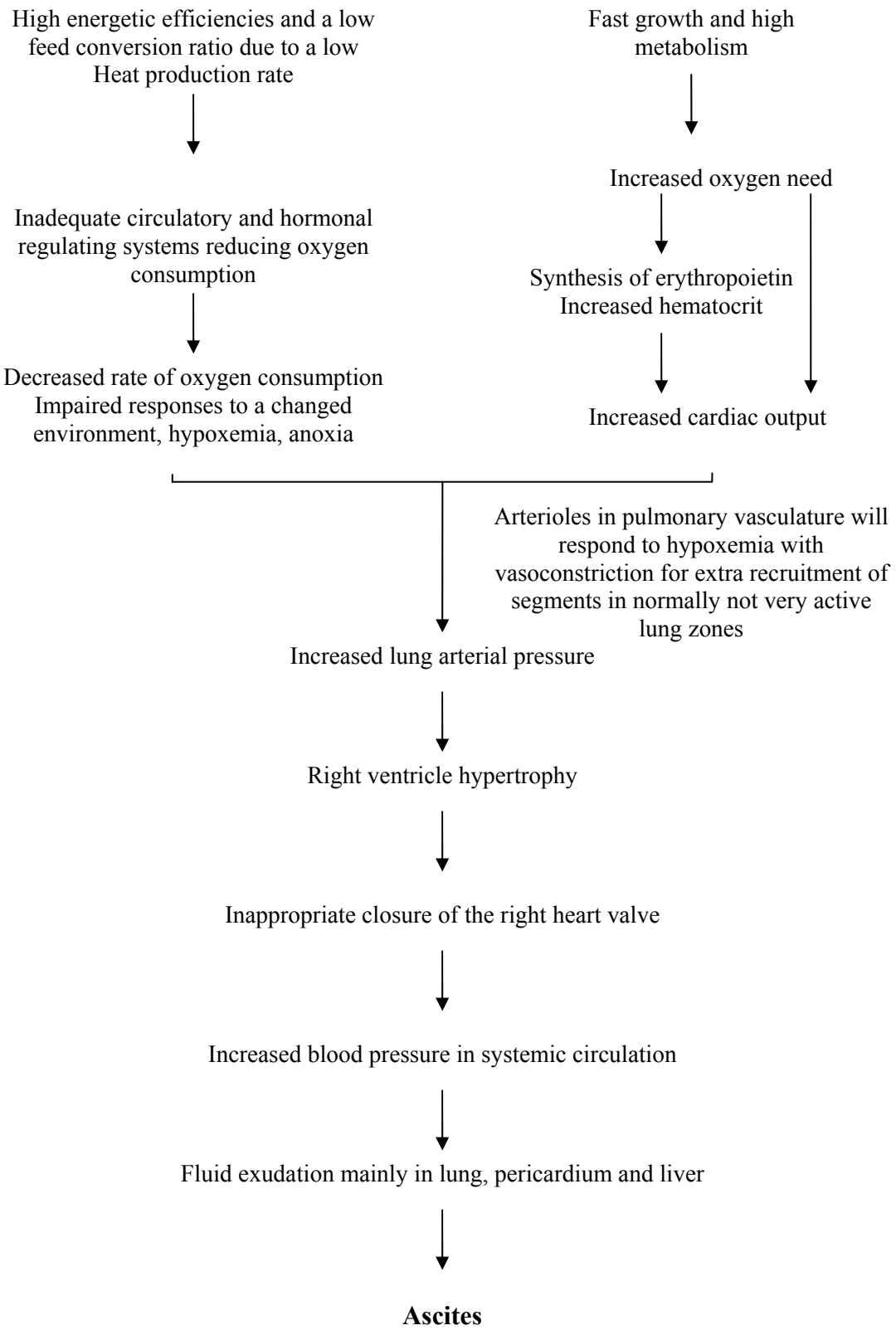

FIGURE 1. Flow chart showing the development of the ascites syndrome in broilers (Decuypere *et al*., 2000).

OBJECTIVES AND OUTLINE

This dissertation deals with the genetic and statistical analysis of data to investigate the relation between a number of traits related to the ascites syndrome, and to evaluate the opportunities to genetically change the prevalence of this metabolic disorder in broiler chickens. Chapter 2 deals with the estimation of heritabilities for ascites-related traits measured under cold stress conditions and to assess the importance of maternal genetic effects for these traits in broilers. Chapter 3 deals with the estimation of genetic and phenotypic correlations among ascites-related traits measured under cold conditions, genetic and phenotypic correlations among ascites-related traits measured under normal temperature conditions and genetic correlations between ascites-related traits measured under cold and normal conditions. Chapter 4 deals with the estimation of genetic correlations among ascites-related traits, carcass traits and feed efficiency traits. Chapter 5 shows the results of a study to confirm Quantitative Trait Loci (QTL) affecting ascites-related traits. Chapter 6 deals with the optimization of the breeding schemes using simulation which aim at controlling resistance to ascites susceptibility as well as improving body weight. In the simulation study, the effect of different types of indicator traits for ascites and different environments in the breeding program were investigated. Finally chapter 7 discusses the results of this thesis and a number of additional topics that were not covered in the previous chapters.

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Chapter 2

Direct and Maternal Genetic Effects for Ascites-Related Traits in Broilers

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ABSTRACT The objective of the present study was to estimate heritabilities for ascites-related traits in broilers and to assess the importance of maternal genetic effects for these traits. Several traits related to ascites were measured on more than 4,000 broilers kept under cold conditions. Heritabilities were estimated using an animal model with a direct genetic effect and a model with direct and maternal genetic effects. Estimated heritabilities from the direct genetic effects model were 0.46 for hematocrit value, 0.42 for BW, 0.47 for right ventricular weight, 0.46 for total ventricular weight, 0.45 for ratio of right ventricular weight to the total ventricular weight, 0.32 for total mortality, and 0.18 for fluid accumulation in the heart sac. Maternal effects significantly influenced the traits BW, total ventricular weight, and total mortality. Direct and maternal heritabilities, respectively, for BW were 0.21 and 0.04, for total ventricular weight were 0.29 and 0.03, and for total mortality were 0.16 and 0.05. The heritability estimates for ascites-related traits and the significance of maternal genetic effects for most of these traits indicate that direct and maternal genetic effects play an important role in the development of the ascites syndrome.
(*Key words:* broiler, ascites, heritability, cold stress, maternal genetic effect)

INTRODUCTION

In all major poultry-producing countries, cases of ascites in broilers have been reported. Ascites syndrome, or water belly, is an increase in the amount of lymph normally found in the peritoneal space (Julian, 1993). This syndrome is a serious economic concern because it results in a loss of broilers (Shapiro, 1993) and has a negative impact on animal welfare. In the survey (Maxwell and Robertson, 1997), information on 18 countries from four continents showed that ascites affects 4.7 % of all live broilers worldwide.

Genetically, the modern broiler seems to be more prone to develop ascites, which is probably due to selection for growth rate or feed conversion ratio, which puts high demands on metabolic processes and on the oxygen demand (Decuypere et al., 2000). To alter the metabolic load placed on the birds, the producer can reduce the growth rate, change the diet, or change other aspects of the management system, e.g. by raising the temperature (e.g. Bendheim et al., 1992). Alternatively it might be possible to select for birds that can maintain a high rate of growth without succumbing to the penalties imposed on their health and, consequently, on their welfare. This requires alternative selection strategies, traits that indicate the susceptibility of birds to ascites and genetic parameters for these traits. Several studies have suggested traits that can be used as indicator traits for ascites. Lubritz et al. (1995) clearly demonstrated that ascites is strongly related to the ratio of right ventricular weight (RV) to the total ventricular weight (TV). Shlosberg et al. (1996) showed that broilers with high hematocrit values have an increased chance of developing ascites when exposed to cold temperatures and suggested that hematocrit values might be a useful selection tool. Maxwell et al. (1998) indicated that in the presence of ascites, plasma troponin T, an indicator of heart muscle damage, is heritable. Moghadam et al. (2001) showed that heart defects, e.g., including pulmonary hypertension, right ventricular failure, and fluid accumulation in the peritoneal cavity, are heritable and had a positive genetic correlation with BW. De Greef et al. (2001) estimated genetic parameters for a number of ascites-related traits. However, they also demonstrated that genetic parameters varied considerably with the severity of the disease.

Koerhuis and Tompson (1997) reported maternal genetic effects on juvenile broiler BW. Other studies have shown positive phenotypic effects of egg weight on juvenile broiler BW (e.g., Chambers, 1990). Further, Dewil et al. (1996) demonstrated that selection for ascites resistance is linked to several physiological variables at the embryonic stage. These results suggest that maternal genetic effects might play a role in the susceptibility of birds to ascites. To our knowledge no studies have actually established the significance of maternal genetic effects on ascites-related traits. The

objective of the current study was to estimate heritabilities for ascites-related traits and to assess the importance of maternal genetic effects for these traits in broilers.

MATERIAL AND METHODS

Birds and Traits

Birds. Ascites-related traits were recorded on 4,202 chickens, 1,736 females and 2,466 males. The experimental population was the result of a cross between two genetically different outcross broiler dam lines (Hybro) originating from the White Plymouth Rock breed. The maternal line had a relatively high reproductive performance and was fast-feathering and the paternal line had a relatively high growth performance and was slow-feathering. The total pedigree file consisted of 5,096 birds of which 36 were pure line birds (F_0), 29 were F_1 birds, 829 were F_2 birds and 4,202 were F_3 birds. Observations were on F_3 birds. A more detailed description of the experimental set up was given by Van Kaam et al. (1998).

The experimental birds hatched at 6 different wk in 1994 and 1995. Broilers were kept in four different pens; however, most were kept in one pen. Nine batches were allotted by hatching day and pen number. In order to identify individuals that were susceptible to ascites, a cold stress temperature schedule was applied (Figure 1). At the time of hatching, the temperature was 30 ^{o}C and then was gradually decreased to 10 ^{o}C by 22 d of age. The temperature remained at 10 ^{o}C until the end of the experiment. A normal temperature schedule starts at 33 to 34 ^{o}C and then gradually decreases to 17 to 18 ^{o}C by 35 d of age. Except for the adjusted temperature schedule, birds were kept under circumstances that closely resemble commercial practice, i.e. a standard commercial feed, artificially lighted housing for 23 h / d, and group housing with 20 birds / m^2.

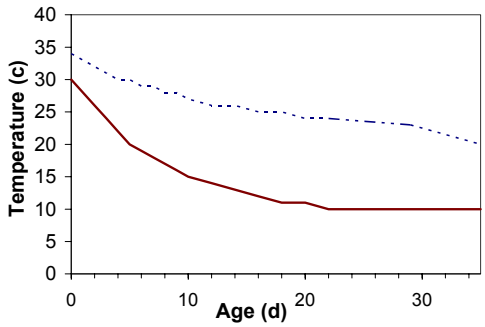

FIGURE 1. The normal temperature schedule (-----) and the cold-stressed temperature schedule (‾‾‾‾).

Traits. The hematocrit value (HCT) and BW of birds were measured 1 d before slaughtering at 5 wk of age. After birds were slaughtered, several ascites-related traits were measured. Livers and hearts were removed and visually inspected. Liver

abnormalities (LIVER) were scored as follows: 0 represented no abnormalities observed, 1 represented an abnormal liver, and 2 represented serious liver abnormalities. Liver abnormalities were a lighter color, an irregular liver surface, or both. Accumulation of fluid in the heart sac (HEART) was scored with 0 if no fluid had accumulated, 1 if fluid accumulation was observed, and 2 if there was serious accumulation of fluid in the heart sac. Further, the weights of RV and TV were measured. From these measurements, the RV:TV, RV as a percentage of total BW (%RV), and TV as a percentage of total BW (%TV) were derived. The accumulation of fluid in the abdomen (ABDOMEN) was scored as 0, 1, or 2. A score of 0 indicated no fluid, 1 indicated the presence of fluid in the abdomen, and 2 indicated a serious accumulation of fluid in this section. For color of the breast (BREAST), a score of 0 represented normal color, 1 represented a color deviation, and 2 represented serious color deviation. In general a deviation of breast color meant that the color was more red. Also the total mortality (MORT-TOT) of the birds was recorded with 0 or 1. A score of 0 represented a bird that was alive at the end of the experiment, and a score of 1 indicated a bird that died before the end of the experiment. For the first three batches of birds, mortality was not recorded. No observations were recorded for other traits of birds died before the end of experiment.

In addition, information from 795 birds kept under a normal temperature schedule (Figure 1) was available. These birds originated from the same F_2 parents and, except for temperature, were kept under similar conditions as the birds kept under cold conditions. These birds were slaughtered between 6 and 7 wk, and the measurements for BW, HCT, RV, TV, and RV:TV were available. These birds were previously used in an experiment by Van Kaam et al. (1998). The data was only used to describe the mean and the distribution of traits under a normal temperature schedule and was not included in genetic analyses.

Genetic Analysis

An animal model including maternal genetic effects was used to calculate direct heritabilities and maternal genetic heritabilities (Model 1);

$$Y_{ijklmn} = \mu + Sex_i + Feather_j + Batch_k + Group_l + d_m + a_n + e_{ijklmn}$$

where: Y_{ijklmn} = the dependent variable on chicken n from dam m of sex i, feathering class j from batch k in group l; Sex_i = fixed effect of sex i (i=1,2 female or male); $Feather_j$ = fixed effect of feathering j (j=1,2 fast or slow); $Batch_k$ = fixed effect of batch k of the birds (k=1,2…9), classes were formed based on a combination of hatching day and pen; $Group_l$ = fixed effect of group (l=1,2…46), classes were based on the age of dam and the hatching day of the experimental birds; d_m= random genetic effect of dam m; a_n= random direct genetic effect of individual n; e_{ijklmn} = random residual effect.

In matrix notation: $\mathbf{y} = \mathbf{Xb} + \mathbf{Z}_1\mathbf{a} + \mathbf{Z}_2\mathbf{m} + \mathbf{e}$ where **y** is a vector of observations, **b** is a vector of fixed effects, **a** is a vector of direct genetic effects, **m** is a vector of maternal genetic effects, and **e** is a vector of residual effects. **X** is incidence matrix relating observations to fixed effects. $\mathbf{Z}_1$ and $\mathbf{Z}_2$ are incidence matrices relating observations to random effects **a** and **m** respectively. The covariance structure for this model was:

$$V\begin{bmatrix}\mathbf{a}\\ \mathbf{m}\\ \mathbf{e}\end{bmatrix} = \begin{bmatrix}\mathbf{A}\sigma_a^2 & \mathbf{A}\sigma_{am} & 0\\ \mathbf{A}\sigma_{am} & \mathbf{A}\sigma_m^2 & 0\\ 0 & 0 & \mathbf{I}\sigma_e^2\end{bmatrix}$$

where σ_a^2 = direct genetic variance, σ_m^2 = maternal genetic variance, σ_e^2 = error variance and σ_{am} = covariance between direct genetic effects and maternal genetic effects. Estimates of variance components were obtained using the ASREML software (Gilmour et al., 2000).

An animal model without a maternal genetic effect (Model 2) was used;

$$Y_{ijkln} = \mu + Sex_i + Feather_j + Batch_k + Group_l + a_n + e_{ijkln}$$

Fixed effects in this model were identical to fixed effects in Model 1. To test the significance of the maternal genetic effect, a likelihood ratio test with two degrees of freedoms was used:

$$\chi_2^2 = 2\log_e L(F) - 2\log_e L(R)$$

where L(F) = likelihood of the full model (Model 1), and L(R) = likelihood of the residual model (Model 2).

In addition to the analyses described, score traits were also analyzed using a binary model and ASREML software (Gilmour et al., 2000). Fixed and random effects in this model were identical to the effects in Model 2. Because some traits were scored using three classes (0, 1, and 2), scores in classes 1 and 2 were combined into one class.

RESULTS

Description of Traits

Means and standard deviations for the traits measured under cold conditions are presented in Table 1. The average weight of broilers at 5 wk was 1,604 g, and the total mortality in the current experiment was 16%. Figure 2 shows the distribution of HCT, RV and RV:TV under cold and normal conditions. Under cold conditions the mean and SD HCT of the birds was 35.4% ± 4.2 and 28.3% ± 2.3 under normal conditions. This difference in mean, as well as in variance, between traits measured in normal or cold conditions is clearly illustrated in Figure 2. Mean values and SD for other ascites-related traits under normal conditions were 1.15 g. (± 0.30) for RV, 5.60 g (± 0.94) for TV, and 20.64% (± 4.66) for RV:TV.

TABLE 1. Statistical description of the traits in cold conditions

Trait	Abbreviation	Number	Mean	SD
Hematocrit value (%)	HCT	3547	35.40	4.21
BW at 5 wk (g).	BW	3693	1604	263
Right ventricular weight (g).	RV	3660	1.95	0.68
Total ventricular weight (g).	TV	3658	6.97	1.17
Ratio of right ventricular weight to total ventricular weight (%)	RV:TV	3658	27.94	8.07
Right ventricular weight as percentage of BW (%)	%RV	3646	0.125	0.05
Total ventricular weight as percentage of BW (%)	%TV	3644	0.439	0.07
Total mortality[1]	MORT-TOT	2494	0.16	0.37
Fluid in the abdomen[2]	ABDOMEN	3697	0.08	0.38
Color of the breast[2]	BREAST	3697	0.03	0.18
Liver abnormalities[2]	LIVER	3697	0.07	0.29
Fluid in the heart sac[2]	HEART	3696	0.59	0.62

[1] Trait scored as 0 or 1. The number of birds for each class: $N_0 = 2,095$ and $N_1 = 399$.
[2] Trait scored as 0, 1 or 2. The number of birds for each class: fluid in the abdomen: $N_0 = 3,542$, $N_1 = 23$, and $N_2 = 132$, color of the breast: $N_0 = 3,585$, $N_1 = 110$, and $N_2 = 2$, liver abnormalities: $N_0 = 3,488$, $N_1 = 170$, and $N_2 = 39$, fluid in the heart sac: $N_0 = 1,781$, $N_1 = 1,653$, and $N_2 = 262$.

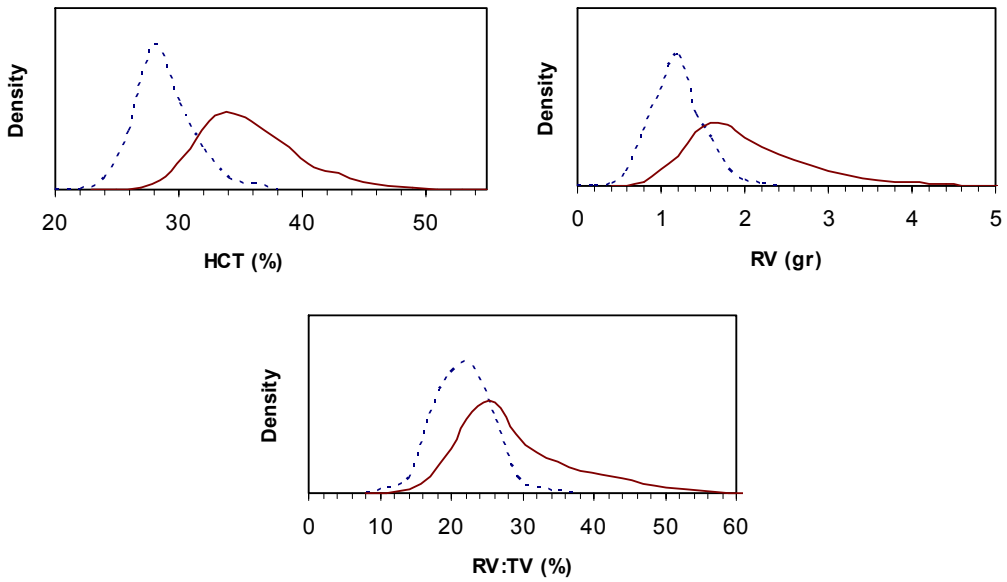

FIGURE 2. The distribution of hematocrit value (HCT), right ventricular weight (RV) and ratio of right ventricular weight to total ventricular weight (RV:TV) in normal (…..) and cold (——) conditions.

Sex had significant effects on all traits analyzed, except for BREAST and LIVER. The most pronounced effects of sex were found for BW, RV:TV, MORT-TOT, and ABDOMEN. The average weight of males was 1,676 g, whereas this value was 1,503 g for females. For RV:TV the average for male was 29.3% and for females it was 26.0%. The MORT-TOT in males was 17.7% and in females 14.2%, and the mean value of ABDOMEN in males was 0.10 and in female was 0.04.

Feathering had significant effect on all continuous traits analyzed; however, no significant effects of feathering on score traits were found. The most pronounced effects of feathering were found for HCT and RV:TV. The average HCT for slow-feathering birds was 35.7% and in fast-feathering birds it was 34%. Also RV and TV were higher for slow-feathering birds, but the increase in RV was higher than the increase in TV, which resulted in a higher RV:TV ratio for slow-feathering birds. The average of RV:TV ratio in slow-feathering birds was 28.2% and in fast-feathering birds it was 25.9%.

TABLE 2. Genetic parameters of ascites-related traits using a maternal genetic effects model (Model 1) or a direct genetic effects model (Model 2)

Traits [1]	Model 1 [2]			Model 2	Likelihood ratio test [3]
	h_a^2	r_{am}	h_m^2	h_a^2	
HCT	NC [4]	NC	NC	0.46(0.05) [5]	NC
BW	0.21(0.06)	0.57(0.40)	0.04(0.02)	0.42(0.05)	13.76** [4]
RV	NC	NC	NC	0.47(0.05)	NC
TV	0.29(0.07)	0.30(0.40)	0.03(0.03)	0.46(0.05)	9.14*
RV:TV	0.28(0.06)	0.90(0.43)	0.02(0.02)	0.45(0.05)	6.72*
%RV	0.22(0.06)	0.86(0.31)	0.04(0.02)	0.45(0.05)	12.44**
%TV	0.31(0.07)	0.44(0.43)	0.03(0.02)	0.46(0.05)	7.53*
MORT-TOT	0.16(0.07)	0.21(0.45)	0.05(0.04)	0.32(0.06)	8.50*
ABDOMEN	0.07(0.03)	0.00(0.00)	0.00(0.01)	0.08(0.03)	0.24
BREAST	NC	NC	NC	0.03(0.02)	NC
LIVER	0.06(0.03)	0.05(0.75)	0.00(0.00)	0.08(0.03)	0.52
HEART	NC	NC	NC	0.18(0.04)	NC

[1] HCT = hematocrit value; RV = right ventricular weight; TV = total ventricular weight; RV:TV = ratio of right ventricular weight to total ventricular weight; %RV= right ventricular weight as percentage of BW; %TV = total ventricular weight as percentage of BW; MORT-TOT = Total mortality; ABDOMEN = Fluid in the abdomen; BREAST = Color of the breast; LIVER = Liver abnormalities; and HEART = Fluid in the heart sac.

[2] h_a^2 = heritability of direct genetic effect; r_{am} = genetic correlation between direct and maternal effect; h_m^2 = heritability of maternal genetic effect.

[3] Test if Model 1 fit better than Model 2.

[4] NC = convergence problems.

[5] Empirical standard errors are in parentheses.

* $P \leq 0.05$.

** $P \leq 0.01$.

Genetic Parameters

The genetic parameters for ascites-related traits from Model 1 and Model 2 are presented in Table 2. For continuous traits, heritabilities obtained using Model 2 were around 0.45, but for score traits, heritabilities were lower, especially for ABDOMEN, BREAST, and LIVER. For most of the continuous trait the maternal genetic effects model (Model 1) gave a significantly better fit. Heritabilities for maternal genetic

effects were low (0.02 to 0.05). Heritabilities for direct genetic effects of the continuous traits under Model 1 ranged from 0.2 to 0.3. Genetic correlations between direct genetic effects and maternal effects showed moderately positive values, but the high SD of the estimates indicated that this parameter could not be accurately estimated. For the traits HCT, RV, BREAST, and HEART, convergence problems were encountered when using the maternal genetic effects model. For these traits no estimates are reported for Model 1.

Additional analyses for binary traits were performed using a binary model. Estimated heritabilities using this model were higher than heritabilities reported in Table 2. Using a binary model without a maternal genetic effect resulted in heritability estimates for the direct genetic effect of 0.46 (± 0.07) for MORT-TOT, 0.49 (± 0.09) for ABDOMEN, 0.47 (± 0.12) for BREAST, 0.36 (± 0.10) for LIVER, and 0.23 (± 0.06) for HEART.

DISCUSSION

Susceptibility to Ascites

In the present experiment, traits that are related to ascites were analysed. Birds that were most susceptible to ascites probably died before the end of the experiment. However, no information was available with respect to the cause of death, and therefore MORT-TOT did not fully identify the birds that were most susceptible to ascites. Also no measurements for HCT, RV:TV and other traits were available on the birds that died before 5 wk of age.

Ascites is defined as accumulation of fluid in the abdominal cavity and therefore is best described by the trait “ABDOMEN”. Birds with a score of 1 or 2 for ABDOMEN showed ascites symptoms and, therefore, also could be qualified as susceptible towards ascites. However, theses birds were less susceptible than birds that actually died due to ascites. The third category of birds that could be distinguished is birds that have not yet accumulated fluid in the abdomen but have high values for RV:TV, HCT, or both.

Effect of Cold Stress, Sex, and Feathering

Cold stress increases metabolic demands for oxygen and elevates HCT values and RV:TV (Shlosberg et al., 1992; Lubritz and Mcpherson, 1994). In the present study cold stress had a marked effect on the mean values for HCT, RV, and RV:TV as well as on the variance of these traits (Figure 2). These results indicate that birds react to the cold stress by increased values for HCT and RV. Apparently, the adaptive capacity of some of the birds is insufficient to meet the increased oxygen demands and results in increased incidence of ascites.

In the present study birds under cold conditions (5 wk) were younger than those under normal conditions (6 to 7 wk). Therefore, results might be influenced by an effect of age. From the results of Shlosberg et al. (1992) it can be concluded that there is no significant difference between HCT values at 5, 6 and 7 wk of age. However, there is a significant increase of RV:TV from weeks 5 to 7. In the current study, the younger birds under cold conditions (5 wk) showed higher RV:TV than the older birds under normal conditions (6 to 7 wk). These results emphasize that cold conditions markedly increased RV:TV.

In the present study, total mortality was recorded, but no information was available about mortality due to ascites. In comparison to the rate of mortality under normal conditions (4 to 5%), mortality under cold conditions was relatively high (16%). Therefore it can be concluded that cold stress resulted in higher mortality, which was likely due to ascites.

Higher mean values for ascites-related traits in male broilers suggest that males are more prone to develop ascites. These results confirm previous reports that ascites is more prevalent in male broilers (e.g. Fredric, 1988). Also higher mean values for ascites-related traits in slow-feathering birds suggest that under cold conditions, slow-feathering birds are more susceptible to ascites.

Maternal Genetic Effects

The heritabilities for continuous traits related to ascites under the cold conditions indicated that direct genetic effects play an important role. The significance of maternal genetic effects for most of the continuous traits suggested that maternal effects play a role in the development of the ascites syndrome. However, maternal genetic effects might be partly confounded with dominance effects, especially if maternal genetic effects were estimated based on full-sib family relationships. In the presence of additive genetic, maternal genetic, and dominance effects, resemblance of full-sibs is $½\sigma_a^2 + r_a\sigma_a\sigma_m + \sigma_m^2 + ¼\sigma_d^2$ where σ_d^2 = variance due to dominance effects. In the current study, however, information regarding maternal genetic effects is also based on maternal half-sibs family relationships. Resemblance between maternal half sibs is $¼\sigma_a^2 + r_a\sigma_a\sigma_m + \sigma_m^2$ and not affected by dominance effects. To investigate the presence of dominance effects, additional analyses were performed. In this analysis, a random full-sib family effect was included in the model in addition to additive genetic and maternal genetic effects. This effect should account for “additional“ resemblance between full-sib family members due to dominance effects. Analyses showed that the variance component of full-sib families was very small and not significant for all traits. This finding suggests that the significantly better fit of Model 1 was due to “true” maternal genetic effects.

Egg characteristics such as shell conductance or shell porosity, volume of air cell, and weight or the composition of the egg might influence the early embryonic development and, thereby, susceptibility towards ascites. Chineme et al. (1995) indicated that interference with egg shell conductance during incubation can increase postnatal HCT. Other findings suggest possible effects of hatching conditions, the length of incubation, and interval between internal pipping (start of breathing) and hatching on the incidence of ascites (Visschedijk, 1968a,b; Coleman and Coleman, 1991; and Dewil et al., 1996). These effects might be due to maternal effects or due to direct effects of the embryo itself.

Clément et al (2001) demonstrated that if maternal genetic effects exist but are neglected in the model, the direct heritability is overestimated. Sometimes this results in a direct heritability that is more than twice the true direct heritability (Clément et al., 2001). In the current study, large increases in the direct heritability were found for traits with a significant maternal genetic effect when this factor was neglected from the model (Model 2). For BW, the heritability of the direct genetic effect increased from 0.21 under Model 1 to 0.42 under Model 2. This finding indicated that heritabilities that have been reported for some of the ascites-related traits are likely to be overestimates of the true heritability.

Literature

De Greef et al. (2001) estimated heritabilities for some ascites-related traits on 2,788 chicks in cold-stressed conditions. Heritability estimates were 0.50 for HCT, 0.15 for ABDOMEN, 0.41 for RV, 0.54 for RV:TV, 0.17 for liver cirrhosis, 0.57 for BW, and 0.22 for MORT-TOT. These estimates are in agreement with the results reported using Model 2. Also Lubritz et al. (1995) estimated heritabilities for two ascites-related traits using a paternal half-sib model in all-male populations (n = 3,436) originating from three different lines. Heritability estimates for ABDOMEN ranged from 0.11 to 0.44, and for RV:TV estimates ranged from 0.21 to 0.27. The estimate for ABDOMEN using Model 1 was lower (0.07), but for RV:TV the estimates are similar.

In the present study information of F_3 individuals was used to estimate genetic parameters for base population. If the two pure lines differed with respect to allele frequencies of genes involved in the traits under study, it was expected that the genetic variation in the F_2 and F_3 would be increased. Therefore, heritability estimates in the present study might be somewhat higher when compared to previously reported estimates.

Score Traits

For discrete or score traits heritabilities might be underestimated using a linear model, especially when the incidences are low (Gianola, 1982). In the current

experiment estimated heritabilities for score traits were especially low for traits for which a majority of individuals had a score of 0 and therefore a low mean value. When the data were analyzed using a binary model, the estimated heritabilities for these traits increased. The heritability estimates from a binary model were in agreement with estimates that were obtained by transforming the heritabilities from the linear model to the underlying scale (Lynch and Walsh, 1998).

Prospects

The present study showed that some of the ascites-related traits were significantly influenced by maternal genetic effects. Heritability estimates for ascites-related traits suggested that selection for these traits is possible. However, selection should done, taking into account maternal genetic effects. Before a selection strategy to reduce the incidence of ascites can be implemented, correlations among traits measured in the present study and genetic correlations between production traits measured under commercial circumstances and under cold-stressed circumstances are required.

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Chapter 3

Genetic and Phenotypic Correlations for Ascites-Related Traits in Broilers Measured under Cold and Normal Conditions

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ABSTRACT Ascites syndrome is a growth-related disorder of broilers that occurs more often in fast growing birds and at low temperatures. The objective of this study was to estimate genetic and phenotypic correlations among ascites-related traits measured under cold conditions, to estimate genetic and phenotypic correlations among ascites-related traits measured under normal temperature conditions and to estimate genetic correlations between ascites-related traits measured under cold and normal conditions. Several traits related to ascites were measured on more than 4,000 chickens under cold conditions and on more than 700 chickens under normal conditions. The heritability estimates for BW measured under cold and normal conditions were 0.42 and 0.50 respectively, for hematocrit value 0.46 and 0.17 respectively and for ratio of right to total ventricular weight (RV:TV) 0.45 and 0.12 respectively. The genetic correlation between BW and hematocrit value under cold conditions was -0.23 and between BW and RV:TV -0.27. Under normal conditions, however, these genetic correlations were 0.55 and 0.50 respectively. These results demonstrate that the heritability estimates of ascites-related traits as well as genetic correlations between ascites-related traits and BW depend on the conditions under which animals are kept. Strong positive genetic correlations (around 0.8) were observed between total mortality, fluid in the abdomen and RV:TV under cold conditions. The genetic correlation between RV:TV measured under cold and normal conditions was strong (0.91). These results suggest that ratio of right to total ventricular weight measured under normal temperature conditions might serve as a good indicator trait for ascites.

(*Key word:* broiler, ascites, genetic correlation, cold stress, genotype by environment interaction)

INTRODUCTION

Ascites, also known as water belly, is a growth-related disorder of broilers that occurs more often in fast growing birds, at high altitudes and low temperatures. The most critical trigger for ascites in broilers is a high oxygen requirement (Julian, 1998). The ascites syndrome has been a worldwide source of concern to the poultry industry for several decades. It has been estimated that ascites accounts for losses of about US $ 1 billion annually worldwide (Maxwell and Robertson, 1997). For developing selection strategies to reduce ascites, genetic parameters such as heritabilities and genetic correlations among ascites-related traits should be known.

Several studies have reported moderate to high heritabilities for ascites-related traits (De Greef et al., 2001; Lubritz et al., 1995; Maxwell and Robertson, 1997; Pakdel et al., 2002). This offers perspectives for selection against this syndrome. Only a few studies have reported genetic correlations among ascites-related traits and those studies only comprised a limited number of ascites-related traits. For instance under normal climatic conditions, Moghadam et al. (2001) found a positive genetic correlation between ascites and BW. However, under cold conditions, De Greef et al. (2001) reported a negative genetic correlation between ascites and BW.

Deeb et al. (2002) found that birds that have a higher potential for growth rate under normal temperature conditions are more likely to suffer from ascites under cold stress conditions as compared to birds with a lower potential for growth rate. Therefore, it seems that there is an interaction among traits such as BW and susceptibility to ascites and temperature. Ascites develops more often in low ambient temperatures (Shlosberg et al., 1992; Yahav and Hurwitz, 1996; Yahav et al., 1997), which increases the possibilities of identifying birds that are susceptible to ascites. At present, selection for economical important traits in broilers is usually carried out under normal temperature conditions. However, for designing optimal selection strategies against ascites incidence it might be optimal to test birds under cold conditions. To decide which strategy is optimal, correlations between traits measured under both conditions are required.

The objective of this study was to estimate genetic and phenotypic correlations among ascites-related traits measured under cold conditions, to estimate genetic and phenotypic correlations among ascites-related traits measured under normal temperature conditions and to estimate genetic correlations between ascites-related traits measured under cold and normal conditions.

MATERIAL AND METHODS

Birds and Traits

Birds. The experimental population was the result of a cross between two genetically different outcross broiler dam lines (Hybro) originating from the White Plymouth Rock breed. The maternal line had a relatively high reproductive performance and was fast-feathering and the paternal line had a relatively high growth performance and was slow-feathering. 36 birds (18 males and 18 females) from the two lines were crossed to produce the F_1. From the F_1, 29 birds were parents of the F_2 generation, which consisted of 829 birds. The F_2 population was used to produce different groups of F_3 generation (offspring). In the present study 4,202 birds were kept under cold conditions and 795 birds, originating from the same F_2 parental population, were kept under normal temperature conditions.

The birds in F_3 generation were divided in different groups. The first group consisted of 4,202 birds and hatched in 6 different wk in 1994 and 1995. These birds were kept in four different pens. Nine batches were allotted by hatching day and pen number. In order to identify individuals that were susceptible to ascites, a cold stress temperature schedule was applied (Figure 1) for this group of birds. At the time of hatching, the temperature was 30 ^{o}C and then was gradually decreased to 10 ^{o}C by 22 d of age. The temperature remained at 10 ^{o}C until the end of the experiment. Except for the adjusted temperature schedule, birds were kept under circumstances that closely resemble commercial practice, i.e. a standard commercial feed, artificially lighted housing for 23 h /d, and group housing with 20 birds / m^2.

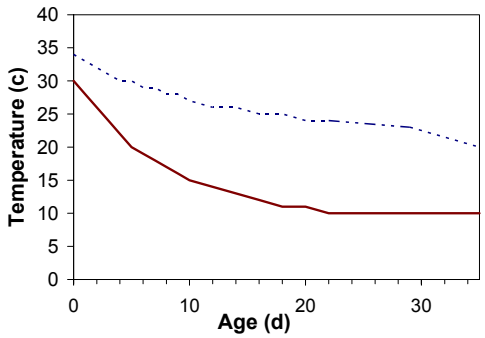

FIGURE 1. The normal temperature schedule (----) and the cold-stressed temperature schedule (——)

The second group consisted of 795 F_3 birds kept under a normal temperature schedule. About 85% of the sires and more than 88% of dams that had offspring which were kept under cold temperature conditions also had offspring kept under normal temperature conditions. A normal temperature schedule starts at 33 to 34 ^{o}C and then gradually decreases to 17 to 18 ^{o}C by 35 d of age (Figure 1). Except for temperature, these groups of birds were kept under similar conditions. The birds kept under normal temperature conditions hatched in 2 different wk in 1995 and were kept in two different

pens. Depending on the hatching day and the pen number, two different batches were defined for these birds.

Traits. Birds exposed to cold stress conditions were slaughtered at 5 wk of age. The BW and hematocrit value (HCT) of birds were measured 1 d before slaughtering. After slaughtering, a number of ascites-related traits were measured. Livers and hearts were removed and visually inspected. Liver abnormalities (LIVER) were scored as follows: 0 represented no abnormalities observed, 1 represented an abnormal liver, and 2 represented serious liver abnormalities. Liver abnormalities were a lighter color, an irregular liver surface, or both. Accumulation of fluid in the heart sac (HEART) was scored with 0 if no fluid had accumulated, 1 if fluid accumulation was observed, and 2 if there was serious accumulation of fluid in the heart sac. Further, the weight of right ventricular (RV) and total ventricular (TV) were measured. From these measurements the ratio of RV:TV, RV as a percentage of total BW (%RV) and TV as a percentage of total BW (%TV) were derived. The accumulation of fluid in the abdomen (ABDOMEN) was scored as 0, 1, or 2. A score of 0 indicated no fluid, 1 indicated the presence of fluid in the abdomen, and 2 indicated a serious accumulation of fluid in this section.

For color of the breast (BREAST), a score of 0 represented normal color, 1 represented a color deviation, and a score of 2 represented serious color deviation. In general a deviation of breast color meant that the color was more red. Also the total mortality (MORT-TOT) of the birds were recorded as 0 or 1. A score of 0 represented a bird that was alive at the end of the experiment and a score of 1 indicated a bird that died before the end of the experiment. For the first three batches of birds, mortality was not recorded. No observations were recorded for other traits of birds that died before the end of experiment.

The birds exposed to normal temperature conditions were slaughtered at 7 wk of age and the measurements for BW, HCT, RV, TV, and RV:TV were available for these birds. BW and hematocrit value (HCT) of this group of birds were also measured 1 d before slaughtering.

Genetic Analysis

An animal model was used to calculate heritabilities and genetic correlations of ascites-related traits;

$$Y_{ijklm} = \mu + Sex_i + Feather_j + Batch_k + Group_l + a_m + e_{ijklm}$$

where: Y_{ijklm} = the dependent variable on chicken m of sex i, feathering class j from batch k in group l; Sex_i = fixed effect of sex i (i=1,2 female or male); $Feather_j$ = fixed effect of feathering j (j = 1,2 fast or slow); $Batch_k$ = fixed effect of batch k (k = 1,2…9

for birds kept under cold conditions and k = 1,2 for birds kept under normal conditions), classes were formed based on a combination of hatching day and pen; $Group_l$ = Fixed effect of group (l=1,2…46 for birds kept under cold conditions and l = 1,2…18 for birds kept under normal conditions), classes were formed based on the age of the dam and the hatching day of the experimental birds ; a_m= random direct genetic effect of individual m; e_{ijklm} = random residual effect. The fixed and random effects used were the same for all the traits under study. Bivariate analyses were performed to compute correlations between all combinations of traits. Estimates of variance components were obtained using the ASREML software (Gilmour et al., 2000).

RESULTS AND DISCUSSION

Descriptive statistics

Descriptive statistics of the traits measured under cold and normal conditions are presented in Table 1. Under cold conditions and at 5 wk of age, the broilers weighted 1,604 g on average and total mortality was 16%. Under normal conditions and at 7 wk of age, the broilers weighted 2,060 g on average. In general the standard deviation of traits under cold conditions was higher than standard deviation of traits under normal conditions. However, this was not the case for BW, but for this trait the coefficient of variation under cold conditions was higher than variation coefficient under normal conditions. Although birds exposed to cold conditions were younger than birds exposed to normal conditions, they showed higher RV:TV which is mainly due to higher values for RV. The hematocrit value (HCT) of birds kept under cold conditions was also higher. The data in Table 1 shows that there is a marked difference between the means and the standard deviations of ascites-related traits measured under cold and normal conditions. This difference can be either due to the effect of temperature or the difference in age. Shlosberg et al. (1992) concluded that there is no significant difference between HCT values at 5, 6 and 7 wk of age. This suggests that the significant difference in HCT values in Table 1 is the result of the effect of temperature. Further, Shlosberg et al. (1992) indicated that there is a significant increase of RV:TV from weeks 5 to 7. In the current study, the younger birds under cold conditions (5 wk) showed higher RV:TV values than the older birds under normal conditions (7 wk) which also points to a clear effect of temperature.

Effects of Sex and Feathering

The estimated effects of the male sex and slow-feathering on ascites-related traits obtained from the univariate analysis are presented in Table 2. In the analysis, the effects of female sex and fast-feathering were fixed at zero. Sex had significant effects

TABLE 1. Statistical description of the traits measured under cold and normal conditions

Traits	Abbreviation	Cold [1]			Normal [2]		
		Number	Mean	SD	Number	Mean	SD
Body weight (g)	BW	3,693	1,604	263	770	2,060	310
Hematocrit value (%)	HCT	3,547	35.40	4.21	780	28.28	2.30
Right ventricular weight (g)	RV	3,660	1.95	0.68	659	1.15	0.31
Total ventricular weight (g)	TV	3,658	6.97	1.17	746	5.60	0.94
Ratio of right ventricular weight to total ventricular weight (%)	RV:TV	3,658	27.93	8.07	659	20.63	4.66
Right ventricular weight as percentage of BW (%)	%RV	3,646	0.125	0.05	652	0.06	0.01
Total ventricular weight as percentage of BW (%)	%TV	3,644	0.439	0.07	738	0.27	0.04
Total mortality [3]	MORT-TOT	2,494	0.16	0.37	- [5]	-	-
Fluid in the abdomen [4]	ABDOMEN	3,697	0.08	0.38	-	-	-
Color of the breast [4]	BREAST	3,697	0.03	0.18	-	-	-
Liver abnormalities [4]	LIVER	3,697	0.07	0.29	-	-	-
Fluid in the heart sac [4]	HEART	3,696	0.59	0.62	-	-	-

[1] Traits measured at 5 wk of age under cold conditions.
[2] Traits measured at 7 wk of age under normal conditions.
[3] Trait scored as 0 or 1. The number of birds for every class: $N_0 = 2,095$ and $N_1 = 399$.
[4] Trait scored as 0, 1 or 2. The number of birds for every class: fluid in the abdomen: $N_0 = 3,542$, $N_1 = 23$, and $N_2 = 132$, color of the breast: $N_0 = 3,585$, $N_1 = 110$, and $N_2 = 2$, liver abnormalities: $N_0 = 3,488$, $N_1 = 170$, and $N_2 = 39$, fluid in the heart sac: $N_0 = 1,781$, $N_1 = 1,653$, and $N_2 = 262$.
[5] Score traits were not recorded under normal conditions

on most of the ascites-related traits under cold as well as under normal conditions. Under both temperature conditions male broilers had lower HCT values and higher values for BW, RV and TV than the females. Under cold conditions, male birds had a stronger increase of RV than female birds which resulted in a higher RV:TV value for male birds (data not shown).

Under cold conditions feathering also had a marked effect on most of the ascites-related traits (Table 2). Under these conditions slow-feathering birds had a lower BW and higher values for HCT and RV:TV. However, under normal conditions the effect of feathering on these traits was not significant. This suggests that under cold conditions slow-feathering birds are more susceptible to the ascites syndrome, which is probably due to the increased sensitivity of these birds to the cold temperature.

TABLE 2. The estimated effect of male sex and slow-feathering on ascites-related traits under cold and normal conditions [1]

Traits [2]	Sex effect		Feathering effect	
	Cold [3]	Normal [4]	Cold [3]	Normal [4]
BW (g)	191.46 *** [5]	263.74 ***	-55.95 ***	-8.14 ns
HCT (%)	-1.10 ***	-0.57 ***	1.13 ***	0.25 ns
RV (g)	0.51 ***	0.30 ***	0.15 ***	0.06 *
TV (g)	1.17 ***	1.24 ***	0.15 ***	0.13 *
RV:TV (%)	2.62 ***	0.79 *	1.79 ***	0.59 ns
%RV	0.018 ***	0.007 ***	0.014 ***	0.003 **
%TV	0.024 ***	0.029 ***	0.025 ***	0.010 **

[1] In the analysis the effect female sex and fast-feathering were fixed at zero.

[2] HCT = hematocrit value, RV = right ventricular weight, TV = total ventricular weight, RV:TV = ratio of right ventricular weight to total ventricular weight, %RV= right ventricular weight as percentage of BW, %TV = total ventricular weight as percentage of BW.

[3] Trait measured at 5 wk of age under cold conditions.

[4] Traits measured at 7 wk of age under normal conditions.

[5] Significance of the sex or the feathering effect: * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$ and ns = non significant.

Genetic Parameters under Cold Conditions

Heritability estimates obtained from the univariate analyses (Table 3) were in general consistent with estimates from the bivariate analyses. However, for bivariate analyses that comprise mortality, deviating heritability estimates were obtained, e.g. for BW the estimated heritability was 0.32 and for ABDOMEN it was 0.21. Reason for this might be that birds that died during the experiment do not have observations for the other traits. The standard errors for the heritability estimates were between 0.02 and 0.05.

The estimated genetic and phenotypic correlations among ascites-related traits under cold conditions are presented in Table 3. The standard errors for genetic correlations were between 0.01 and 0.30. For phenotypic correlations standard errors

TABLE 3. Estimates of genetic parameters of ascites-related traits measured under cold conditions [1]

Traits [2]	BW	HCT	RV	TV	RV:TV	%RV	%TV	MORT-TOT	ABDOMEN	BREAST	LIVER	HEART
BW	**0.42**	-0.23	0.06	0.58	-0.27	-0.41	-0.50	-0.06	0.00	-0.38	-0.17	-0.12
HCT	-0.37	**0.46**	0.54	0.20	0.56	0.63	0.52	0.72	0.66	0.61	0.66	0.67
RV	0.06	0.40	**0.47**	0.60	0.89	0.86	0.59	0.43	0.74	0.48	0.75	0.91
TV	0.63	-0.03	0.49	**0.46**	0.15	0.26	0.40	-0.25	0.22	-0.03	0.18	0.40
RV:TV	-0.30	0.50	0.86	0.01	**0.45**	0.94	0.50	0.62	0.82	0.62	0.85	0.90
%RV	-0.46	0.57	0.79	0.09	0.92	**0.45**	0.77	0.70	0.81	0.64	0.85	0.91
%TV	-0.53	0.44	0.46	0.29	0.39	0.70	**0.46**	0.58	0.34	0.36	0.44	0.57
MORT-TOT	0.42	0.34	0.04	-0.11	0.11	0.37	0.53	**0.32**	0.96	1.00	0.97	0.78
ABDOMEN	-0.33	0.29	0.29	-0.15	0.46	0.51	0.30	0.57	**0.08**	0.87	1.01	0.70
BREAST	-0.11	0.09	0.10	-0.04	0.16	0.19	0.11	0.88	0.28	**0.03**	0.96	0.13
LIVER	-0.29	0.27	0.26	-0.11	0.40	0.46	0.29	0.67	0.72	0.31	**0.08**	0.76
HEART	-0.15	0.27	0.36	0.05	0.41	0.42	0.26	0.19	0.43	0.14	0.41	**0.18**

[1] Genetic correlations above, Phenotypic correlations below and heritabilities are on the diagonal. Heritabilities obtained in univariate analysis, but genetic and phenotypic correlations obtained in bivariate analysis. The s.e. for genetic correlation were in the range 0.01-0.30, for phenotypic correlation were in the range of 0.00-0.04, and for heritabilities were in the range of 0.02-0.05.

[2] HCT = hematocrit value, RV = right ventricular weight, TV = total ventricular weight, RV:TV = ratio of right ventricular weight to total ventricular weight, %RV= right ventricular weight as percentage of BW, %TV = total ventricular weight as percentage of BW, MORT-TOT = Total mortality, ABDOMEN = Fluid in the abdomen, BREAST = Color of the breast, LIVER = Liver abnormalities, and HEART = Fluid in the heart sac

were between 0.00 and 0.04. The standard errors of estimated genetic correlations were high for those bivariate analysis where one or both of the traits were score traits. Some of the estimated genetic correlations among score traits were outside the parameter space. With a few exceptions, the genetic correlations reported in Table 3 are all positive. However, BW had negative genetic correlations with HCT (-0.23) and RV:TV (-0.27). These estimates indicate that, under the applied experimental conditions (cold stress), those broilers that have a higher genetic potential for growth, have a lower genetic potential for HCT and RV:TV. The positive genetic correlation between BW and TV (0.58) indicates that fast growing birds have a larger total ventricular weight.

At first sight, the correlations between BW and ascites-indicator traits like HCT and RV:TV might seem unexpected as research generally showed that higher productivity in broiler leads to higher O_2 requirements and consequently results in an increased incidence of the ascites syndrome (e.g., Julian, 1993; Moghadam et al., 2001; Summers, 1994). Therefore, one might expect faster growing birds to have higher HCT values and higher RV:TV's, corresponding to a higher incidence of ascites. Apparently, under the present experimental conditions (cold stress), these relationships are influenced by the susceptibility of birds against ascites: birds can only achieve a high body weight in case they show a certain degree of resistance against ascites. These results are in agreement with the results previously obtained by De Greef et al. (2001) and Deeb et al. (2002). De Greef et al. (2001) estimated a negative genetic correlation between 5-wk body weight and ascites candidate traits; -0.54 between BW and HCT and -0.26 between BW and RV:TV. However, in the undiseased subpopulation De Greef et al. (2001) estimated a positive genetic correlation between BW and RV:TV (0.29). Therefore, De Greef et al.(2001) concluded that the genetic correlation between productivity and ascites is sensitive to the disease status of the birds. Deeb et al. (2002) found that chickens that reached a higher BW at 37 d under normal temperature conditions, had a higher mortality due to ascites under cold stress conditions. Further, Deeb et al. (2002) reported that the correlation between sire family means for potential growth rate and actual growth rate (weight gain between 37 to 47 d) changed from positive (0.43) under normal conditions to negative (-0.12) under cold conditions and demonstrated that fast-growing birds are more susceptible to cold stress vs. slow-growing birds.

Ascites is defined as accumulation of fluid in the abdominal cavity and therefore is best described by the trait ABDOMEN. The genetic correlation between ABDOMEN and MORT-TOT was very strong (0.96). In the present experiment, MORT-TOT was defined as the total mortality, but most likely mortality was mainly due to ascites. Also there was a high genetic correlation between ABDOMEN and other score traits which suggests that these traits all represent a similar phenomenon. The high genetic correlation between ABDOMEN and RV:TV (0.82) suggests that RV:TV is a good

indicator trait for ascites. The ratio of RV:TV quantifies the degree of hypertrophy of the heart and it is an index of pulmonary hypertension (Huchzermeyer and de Ruyck, 1986). Lubritz et al. (1995) found genetic correlations between ABDOMEN and RV:TV in broilers exposed to cold temperatures varying from 0.46 to 0.78, depending on the broiler line and the growth rate.

The hematocrit value (HCT) is a physiological regulator of oxygen transport capacity. A high value for HCT in broilers with a high metabolic rate and under cold stress is an adaptive advantage because the blood's oxygen carrying capacity is enhanced. However, the down side of high HCT values is that the blood becomes more viscous and resistant to flow and as a result the pulmonary vascular pressure increases (Maxwell et al, 1992). In the current study the genetic correlation between HCT and MORT-TOT was relatively high (0.72). The genetic correlation between HCT and other traits was moderate, e.g. the genetic correlation between HCT and RV:TV was 0.56 and between HCT and ABDOMEN was 0.66. These results indicate that under cold conditions, the incidence of ascites is higher in those birds that have a higher genetic potential for hematocrit value. Shlosberg et al. (1996) showed that in cold conditions birds with high HCT were more susceptible to die due to ascites (41%), and birds with low HCT were more likely to die from other causes (26%).

Genetic Parameters under Normal Conditions

The estimated heritabilities and genetic and phenotypic correlations among ascites-related traits measured under normal conditions are presented in Table 4. The accuracy of the estimates under normal conditions was relatively low due to the smaller data set: the standard errors for genetic correlations were in the range of 0.10 to 0.54, for phenotypic correlations between 0.02 and 0.05, and for heritabilities between 0.05 and 0.12. The heritability estimates of ascites-related traits under normal conditions were in general lower than those obtained under cold conditions, e.g. the heritability estimate for HCT was 0.17, and for RV:TV, the estimated heritability was 0.12. This is probably because under cold conditions, genetic differences in ascites susceptibility become more evident. Genetic correlations among ascites-related traits are shifted to more positive values under normal conditions as compared to the estimates under cold conditions. For instance the genetic correlation between BW and HCT changed from -0.23 under cold conditions to 0.55 under normal conditions and the genetic correlation between BW and RV:TV changed from -0.27 to 0.50. The high and positive genetic correlations between BW and HCT or BW and RV:TV under normal conditions indicated that birds with high genetic potential for BW have a high genetic potential for HCT or RV:TV. These results also suggest that the genetic parameters for these traits are very sensitive to the applied temperature schedule, which is related to the incidence

of the disease. It should be noted, however, that under normal temperature conditions the birds are older (7wk) as compared to the birds kept under cold temperature conditions (5 wk). Therefore, they are expected to have a higher BW and it cannot be excluded that part of the differences in correlations found under cold and normal temperature conditions might actually be due to the difference in age at which BW is recorded.

The high genetic correlation between BW and heart characteristics like RV and TV suggest that under normal conditions those broilers that have higher genetic potential for growth, have higher genetic values for RV and TV values as well. This agrees with the finding of Wideman, (2001) who indicated that for clinically healthy broilers any increase in BW is associated with proportional increases in TV, cardiac output and stroke volume.

TABLE 4. Estimates of genetic parameters of ascites-related traits under normal conditions [1]

Traits [2]	BW	HCT	RV	TV	RV:TV	%RV	%TV
BW	**0.50**	0.55	0.90	0.79	0.50	0.41	-0.36
HCT	-0.08	**0.17**	0.80	0.59	0.71	0.61	0.09
RV	0.41	0.08	**0.13**	0.73	0.88	1.12	-0.50
TV	0.59	0.04	0.57	**0.54**	-0.19	0.73	0.39
RV:TV	0.11	0.08	0.72	-0.08	**0.12**	0.93	-0.69
%RV	-0.13	0.11	0.73	0.30	0.61	**0.05**	0.00
%TV	-0.51	0.14	0.16	0.40	-0.15	0.43	**0.17**

[1] Genetic correlations above, Phenotypic correlations below and heritabilities are on the diagonal. Heritabilities obtained in univariate analysis, but genetic correlations obtained in bivariate analysis. The s.e. for genetic correlation were in the range 0.1-0.54, for phenotypic correlation were in the range of 0.02-0.05, and for heritabilities were in the range of 0.05-0.12.

[2] HCT = hematocrit value, RV = right ventricular weight, TV = total ventricular weight, RV:TV = ratio of right ventricular weight to total ventricular weight, %RV= right ventricular weight as percentage of BW, %TV = total ventricular weight as percentage of BW.

Cold and Normal Conditions

The unique set up of the present experiment, where parents have offspring under both cold and normal temperature conditions, enables the estimation of genetic correlations between traits measured under both conditions (Table 5). Except for BW, the genetic correlations between the same traits measured under cold and normal temperatures were high, e.g. 0.93 for HCT, 0.89 for RV, 0.80 for TV and 0.91 for RV:TV. These results indicate that mainly the same genes affect these traits in both environments. In contrast the low genetic correlation for BW measured in different environments (0.29) suggests that this trait is very sensitive to temperature. However, this correlation is not only the result of differences in environmental conditions but also the difference in age between the groups of birds should be considered. Most of the reported genetic correlations among body weights of broilers at various ages are high

e.g. Chambers et al. (1984) estimated genetic correlations larger than 0.8 among BW measured at 4, 6 and 7 wk of age and Wang et al. (1991) estimated a genetic correlation of 0.94 between 4- and 6-wk BW based on maternal relationships and a genetic correlation of 0.83 between these traits based on paternal relationships. Therefore, it can be concluded that the low genetic correlation between BW measured under cold and normal conditions in the present study is mainly due to the temperature effect. This correlation therefore indicates genotype by environment interaction and consequently broilers with high genetic values for BW under normal conditions do not necessarily have high genetic values for BW under cold conditions. Fast growing broilers have high metabolic requirements for oxygen which requires a high volume of blood flow through their lungs (Julian, 1993). High oxygen requirement is the most critical trigger for ascites in broilers especially under cold stress conditions (Julian, 1998). Also to maintain normal body temperature in a cold environment, the metabolic rate rises to increase heat production (Julian, 1998). Therefore, when the environmental conditions give rise to ascites syndrome (cold stress or high altitudes), broilers with higher genetic potential for growth rate are especially affected.

TABLE 5. Genetic correlation among ascites-related traits in cold and normal conditions

		Normal temperature conditions						
	Traits [1]	BW	HCT	RV	TV	RV:TV	%RV	%TV
Cold temperature conditions	BW	**0.29**	0.15	-0.12	0.09	-0.07	-0.77	-0.14
	HCT	0.31	**0.93**	0.80	0.38	0.77	0.98	0.07
	RV	0.58	0.62	**0.89**	0.73	0.77	0.90	0.36
	TV	0.48	0.40	0.33	**0.80**	-0.29	-0.01	0.80
	RV:TV	0.40	0.46	0.91	0.41	**0.91**	0.94	-0.01
	%RV	0.38	0.44	0.86	0.59	0.73	**0.96**	0.35
	%TV	0.21	0.23	0.45	0.69	-0.20	0.74	**0.83**
	MORT-TOT	0.17	0.51	0.50	0.12	0.63	0.57	-0.33
	ABDOMEN	0.20	0.51	0.61	0.31	0.63	1.36	0.02
	BREAST	-0.08	0.45	1.29	-0.67	0.92	0.43	-0.68
	LIVER	0.21	0.58	0.70	0.29	0.76	0.77	-0.04
	HEART	0.30	0.57	0.77	0.53	0.64	0.87	0.31

[1] HCT = hematocrit value, RV = right ventricular weight, TV = total ventricular weight, RV:TV = ratio of right ventricular weight to total ventricular weight, %RV= right ventricular weight as percentage of BW, %TV = total ventricular weight as percentage of BW, MORT-TOT = Total mortality, ABDOMEN = Fluid in the abdomen, BREAST = Color of the breast, LIVER = Liver abnormalities, and HEART = Fluid in the heart sac.

The genetic correlation between BW measured under cold conditions and other ascites-related traits measured under normal conditions (Table 5) was higher than estimates among the same traits under cold conditions (Table 3), but they were lower than estimates among the same traits under normal conditions (Table 4). For other traits there was no obvious difference between estimates under cold, normal and cold +

normal conditions. Because of low genetic correlation between BW under cold and normal conditions these results were expected.

Maternal Genetic Effects

Pakdel et al. (2002) indicated that under cold conditions, the traits BW, TV, RV:TV, %RV, %TV and MORT-TOT are significantly affected by maternal genetic effects and there is an overestimation of the direct heritability when the maternal genetic effect was neglected. In the current study, no significant maternal genetic effects could be detected for traits measured under normal conditions, which might be due to the smaller number of observations. Including maternal genetic effects in bivariate analyses leads to a strong increase in the number of parameters that needs to be estimated and greatly complicates the calculations. Therefore, in the present study results are presented for a model without maternal genetic effects. When, under cold conditions, the maternal genetic effect was included in the model, the genetic correlations between BW and other ascites-related traits increased, e.g. the correlation between BW and HCT changed from -0.23 ($\pm$ 0.10) to 0.06 ($\pm$0.17) and the correlation between BW and RV changed from 0.06 ($\pm$0.10) to 0.27 ($\pm$0.16). However, for most of the traits there was no obvious difference between genetic correlations estimated using a model with and without maternal genetic effects.

Prospects

Animals that are not fully resistant to a certain disease may show a decreased production when infected. A high infection pressure combined with a low level of resistance may cause production to drop dramatically, while when the level of resistance is high, infection may have little or no influence on performance (Van der Waaij et al., 2000). From the economical as well as ethical point of view it is important to increase the level of ascites resistance in broilers to a level where the influence of this syndrome on production is negligible. In this study we report genetic parameters for traits which might serve as indicators for ascites susceptibility. Designing effective selection strategies for ascites resistance not only has to deal with the identification of good indicator traits, but also concerns the choice of the selection environment, i.e. normal and cold temperature conditions. Therefore, it is important to determine the degree of genotype by environment interaction for BW and ascites indicator traits. This study is the second to report on genetic correlations among traits related to the ascites syndrome measured under cold and normal conditions. In spite of difference in age of measurement of the traits under both environmental conditions, the results suggest that there is an interaction between temperature and BW, which can be attributed to genetic variation in the susceptibility of birds to ascites. From the results it can be concluded

that a high-observed production under cold conditions is due to a favorable combination of resistance to ascites and production potential. Under normal conditions however, the production potential of birds is important whereas genetic differences in resistance to ascites syndrome are less relevant. The evidence for genotype by environment interactions in modern broilers and various suboptimal conditions also emphasize the need for breeding programs aimed at improving performance under particular stressful environments.

The results of present study showed high genetic correlations between the same ascites-related traits measured under cold and normal conditions. Therefore it is possible to select against ascites by measuring birds ascites-related traits under normal conditions. Strong positive genetic correlations were found among total mortality, fluid in the abdomen and ratio of RV:TV (around 0.8) under cold conditions. The genetic correlation between RV:TV measured under normal conditions and ascites indicator traits (e.g. HCT, MORT-TOT, ABDOMEN, BREAST and LIVER) measured under cold conditions was relatively high. Because ascites is best described by the trait fluid in the abdomen, these results suggest that ratio of RV:TV that quantify the degree of hypertrophy of the heart is a good indicator for ascites.

The results of the present study provide important information for developing an effective selection strategy to reduce the incidence of ascites syndrome in broilers. This will form the basis for the design of a well-balanced breeding scheme for broilers.

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Chapter 4

Genetic Correlations among Ascites-Related Traits and Performance Traits in Broilers

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ABSTRACT 1. Pulmonary hypertension syndrome followed by ascites is a metabolic disorder in broilers that occurs more often in fast growing birds and at cool temperatures. 2. Knowledge of the genetic relationships among ascites-related traits and performance traits like carcass traits or feed efficiency traits are required to design breeding programs that aim to improve the degree of resistance to ascites syndrome as well as production traits. The objective of this study was to estimate these genetic correlations.

3. Three different experiments were set up to measure ascites-related traits (4202 birds), feed efficiency traits (2166 birds) and carcass traits (2036 birds). All the birds in different experiments originated from the same group of parents, which enabled the estimation of genetic correlations among different traits.

4. The ratio of right to total ventricular weight (RV:TV) quantifies the degree of hypertrophy of the heart. The genetic correlation of BW under normal conditions with RV:TV under cold conditions was 0.30. The estimated genetic correlation indicated that single-trait selecting for BW leads to an increase occurrence of the ascites syndrome but that there are good opportunities of multi-trait selection of birds for improved BW and resistance to ascites.

5. Weak but positive genetic relationships were found between FE and ascites related traits suggesting that more efficient birds tend to be slightly more susceptible towards ascites.

6. The results of present study showed considerable genotype by environment interaction for trait BW which suggest that to achieve a higher selection response in broilers, breeding program aimed at improving performance under particular stressful environment (cold-stress conditions).

INTRODUCTION

Consistent selection by poultry breeding companies have dramatically increased growth rate of broilers stocks. As a result, today's chickens as compared to typical broilers from 1950s, consume more feed per unit time, have better feed efficiency, grow faster and have greater carcass yield (Havenstein et al., 1994). However, apart from a favorable increase in production traits, birds that have been selected for high production efficiency seem to be more sensitive to suboptimal conditions. Further, there seems to be an increase in the incidence of metabolic and physiological disorders of which ascites syndrome is an example (Julian, 1998, Rauw et al., 1998). Ascites syndrome refers to the accumulation of fluid in the abdominal cavity, and the lay term "waterbelly" is an appropriate description of its appearance in affected chickens. It occurs when broilers fail to take up sufficient oxygen to support their metabolic demands. This syndrome is a challenge to the poultry industry because it is an end-stage lesion with multiple causes and the heavy, rapidly growing broilers appear to be more susceptible as a result of an increased metabolic rate (Hoerr, 1988).

Previous studies showed that traits related to ascites syndrome have a relatively high heritability (Lubritz et al., 1995; De Greef et al., 2001 and Pakdel et al., 2002). This indicates that selection against this syndrome should be feasible. Furthermore, Pakdel et al. (2004) indicated that there is a strong genetic correlation between the same ascites-related trait measured under cold and normal conditions, which indicates that the same genes affect these traits in both environments. Genetic correlations among ascites-related traits and productivity traits like BW have been reported (Moghadam et al., 2001, Pakdel et al., 2004, De Greef et al., 2001), but they seem to depend on the environmental conditions. Little information is available on genetic correlations with feed efficiency or carcass traits. Under normal climatic conditions a positive genetic correlation was reported between ascites-related traits and BW (Moghadam et al., 2001, Pakdel et al., 2004). However, under cold conditions a negative genetic correlation was reported between ascites and BW (De Greef et al., 2001, Pakdel et al., 2004). Deeb et al., (2002) found that birds that have a higher potential for growth rate under normal temperature conditions are more likely to suffer from ascites under cold-stress conditions as compared to birds with a lower potential for growth rate. Pakdel et al. (2004) reported that the genetic correlation between ascites-related traits and BW depends upon the conditions under which birds are kept. They suggest that a high-observed production of birds under cold conditions is due to a favorable combination of resistance to ascites and production potential. Under normal conditions however, the production potential of animals is important whereas genetic differences in resistance to ascites syndrome are less relevant.

Knowledge of the genetic relationships among ascites-related traits and performance traits like carcass traits or feed efficiency traits are required to design breeding programs that aim to improve the degree of resistance to ascites syndrome as well as production traits. The objective of this study was to estimate these genetic correlations.

MATERIAL AND METHODS

Birds and traits

Birds. The experimental population is the result of a cross between two genetically different outcross broiler dam lines (Hybro) originating from the White Plymouth Rock breed. The maternal line had a relatively high reproductive performance and was fast feathering and the paternal line had a relatively high growth performance and was slow feathering. 36 birds from the two lines were crossed to produce the F_1 generation. From the F_1, 29 birds were parents of the F_2 generation, which consisted of 829 birds. The same F_2 parents were used to produce three groups of F_3 birds, which were subject to three different experiments.

Ascites experiment: this experiment was used to measure ascites-related traits under cold conditions. This group consisted of 4,202 birds and hatched in 6 different wk. These birds were kept in four different pens. Nine batches were allotted by hatching day and pen number. In order to identify individuals that were susceptible to ascites, a cold-stress temperature schedule was applied for this group of birds. At the time of hatching, the temperature was 30 ^{o}C and then was gradually decreased to 10 ^{o}C by 22 d of age. The temperature remained at 10 ^{o}C until the end of the experiment. Except for the cold stress temperature schedule, birds were kept under circumstances that closely resemble commercial practice. More details on the experiment are given by Pakdel et al.(2002).

Carcass experiment: this experiment was used to measure carcass traits. This group consisted of 2,036 birds, and hatched in 6 different wk. They were raised in six hatches and housed in a litter system until the age of 48 d. These birds were kept under normal temperature schedule. A normal temperature schedule starts at 33 to 34 ^{o}C and then gradually decreases to 17 to 18 ^{o}C at 35 d of age. The animals were in the same pen starting from day 0, where they received feed and water for *ad libitum* consumption. The birds in this experiment have been used previously to detect QTL affecting carcass traits (Van Kaam et al., 1999a). In addition to the carcass traits, information on ascites-related traits were collected on 795 birds in this experiment.

Feed efficiency experiment: this experiment was used to measure traits related to feed efficiency. This group consisted of 2,166 birds, hatched in 5 different wk. They were raised consecutively in the same floor pens up to 22 d of age and housed individually in another building between the age of 22 and 48 d. Individual cages were used to enable individual measurements of feed intake. During the lifetime of the

broilers, feed and water were supplied *ad libitum*. The temperature schedule of this group of birds was normal and it was similar to the carcass experiment. The birds in this experiment have been used previously to detect QTL affecting feed efficiency traits (Van Kaam et al., 1999b).

All three groups of birds originated from the same parents, which provide the possibility to estimate genetic correlations between traits measured in different experiments. A few important differences exist among the housing conditions of the three experimental groups, which need to be emphasized. In the ascites and carcass experiment, birds were kept in group housing (20 birds / m^2), whereas in the feed efficiency experiment birds were housed individually. Further, in the ascites experiment birds were kept under cold conditions whereas in the two other experiments a normal temperature schedule was applied. Except for these differences, all three groups of birds were kept under similar conditions, i.e. a standard commercial broiler feed, consisting of crumbled concentrates containing 12,970 kJ/kg and 21% protein and artificially lighted housing for 23 h/d.

Traits. Ascites experiment: birds were slaughtered at 5 wk of age. The body weight (BW_{AS-35}) and hematocrit value (HCT) of birds were measured 1 d before slaughtering. After slaughtering a number of ascites-related traits were measured. Livers and hearts were removed and visually inspected. Liver abnormalities (LIVER) were scored as follow: 0 represented no abnormalities observed, 1 represented an abnormal liver, and 2 represented serious liver abnormalities. Liver abnormalities were a lighter color, an irregular liver surface, or both. Accumulation of fluid in the heart sac (HEART) was scored with 0 if no fluid had accumulated, 1 if fluid accumulation was observed, and 2 if there was serious accumulation of fluid in the heart sac. Further, the weight of right ventricular (RV) and total ventricular (TV) were measured. From these measurements the ratio of RV:TV, RV as a percentage of total BW (%RV) and TV as a percentage of total BW (%TV) were derived. The accumulation of fluid in the abdomen (ABDOMEN) was scored as 0, 1, or 2. A score of 0 indicated no fluid, 1 indicated the presence of fluid in the abdomen, and 2 indicated a serious accumulation of fluid in this section. For color of the breast (BREAST), a score of 0 represented normal color, 1 represented a color deviation, and a score of 2 represented serious color deviation. In general a deviation of breast color meant that the color was reddish. Also the total mortality (MORT-TOT) of the birds were recorded as 0 or 1. A score of 0 represented a bird that was alive at the end of the experiment and a score of 1 indicated a bird that died before the end of the experiment. For the first three batches of birds, mortality was not recorded. No observations for other traits were available for birds, which died before the end of experiment.

Carcass experiment: Around day 47, the legs of the birds were scored on a scale from 1 to 9, by looking at the lateral deviation of the legs (the hock-joints). Straight legs

were considered as the optimal and received a score of 9. Birds with legs further away from this optimum received a lower score. Leg problems were considered as an effect of weak hock ligaments or tendons, which could result in both *varus* (proximal hocks) as well as *valgus* (distal hocks). Therefore, both *varus* and *valgus* birds had a score below the maximum. In practice, the majority of the birds with leg abnormalities showed *varus*. At 48 d, the body weight (BW_{C-48}) was measured and animals were slaughtered and carcass weight (CW) was measured. Carcass weight was measured on the chilled carcass after removal of feathers, head, lungs, liver, kidneys, gastrointestinal tract, abdominal body fat, subcutaneous leg fat and lower legs and after loss of part of the animals blood due to bleeding. For one hatch, CW was measured on 2 days. On the same day that CW was measured, the meat color (MC) was measured at three spots on the chilled breast fillet, using a fibre optic meat probe [2]. These three measurements were considered as repeated measurements of the same traits and were averaged to obtain a single value for MC. The last hatch of birds was measured on a different scale due to problems with the fibre optic meat probe. To remove this effect, the data was standardized within every hatching wk (by dividing the deviation of each observation from the mean with standard deviation). For about 700 birds in this experiment measurements for ascites-related traits HCT, RV, TV, and RV:TV were available. BW and hematocrit value (HCT) of this group of birds were also measured 1 d before slaughtering.

Feed efficiency experiment: Traits measured were BW at 23 d of age (BW_{FE-23}), BW at 48 d of age (BW_{FE-48}) and feed intake from 23 d to 48 d (FI). Inferred traits were growth between 23 d and 48 d (GAIN), feed efficiency (in percentage) between 23 d and 48 d (FE) and residual feed intake (RFI). FE was defined as the ratio between GAIN and FI and can be seen as gross efficiency. Residual feed intake (RFI) is a measure of net feed efficiency, which accounts for both maintenance and growth requirements. RFI was calculated as:

$$RFI = FI - [a + (b_1 * BW_{FE-23}) + (b_2 * GAIN)]$$

where a is the intercept and b_1 and b_2 are the partial regression coefficients of FI on BW_{FE-23} and GAIN, respectively (Van Bebber and Mercer, 1994)

Genetic Analysis

An animal model was used to calculate heritabilities and genetic correlations of the traits;

$$Y_{ijklm} = \mu + Sex_i + Feather_j + Batch_k + Group_l + a_m + e_{ijklm}$$

where: Y_{ijklm} = the dependent variable on chicken m of sex i, feathering class j from batch k in group l; Sex_i = fixed effect of sex i (i=1,2 female or male); $Feather_j$ = fixed

[2] TBL Fibre optics Ltd., Leeds, LS10 1AT, U. K.

effect of feathering j (j = 1,2 fast or slow); $Batch_k$ = fixed effect of batch k (k = 1,2…9 only for birds in the ascites experiment), classes were formed based on a combination of hatching day and pen; $Group_l$ = Fixed effect of group (l=1,2…46 for birds in the ascites experiment, l = 1,2…47 for birds in the carcass experiment and l = 1, 2 … 40 for birds in the feed efficiency experiment), classes were formed based on the age of the dam and the hatching day of the animals ; a_m= random direct genetic effect of individual m; e_{ijklm} = random residual effect. The model was based on previous analysis reported by Pakdel et al. (2004). Except for the Batch effect, which was included only in the model for birds in the ascites experiment, fixed and random effects in the model were identical for all experiments. Bivariate analyses were performed to compute correlations between all combinations of traits. Estimates of variance components were obtained using the ASREML software (Gilmour et al., 2000).

RESULTS

Descriptive statistics

Descriptive statistics of the traits measured in the three experiments are presented in Table 1. In the ascites experiment, the broilers weighted 1,604 g on average at 35 d of age and total mortality in this experiment was 16%. Under normal conditions (carcass and feed efficiency experiment) the broilers weighted around 2,199 g on average at 48 d of age and total mortality was 4% in the carcass experiment (data not shown). For a more detailed description of ascites-related traits under cold and normal conditions, we refer to Pakdel et al. (2004).

In the feed efficiency experiment, the average feed intake of birds from 23 d to 48 d of age was 3,222 g and the average weight gain during this time period was 1,582 g. The corresponding average feed efficiency is 49%. The average residual feed intake is by definition equal to zero and the standard deviation was 253 g.

The mean weight of 48-d old birds in the carcass experiment was 2,212 g and the corresponding carcass weight was 1,495 g. This corresponds to a carcass percentage (CP) of 67 %.

Genetic parameters for feed efficiency and carcass traits

The estimated heritabilities and genetic correlations among feed efficiency traits and carcass traits are presented in Table 2. Heritability estimates for most of the traits in the carcass experiment were in the range of 0.3 to 0.4. The heritability for LS was lower and had a value of 0.12. In the feed efficiency experiment heritabilities ranged from 0.16 for GAIN to 0.52 for BW_{FE-23} the estimated genetic correlation between BW_{C-48} and carcass weight (CW) was close to unity (0.97). The genetic correlation between body weight measured when birds were kept in groups (BW_{C-48}) and individually housed birds (BW_{FE-48}) was 0.87. Body weight (BW_{C-48} or BW_{FE-48}) and carcass

TABLE 1. Statistical description of the trais

Trait	Abbreviation	Number	Mean	SD
Ascites experiment[1]				
BW at 35 d of age (g)	BW_{AS-35}	3,693	1,604	263
Hematocrit value (%)	HCT	3,547	35.40	4.21
Right ventricular weight (g)	RV	3,660	1.95	0.68
Total ventricular weight (g)	TV	3,658	6.97	1.17
Ratio of right ventricular to total ventricular weight (%)	RV:TV	3,658	27.94	8.07
Right ventricular weight as percentage of BW (%)	% RV	3,647	0.125	0.05
Total ventricular weight as percentage of BW (%)	% TV	3,644	0.439	0.07
Total mortality [2]	MORT-TOT	2,494	0.16	0.37
Fluid in the abdomen [3]	ABDOMEN	3,697	0.08	0.38
Color of the breast [3]	BREAST	3,697	0.03	0.18
Liver abnormalities [3]	LIVER	3,697	0.07	0.29
Fluid in the heart sac [3]	HEART	3,696	0.59	0.62
Feed efficiency experiment[4]				
BW at 23 d of age (g)	BW_{FE-23}	2,166	603	100
BW at 48 d of age (g)	BW_{FE-48}	2,085	2,187	332
Feed intake between 23 to 48 d (g)	FI	2,085	3,222	490
Growth between 23 to 48 d (g)	GAIN	2,085	1,582	278
Feed efficiency	FE	2,085	0.49	0.05
Residual feed intake from 23 to 48 d (g)	RFI	2,085	0	253
Carcass experiment[4]				
BW at 48 d (g)	BW_{C-48}	1999	2212	337
Carcass weight (g)	CW	1987	1495	237
Carcass percentage	CP	1966	67.42	1.86
Meat color [5]	MC	1943	31.73	4.12
Leg score [6]	LS	1959	5.76	1.98
Hematocrit value (%)	HCT_C [7]	780	28.28	2.30
Right ventricular weight (g)	RV_C	659	1.15	0.31
Total ventricular weight (g)	TV_C	746	5.60	0.94
Ratio of right ventricular to total ventricular weight (%)	$RV:TV_C$	659	20.65	4.66
Right ventricular weight as percentage of BW (%)	% RV_C	652	0.06	0.01
Total ventricular weight as percentage of BW (%)	% TV_C	738	0.27	0.04

[1] Traits measured at 5wk of age under cold conditions.

[2] Trait scored as 0 or 1.

[3] Trait scored as 0, 1 or 2.

[4] Traits measured at 7wk of age under normal conditions.

[5] Higher values represent darker or reddish meat.

[6] Legs scored from 1 to 9. Higher score means the legs are straighter and they were considered as the optimum.

[7] C means trait measured in carcass experiment.

percentage (CP) were genetically unrelated (0 or –0.03). Leg score (LS) had a positive genetic correlation with CP (0.41). No correlations significantly different from zero were found between LS and other traits. Further, no significant correlations were found between meat color (MC) and other traits.

Genetically, birds with a higher initial body weight (BW_{FE-23}) also tend to be heavier at 48 days of age, they have a higher GAIN, a higher feed intake (FI) and a lower FE (Table 2). Genetic correlations of BW_{FE-48} with FI and GAIN were positive and high (0.78 and 0.93, respectively). The correlations between FE and BW_{FE-48} or BW_{C-48} had opposite signs but both correlations did not differ significantly from 0. Chickens with higher GAIN during the 23- to 48-day period consumed more feed, which was reflected in the genetic correlation between GAIN and FI of 0.71. The negative relationship between FI and FE (-0.72) indicates that more efficient birds, i.e. the birds with a higher FE, consumed less feed. Residual feed intake (RFI) showed a strong negative genetic correlation with FE (-0.93) and a positive genetic correlation with FI (0.72).

The Genetic Relationship among Ascites-Related Traits Measured under Cold Conditions and Performance Traits

The estimated genetic correlation among traits measured in the ascites experiment, i.e. measured under cold conditions and traits measured in the carcass and feed efficiency experiments are presented in Table 3. Body weight measured in the ascites experiment (BW_{AS-35}) showed a relatively low genetic correlation (0.49) with body weight measured in the carcass experiment (BW_{C-48}). The genetic correlation between BW_{C-48} and the ascites indicator trait RV:TV was 0.30 and with TOT-MORT the genetic correlation was 0.35. Carcass weight (CW) had very similar genetic correlations with these traits. This was expected given the high genetic correlation between BW_{C-48} and CW. These results suggest that birds with higher genetic potential for body weight measured under normal commercial circumstances (i.e. BW_{C-48}) are more susceptible to ascites.

MC showed a positive genetic correlation with RV:TV (0.32) that differed significantly from zero. A higher value for meat color (MC) represents darker or more reddish meat. The genetic correlations between body weight in the ascites experiment (BW_{AS-35}) and body weights measured in the feed efficiency experiment were 0.36 and 0.53 for BW_{FE-23} and BW_{FE-48}, respectively. These results confirm that BW measured in a high ascites incidence environment (cold temperatures) is a genetically different trait from BW measured in a low ascites incidence environment (normal temperatures). The trait BW_{FE-48} showed a positive genetic correlation with RV (0.47), TV (0.54), and RV:TV (0.27). The genetic correlations between BW_{FE-48} and other ascites-related traits

TABLE 2. Estimates of genetic parameters for feed efficiency traits and carcass traits measured [1]

Trait [2]	Carcass experiment					Feed efficiency experiment					
	BW_{C-48}	CW	CP	MC	LS	BW_{FE-23}	BW_{FE-48}	FI	GAIN	FE	RFI
BW_{C-48}	**0.31 (0.07)** [3]										
CW	0.97 (0.01)	**0.28 (0.06)**									
CP	0.00 (0.16)	0.27 (0.14)	**0.41 (0.07)**								
MC	0.29 (0.16)	0.22 (0.16)	-0.15 (0.14)	**0.36 (0.07)**							
LS	0.10 (0.23)	0.16 (0.23)	0.41 (0.18)	-0.13 (0.22)	**0.12 (0.05)**						
BW_{FE-23}	0.70 (0.12)	0.64 (0.13)	-0.13 (0.13)	0.08 (0.13)	0.21 (0.19)	**0.52 (0.07)**					
BW_{FE-48}	0.87 (0.11)	0.83 (0.12)	-0.03 (0.16)	-0.08 (0.16)	-0.08 (0.24)	0.86 (0.05)	**0.27 (0.06)**				
FI	0.55 (0.15)	0.50 (0.15)	-0.17 (0.14)	-0.05 (0.15)	-0.11 (0.22)	0.73 (0.07)	0.78 (0.06)	**0.35 (0.07)**			
GAIN	0.71 (0.15)	0.70 (0.15)	0.02 (0.19)	-0.14 (0.19)	-0.20 (0.27)	0.64 (0.11)	0.93 (0.02)	0.71 (0.09)	**0.16 (0.05)**		
FE	0.10 (0.17)	0.18 (0.17)	0.26 (0.15)	-0.16 (0.15)	0.06 (0.23)	-0.32 (0.13)	-0.19 (0.18)	-0.72 (0.11)	0.00 (0.20)	**0.29 (0.06)**	
RFI	-0.03 (0.15)	-0.09 (0.15)	-0.22 (0.13)	0.04 (0.14)	-0.10 (0.20)	0.12 (0.12)	0.13 (0.15)	0.72 (0.07)	0.07 (0.18)	-0.93 (0.03)	**0.49 (0.07)**

[1] Genetic correlation below and heritabilities are on the diagonal.

[2] BW_{C-48} = BW at 48 d in carcass experiment, CW = carcass weight, CP = carcass percentage, MC = meat color, LS = leg score, BW_{FE-23} = BW at 23 d in feed efficiency experiment, BW_{FE-48} = BW at 48 d in feed efficiency experiment, FI= =feed intake between 23 to 48 d, GAIN = growth between 23 to 48 d, FE = feed efficiency and RFI = residual feed intake.

[3] The standard error in bracket. The standard errors were high for genetic correlations involving leg score.

did not differ significantly from zero. The genetic correlations between GAIN and BW_{AS-35} and ascites-related traits were similar to those found for BW_{FE-48}. This is expected given the high genetic correlation between BW_{FE-48} and GAIN. FI also showed a positive genetic correlation with BW_{AS-35}, RV and TV. Correlations between FI and ascites indicator traits like RV:TV or MORT-TOT were close to zero. Feed efficiency (FE) was positively correlated to RV:TV (0.20) and ABDOMEN (0.17) suggesting an increased susceptibility towards ascites for more efficient birds. However, these correlations are not very strong and have relatively high standard errors. RFI showed a negative genetic correlation with HEART (-0.31). Correlations between RFI and other ascites-related traits are similar to those found for FE but have opposite signs.

The Genetic Relationship among Ascites-Related Traits Measured under Normal Conditions and Performance Traits

The genetic correlation among ascites-related traits under normal temperature conditions, i.e. in the carcass experiment, and performance traits are presented in Table 4. Ascites-related traits under normal conditions were measured on approximately 700 of the animals in the carcass experiment. Due to this smaller number of animals, the accuracy of the estimated genetic correlations is lower than estimates reported in Table 3.

The trait BW_{C-48} showed a relatively high genetic correlation with heart measurements like RV and TV (0.83 and 0.69, respectively). Positive genetic correlations were found between BW_{C-48} and ascites indicator traits like HCT and RV:TV. MC showed a high positive genetic correlation with RV (0.72) and RV:TV (0.73) which means that birds with high values for MC have a higher right ventricular weight and also a higher RV:TV. No significant correlations were found between LS and ascites-related traits.

Body weight measured at 48 days in the feed efficiency experiment (BW_{FE-48}) had high genetic correlations with heart measurements like RV and TV (0.63 and 0.83, respectively), but the correlation with RV:TV was close to zero. The relationships between GAIN and ascites-related traits were very similar to those for BW_{FE-48} which was to be expected given their high genetic correlation (Table 1). Feed intake (FI) showed a positive genetic correlation with TV (0.46) and %TV (0.59). The genetic correlations between HCT and FE or RFI were of the same magnitude but with opposite signs (0.58 and –0.57 respectively).

TABLE 3. Estimates of genetic correlation among ascites-related traits measured under cold conditions and performance traits measured under normal conditions

Trait [1]	Carcass experiment					Feed efficiency experiment					
	BW_{C-48}	CW	CP	MC	LS	BW_{FE-23}	BW_{FE-48}	FI	GAIN	FE	RFI
BW_{AS-35}	0.49 (0.12) [2]	0.52 (0.12)	0.16 (0.12)	-0.09 (0.13)	-0.36 (0.20)	0.36 (0.10)	0.53 (0.13)	0.43 (0.12)	0.52 (0.15)	-0.10 (0.13)	0.11 (0.11)
HCT	0.21 (0.13)	0.21 (0.13)	0.03 (0.12)	-0.03 (0.13)	0.48 (0.17)	-0.03 (0.11)	-0.10 (0.14)	-0.19 (0.12)	-0.11 (0.16)	0.19 (0.13)	-0.19 (0.11)
RV	0.44 (0.13)	0.40 (0.13)	-0.09 (0.12)	0.22 (0.12)	0.17 (0.18)	0.34 (0.10)	0.47 (0.12)	0.26 (0.12)	0.49 (0.15)	0.16 (0.13)	-0.12 (0.11)
TV	0.42 (0.12)	0.41 (0.12)	-0.01 (0.12)	-0.05 (0.12)	-0.11 (0.19)	0.34 (0.10)	0.54 (0.12)	0.41 (0.11)	0.59 (0.14)	0.03 (0.13)	0.05 (0.11)
RV:TV	0.30 (0.13)	0.27 (0.13)	-0.06 (0.12)	0.32 (0.12)	0.28 (0.18)	0.22 (0.11)	0.27 (0.13)	0.09 (0.13)	0.26 (0.16)	0.19 (0.13)	-0.16 (0.11)
% RV	0.19 (0.13)	0.15 (0.14)	-0.11 (0.12)	0.24 (0.12)	0.35 (0.18)	0.16 (0.11)	0.20 (0.13)	0.07 (0.13)	0.21 (0.16)	0.16 (0.13)	-0.13 (0.11)
% TV	-0.06 (0.13)	-0.10 (0.13)	-0.17 (0.12)	0.05 (0.12)	0.27 (0.19)	-0.04 (0.11)	0.00 (0.14)	-0.03 (0.12)	0.05 (0.16)	0.13 (0.13)	-0.06 (0.11)
MORT-TOT	0.35 (0.16)	0.33 (0.16)	0.02 (0.15)	-0.11 (0.16)	0.09 (0.23)	-0.04 (0.14)	-0.19 (0.18)	-0.04 (0.16)	-0.27 (0.20)	-0.20 (0.17)	0.15 (0.14)
ABDOMEN	0.08 (0.21)	0.06 (0.21)	0.00 (0.20)	0.11 (0.20)	0.25 (0.25)	0.23 (0.17)	0.31 (0.20)	0.20 (0.20)	0.29 (0.23)	0.17 (0.21)	-0.06 (0.19)
BREAST	0.10 (0.29)	0.07 (0.30)	0.10 (0.28)	0.26 (0.25)	0.07 (0.37)	0.34 (0.23)	0.03 (0.31)	-0.01 (0.29)	-0.27 (0.35)	-0.06 (0.30)	-0.09 (0.26)
LIVER	-0.02 (0.22)	-0.03 (0.22)	0.07 (0.20)	0.09 (0.21)	0.37 (0.25)	0.20 (0.18)	0.23 (0.21)	0.05 (0.21)	0.17 (0.25)	0.21 (0.22)	-0.18 (0.19)
HEART	0.28 (0.17)	0.26 (0.17)	-0.09 (0.15)	0.08 (0.16)	0.42 (0.21)	0.00 (0.14)	0.05 (0.18)	-0.18 (0.17)	0.11 (0.21)	0.35 (0.18)	-0.31 (0.15)

[1] HCT = hematocrit value, RV = right ventricular weight, TV = total ventricular weight, RV:TV = ratio of right ventricular weight to total ventricular weight, %RV= right ventricular weight as percentage of BW, %TV = total ventricular weight as percentage of BW, MORT-TOT = Total mortality, ABDOMEN = Fluid in the abdomen, BREAST = Color of the breast, LIVER = Liver abnormalities, HEART = Fluid in the heart sac, BW_{C-48} = BW at 48 d in carcass experiment, CW = carcass weight, CP = carcass percentage, MC = meat color, LS = leg score, BW_{FE-23} = BW at 23 d in feed efficiency experiment, BW_{FE-48} = BW at 48 d in feed efficiency experiment, FI= =feed intake between 23 to 48 d, GAIN = growth between 23 to 48 d, FE = feed efficiency and RFI = residual feed intake

[2] The standard error in bracket, .

TABLE 4. Estimates of genetic correlation among ascites-related traits and performance traits measured under normal conditions

Trait [1]	Carcass experiment					Feed efficiency experiment					
	BW_{C-48}	CW	CP	MC	LS	BW_{FE-23}	BW_{FE-48}	FI	GAIN	FE	RFI
HCT_C [2]	0.47 (0.24) [3]	0.40 (0.25)	0.35 (0.22)	0.21 (0.28)	0.10 (0.34)	-0.25 (0.23)	0.12 (0.29)	-0.33 (0.26)	0.14 (0.31)	0.58 (0.20)	-0.57 (0.19)
RV_C	0.83 (0.14)	0.73 (0.18)	-0.07 (0.32)	0.72 (0.20)	0.18 (0.42)	0.25 (0.30)	0.63 (0.25)	0.32 (0.30)	0.61 (0.26)	0.50 (0.25)	-0.21 (0.29)
TV_C	0.69 (0.13)	0.67 (0.13)	0.04 (0.18)	0.27 (0.17)	0.24 (0.25)	0.46 (0.16)	0.83 (0.14)	0.46 (0.19)	0.78 (0.16)	0.29 (0.18)	-0.11 (0.17)
$RV:TV_C$	0.46 (0.29)	0.35 (0.30)	-0.14 (0.34)	0.73 (0.23)	0.08 (0.41)	-0.13 (0.30)	-0.01 (0.34)	-0.17 (0.33)	-0.04 (0.38)	0.38 (0.30)	-0.19 (0.30)
% RV_C	0.48 (0.38)	0.32 (0.39)	-0.75 (0.54)	0.50 (0.37)	0.96 (0.62)	-0.37 (0.38)	0.42 (0.41)	0.20 (0.44)	0.56 (0.37)	0.56 (0.34)	-0.16 (0.43)
% TV_C	-0.19 (0.26)	-0.05 (0.29)	0.22 (0.28)	-0.33 (0.28)	-0.18 (0.35)	-0.16 (0.26)	0.51 (0.28)	0.59 (0.25)	0.74 (0.23)	0.14 (0.29)	0.32 (0.25)

[1] HCT = hematocrit value, RV = right ventricular weight, TV = total ventricular weight, RV:TV = ratio of right ventricular weight to total ventricular weight, %RV= right ventricular weight as percentage of BW, %TV = total ventricular weight as percentage of BW, BW_{C-48} = BW at 48 d in carcass experiment, CW = carcass weight, CP = carcass percentage, MC = meat color, LS = leg score, BW_{FE-23} = BW at 23 d in feed efficiency experiment, BW_{FE-48} = BW at 48 d in feed efficiency experiment, FI= =feed intake between 23 to 48 d, GAIN = growth between 23 to 48 d, FE = feed efficiency and RFI = residual feed intake

[2] C means trait measured in carcass experiment.

[3] The standard error in bracket.

DISCUSSION

In poultry breeding, traits like growth rate and FE are of great interest as these traits have a large effect on the economic results. Therefore, breeding programs aim to select birds with a higher growth rate and/or a higher FE. However, it has been suggested that the improvement in growth rate or FE is not without undesirable correlated responses such as increased incidence of defects in heart and lung function and reduced adaptability to environmental conditions (McKay et al., 2000; Olkowski et al., 1999). This is in line with the resource allocation theory (Beilharz et al., 1993) which states that when a population is genetically driven towards higher production, and thus allocating a higher proportion of resources to these traits, less resources will be left to respond adequately to other demands, like coping with unexpected stressors. The results of the current study shows that- birds that grow fast under normal commercial circumstances (i.e. normal temperatures) are more susceptible to ascites syndrome. Further, weak but positive genetic relationships were found between feed efficiency and ascites related traits suggesting that more efficient birds tend to be slightly more susceptible towards ascites.

Growth Rate and Susceptibility to Ascites

Birds that grow fast under normal commercial circumstances, that is birds with a high genetic potential for BW_{C-48}, also tend to have larger hearts as is indicated by the genetic correlations with RV and TV. This holds true under both cold and normal temperature conditions. Based on the ascites experiment it can be conclude that these birds are also genetically more susceptible to develop the ascites syndrome as is indicated by the correlation with RV:TV. The ratio of RV:TV is an ascites heart index that quantifies the degree of hypertrophy of the heart in broilers (Huchzermeyer and De-Ruyck, 1986). Literature generally reports that RV:TV is higher for ascitic than non-ascitic broilers (e.g. Wideman and French, 2000). Further, fast growth in the carcass experiment, where the housing system (group housing) was similar to that in the ascites experiment, is positively correlated to MORT-TOT. Based on these results we can conclude that broilers with higher genetic potential for growth rate are more susceptible to ascites. However the estimated genetic correlations among body or carcass weights and ascites-related traits in the present study were moderate which indicates that there is scope for simultaneous improvement of growth rate and susceptibility to ascites.

The favorable genetic correlations between TV measured under cold or normal conditions and productivity traits like BW, CARCASS and GAIN are in agreement with the results previously obtained by Rance et al. (2002). Rance et al. (2002) reported that the genetic correlations between production traits and support organs in broilers were

generally low, however, heart mass was positively correlated with all carcass components; the genetic correlations ranged between 0.55 with breast mass to 0.64 with eviscerated body mass.

Feed Efficiency and Susceptibility to Ascites

The estimated genetic correlations between FE and ascites-related traits measured under cold-stress conditions were in general low. Correlations between FE and the important ascites-related traits RV:TV and ABDOMEN were positive but not very strong. Relationships between RFI and the ascites-related traits were negative but also not very strong. Based on the strong negative genetic correlation between FE and RFI these results were expected. Relations between feed efficiency and RV:TV measured under normal temperatures also indicate that more efficient birds are more susceptible towards ascites. Previous studies have reported that birds with a high feed efficiency have lower heat production and therefore they have less flexibility in metabolic adaptation to a changing environment, which can account for the development of ascites (Scheele et al., 1991, 1996). We found some evidence that supports this hypothesis, however, it should be pointed out that the evidence is not very strong given the high standard errors of the estimated correlations.

It should be realized that the genetic correlations among feed efficiency and ascites-related traits in the present study are not only the result of differences in environmental conditions (including system of housing and temperature effect) but also differences in age between the groups of birds should be considered. Leenstra and Cahaner, (1991) reported that age and temperature have significant effects on feed efficiency. Younger birds (0 to 4 wk) showed higher FE than older birds (4 to 6 wk). On the other hand the FE of birds was higher under normal temperatures than under low temperatures (Leenstra and Cahaner, 1991). In the current study FE is measured under conditions where birds were using feed mainly for growth. However, under cold-stress conditions birds were younger (5 wk of age vs. 7 wk of age) and they might have higher FE than birds under FE experiment. But they used feed also to sustain a normal body temperature and therefore they have lower value for FE than level which is expected.

Genotype by Environment Interaction

If the estimated genetic correlation between the same traits measured under different conditions is significantly less than unity, there is genotype by environmental interaction (Falconer, 1989). In the present study there was a relatively low genetic correlation between body weight measured under cold and normal conditions (around 0.50) which indicates that BW is very sensitive to the applied temperature schedule. Also the difference in age between the groups of birds could have contributed to the lower correlation. However, the genetic correlations among body weights of broilers at

various ages are in general high (Chambers et al., 1984, Wang et al., 1991): in the present study the genetic correlation between BW_{FE-23} and BW_{FE-48} was 0.87. Therefore, it can be conclude that the relatively low genetic correlation between BW measured in the carcass or in the feed efficiency experiments and BW measured in the ascites experiment is mainly due to the temperature effect. The low estimated genetic correlation between BW measured under cold and normal conditions is in agreement with the results obtained in a previous study (Pakdel et al., 2004). In a previous study we reported a genetic correlation between BW_{AS_35} and BW_{C_48} using 770 birds of 0.29, whereas in the current study this correlation was 0.49 and was estimated based on 1999 observations (Pakdel et al., 2004).

Effect of Housing

Different correlations were observed between some of the ascites related traits measured in the ascites experiment and body weight in the carcass experiment (BW_{C-48}) or body weight in the feed efficiency experiment (BW_{FE-48}). Birds with a higher genetic potential for BW_{C-48} showed a higher MORT-TOT and higher HCT values under cold-stress conditions. However, the genetic correlations among BW_{FE-48} and MORT-TOT or HCT were negative. Further, under normal conditions, the genetic correlation among BW_{C-48} and HCT or RV:TV were higher than those obtained for BW_{FE-48}. The other point that suggests correlations are affected by the system of housing is the relationship among BW, ABODOMEN, HEART. The genetic correlation between BW_{C-48} and ABDOMEN was 0.08, and with HEART 0.28. However, the genetic correlation between BW_{FE-48} and ABDOMEN was 0.31 and with HEART 0.05.

Although standard errors of these estimates are relatively high, the difference between the genetic correlations among BW_{C-48} or BW_{FE-48} and ascites-related traits indicate that correlations are affected by a higher incidence of ascites syndrome which might be due to the difference in the housing system: individual versus group housing. It is probable that birds under group housing are more susceptible to the ascites than birds under individual housing: under individual housing birds have less movement and no competition for food as might be the case in the carcass or ascites experiment which influence on the metabolic rate of the chickens and finally on the ascites incidence. Moreover, under group housing (ascites or carcass experiment) stocking density is very high towards the end of the rearing period. The concentration of air pollution and respiratory irritants (ammonia, carbon dioxide, and carbon monoxide) is higher under group housing as well (Madelin and Wathes, 1989). The contamination in the air of broiler houses may increase the incidence of ascites syndrome in susceptible broilers by posing a higher respiratory challenge to the lungs (Wang et al., 2002).

Conclusions

From the relationship found it can be concluded that selecting for BW increases the susceptibility for ascites. However, the weak genetic correlation among BW and ascites-related traits indicate that there is considerable scope for simultaneous selection for birds with high BW and low susceptibility to ascites. Further, the estimated genetic correlations in the present study do not support that selecting for FE will result in an increase of the ascites problem. However, the results showed a considerable genotype by temperature interaction for BW, which suggest that the adaptability of birds is not very high under suboptimal conditions.

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Chapter 5

Confirmation of Quantitative Trait Loci Affecting Susceptibility of Broilers to Ascites

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ABSTRACT Pulmonary hypertension syndrome (PHS) followed by ascites is a major cause of economical losses to the broiler industry. The modern chicken small lung volume and body weight ratio is responsible for the inability of the respiratory system to respond to the broiler's elevated oxygen needs, which leads to ascites syndrome. Quantitative trait locus (QTL) mapping opens a way for breeders to manipulate quantitative trait genes. In a previous study, a three generation population was created for mapping of loci that are involved in the susceptibility of birds to ascites. The results revealed quantitative trait loci (QTL) with suggestive associations on chromosomes 8 and 10 for some of the ascites-related traits. The objective of this study is to confirm the QTL reported previously in subsequent generations. A two generation population including 19 full sib families has been created. In total 14 microsatellite markers were analyzed on all individuals. Twelve ascites-related traits were measured. Two QTLs exceeded the significance thresholds for the traits body weight at 2 and 5 weeks of age (BW2, BW5), right ventricular weight (RV), the ratio of right to total ventricular weight (RV:TV), and total mortality (MORT-TOT). The most significant QTL were located on chromosome 8 for traits BW5 at 24 cM, RV at 19 cM and RV:TV at 15 cM and on chromosome 10 for traits BW2 at 34 cM and MORT-TOT at 59 cM.
(*Key word:* broiler, ascites, QTL mapping, cold stress)

INTRODUCTION

Fast growth, high altitudes and cool temperatures are the primary triggers for ascites syndrome in commercial broilers (Julian, 2000). This syndrome results in significant economic losses to the broiler industry due to high mortality around the world and has a negative impact on animal welfare. A number of studies suggested several traits that can be used as indicator traits for ascites. The large number of organs (heart, lung, liver, etc.) which are involved in the disease makes ascites syndrome complicated. The physiology of this syndrome has been studied extensively (Julian, 2000; Wideman and French, 2000). In addition several studies showed that traits related to ascites syndrome have a relatively high heritability (Pakdel et al., 2002; De Greef et al., 2001; Maxwell and Robertson, 1997; Lubritz et al., 1995). This indicates that genetic factors play a considerable role in susceptibility of birds to ascites and offers perspectives for selection against this syndrome. Pakdel et al. (2004b) estimated a weak but positive genetic correlation among ascites-related traits measured under cold conditions and BW measured under normal conditions and concluded that there is scope for simultaneous selection for birds with BW and susceptibility to ascites. In commercial broiler breeding, genetic improvements for traits like BW can easily be achieved through traditional selection that is based on phenotypic information. However, most of the ascites-related traits are difficult to measure in commercial breeding (e.g. the traits can not be measured on the live birds) and therefore the breeder must rely entirely on information from relatives. It is expected that the availability of molecular information is especially useful in selection for these type of traits (Van der Beek, 1995). Using DNA marker techniques, QTL controlling ascites susceptibility can be identified and used in marker assisted selection. Moreover QTL knowledge for such traits may contribute to a better understanding of the physiological and biological background of ascites. In a previous study (Rabie et al., 2004), a three generation population was created for mapping of loci that are involved in the susceptibility of birds to ascites. The results revealed quantitative trait loci (QTLs) with suggestive association for some of the ascites-related traits on chromosomes 8 and 10. Confirmation of these QTLs is an essential step before an attempt is made towards the fine mapping of the QTL and identification of genes underlying the ascites-related traits. The objective of this study is to confirm the QTL reported previously for ascites-related traits in subsequent generations.

MATERIAL AND METHODS

Experimental Population

For this QTL detection study, a two generation full sib design with 19 families was created. The experimental population used in this study originates from the population that was used by Rabie et al. (2004). In the previous study (Rabie et al., 2004), a three-generation full sib half sib design was created for mapping of loci that are involved in the susceptibility of birds to ascites. G_2 animals of this design were used to produce subsequent generations by random intercrossing in each generation. In the present study, the parents are generation 6 (G_6) or generation 7 (G_7) birds and the full sib offspring are generation 7 or generation 8 (G_8) birds. In total 1,552 individuals were included in the study of which including 5 G_6/G_7 full sib families and 14 G_7/G_8 full sib families. The average number of offspring per family was 82 with a minimum of 61 and a maximum of 103 offspring per full-sib family. The birds in G_6, G_7 and G_8 were typed for genetic markers. Phenotypic observations were collected during in total 33 weeks. In order to identify individuals that were susceptible to ascites, a cold stress temperature schedule was applied. At the time of hatching, the temperature was 30 ^oC and then was gradually decreased to 10 ^oC by 22 d of age. The temperature remained at 10 ^oC until the end of the experiment. Except for the adjusted temperature schedule, birds were kept under circumstances that closely resemble commercial practice, i.e. a standard commercial broiler feed containing 12,970 kJ/kg, artificially lighted housing for 23 h /d, and group housing with 20 birds/m^2.

Traits measured were body weight at 2 and 5 wk of age (BW2 and BW5), right ventricular weight (RV), total ventricular weight (TV) , the ratio of RV to TV (RV:TV), total mortality (MORT-TOT), blood pH (pH), partial pressure of carbon dioxide (PCO_2), partial pressure of oxygen (PO_2), blood bicarbonate concentration (HCO_3), total carbon dioxide content (TCO_2) and oxygen saturation in arterial blood (sO_2). For more information about the blood gas traits see Appendix.

QTL Regions

In the previous QTL analysis, QTL for ascites-related traits were found on different chromosomes of chickens (Rabie et al., 2004). From the results of that analysis chromosomes 8 and 10 were chosen for further analysis in the G_7 and G_8 populations. These two chromosomes were selected because they showed suggestive evidence of QTL effects for BW5, TV, and MORT-TOT.

Genetic Markers

Genotypes for micro satellite markers were determined using DNA derived from blood samples from 10 G_6, 457 G_7 and 1085 G_8 animals. In total 14 informative

markers were mapped to chromosomes 8 and 10. The Haldane mapping function (Haldane, 1919) was used in the current study. Table 1 shows the name, the number of alleles and the relative location of 14 markers on the two linkage groups used in the present study.

TABLE 1. Linkage map of the chromosomes 8 and 10 including marker names, marker positions in centimorgan and number of alleles.

Chromosome	Markers	Position in the current study	Number of alleles
Chromosome 8	ADL301	0	2
	MCW271	13	6
	ROS075	14	4
	ADL278	14	5
	MCW351	24	5
Chromosome 10	MCW194	0	4
	ADL038	7	6
	MCW067	11	3
	MCW035	34	3
	ADL102	40	4
	MCW366	40	7
	ADL158	53	4
	LEI112	59	3
	LEI103	61	4

Analysis of Phenotypic Data

For the analysis of the phenotypic data a two step procedure was applied: first average adjusted progeny trait values were calculated by adjusting phenotypic observations for systematic environmental effects, and secondly a QTL analysis was undertaken using adjusted trait values as dependent variables. Data were adjusted for the fixed effects sex and week of hatching. There was an additional fixed effect "date of measurement" for blood gas traits. This fixed effect is related to the fact that measuring blood gas traits could not be done for all the birds on one day. Adjusted traits values were calculated using MTDFREML software (Boldman et al., 1995).

Full sib QTL Analysis

Full sib QTL analysis was undertaken using the regression interval mapping methodology as described by Van Kaam et al. (1998) in which a single QTL was fitted within each family. This method is an extension of the multi-marker regression method of (Knott et al., 1996) for outbred populations with a half sib family structure. Adjusted

trait values of G_7 and G_8 were regressed on the probabilities of inheriting the first allele of each parent. The across family full-sib model to fit a QTL at position *k* was:

$$Y_{ij} = family_i + b_{s,i}X_{s,ij} + b_{d,i}X_{d,ij} + e_{ij}$$

where:

Y_{ij} = Adjusted trait value for the j^{th} offspring of the i^{th} family

$family_i$ = Family mean

$b_{s,i}$ = Regression coefficient for the sire (*s*) in family *i*

$X_{s,ij}$ = Probability that the j^{th} offspring from sire *s* in family *i* received allele 1

$b_{d,i}$ = Regression coefficient for the dam (*d*) in family *i*

$X_{d,ij}$ = Probability that the j^{th} offspring from dam *d* in family *i* received allele 1.

e_{ij} = Random residual.

The family mean is used to account for polygenic differences between families. In order to test for the alternative hypothesis of the presence of QTL effects, versus the null hypothesis of the absence of QTL effect a test statistics was calculated at each centimorgan. The test statistic is the ratio of the explained mean square of the QTL effect under study in the numerator and the residual mean square of the full model in the denominator. The test statistic at position *k* was calculated as:

$$Test\ statistic_k\ (H_1{:}H_0) = \frac{\left(\frac{RSS_k(H_0) - RSS_k(H_1)}{df_{QTL}}\right)}{\left(\frac{RSS_k(H_1)}{df_{total} - df_{family} - df_{QTL}}\right)}$$

$RSS_k(H_0)$ is the residual sums of squares of the reduced model, i.e. without fitting a QTL:

$$RSS_k(H_0) = \sum_{j=1}^{n}(Y_{ijk} - family_i)^2$$

and $RSS_k(H1)$ is the residual sums of squares after fitting a QTL at position k:

$$RSS_k(H_1) = \sum_{j-1}^{n}(Y_{ijk} - family_i - b_{s,ik}X_{s,ijk} - b_{d,ik}X_{d,ijk})^2$$

and df are the number of F_7 and F_8 genotyped animals (df_{total}), number of family means (df_{family}) fitted and number of QTL effects (df_{QTL}) fitted in each family. In case significant evidence for the presence of a QTL was found, the analyses also were performed for each family individually with the purpose to test for the presence of QTL effects within each family.

Significance Thresholds

The significance thresholds for the test statistics were calculated empirically using the permutation method outlined by Churchill and Doerge (1994). The genomewise

threshold values were derived for each trait by permutating two linkage groups simultaneously. Significance tests for the presence of a QTL were performed at 5 cM interval. This was repeated 1000 times in order to construct the distribution of the test statistic under the null hypothesis.

Permutation was also applied to determine which parents were segregating for a QTL on those locations where a QTL was detected in the across family analysis. Per parent, a test comparing a model with a QTL versus a model without a QTL was applied. Parents with a test statistic above the 10% chromosomewise threshold were considered to be segregating for the QTL. The 10% chromosomewise thresholds were calculated per parent by performing 1000 permutations at 5-cM intervals.

RESULTS

Twelve traits related to ascites have been analyzed in the current study. The statistical descriptions of the traits measured under cold stress conditions are presented in Table 2. The average weight of broilers at 5 wk of age was 1,119 g, the ratio of RV:TV which is an ascites heart index was 24 % and total mortality in the current experiment was 8%.

TABLE 2. Statistical description of the traits

Trait	Abbreviation	Number	Mean	Std Dev
BW at 2 wk of age (g)	BW2	1507	370	111
BW at 5 wk of age (g)	BW5	1382	1119	211
Right ventricular weight (g)	RV	1355	1.22	0.34
Total ventricular weight (g)	TV	1355	5.04	0.91
Ratio of right ventricular weight to total ventricular weight (%)	RV:TV	1355	24.05	4.83
Blood pH	pH	1260	7.38	0.05
Partial pressure of carbon dioxide	PCO_2	1261	45.48	6.41
Partial pressure of oxygen	PO_2	1261	52.42	10.44
Blood bicarbonate concentration	HCO_3	1261	27.10	3.11
Total carbon dioxide content	TCO_2	1260	28.50	3.24
Oxygen saturation in arterial blood	sO_2	1259	84.18	6.47
Total mortality	MORT-TOT	1507	0.08	0.28

Information Content

The information content shows the ratio between the actual variance found in the data and the expected variance under full information (Spelman et al., 1996). The

regions covered in the current study were 24.7 cM for chromosome 8 and 61.4 cM for chromosome 10. The average information content over 2 linkage groups was 0.77 for both males and females. There was a slight difference in the average information content between males and females for each linkage group. Figure 1 shows the sex averaged information content for the 2 linkage groups.

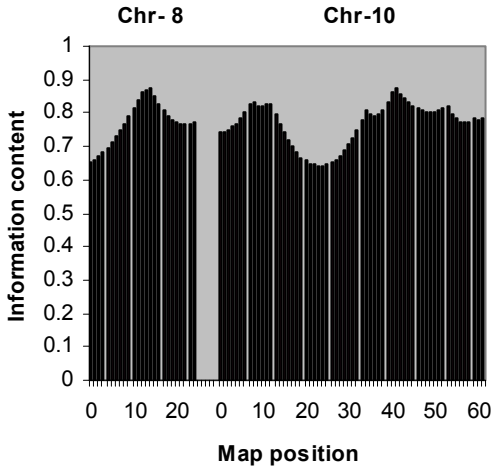

FIGURE 1. Information content for chromosomes 8 (Chr-8) and chromosomes 10 (Chr-10)

Full sib QTL analysis

Table 3 gives the test statistic for the presence of a QTL for each trait at the most likely location. A Quantitative trait locus for RV:TV was located at 15 cM on chromosome 8 as shown in Figure 2 and exceeded the threshold for significant linkage. Furthermore, in the same region QTL affecting the traits RV and BW5 was found and exceeded the threshold for significance linkage (Figure 2). The test statistic for the trait RV peaked at 19 cM and for the trait BW5 at 24 cM. To study the number of families contributing to these QTL, allelic effects were calculated for all families. Results suggest the segregation of the QTL in seven parents (of the 38) for trait RV:TV, in eight parents for trait RV and in eight parents for trait BW5. The absolute average allele substitution effect (α) over these parents was 2.63% for RV:TV, 0.16 g for RV and 98.6 g for BW5.

On chromosome 10, QTL for the traits BW2 and MORT-TOT were found (Table 3). This QTL exceeded the threshold for significant linkage, reaching a 5% significance level for trait BW2 and 7% for MORT-TOT. The peak of the test statistic was located at 34 cM for BW2 and at 59 cM for MORT-TOT. Furthermore, another high test statistic value was found for MORT-TOT on chromosome 10 at 40 cM (Figure 3). Suggestive QTL were detected for the traits TV and PCO2. The test statistic for TV peaked at 23 cM and for PCO2 at 6 cM. Eleven parents showed significant QTL effects for BW2 and eleven parents for MORT-TOT. The absolute average allele substitution effect (α) over these parents for BW2 was 34.5 g and for MORT-TOT was 0.13%.

TABLE 3. Summary of interesting regions per trait. The linkage group, the most likely location in centimorgan, the test statistic and the genomewise significance level of the QTL at this position are indicated per trait.

Trait [1]	Chromosome	Location	Marker bracket	Test statistic	Significance [2]
BW5	8	24 cM	ADL278 - MCW351	1.66	**
RV	8	19 cM	ADL278 - MCW351	1.63	**
RV:TV	8	15 cM	ROS075 - ADL278	1.84	***
PO_2	8	12 cM	ADL301 - MCW271	1.55	ns
sO_2	8	12 cM	ADL301 - MCW271	1.29	ns
BW2	10	34 cM	MCW035 – ADL102	1.72	***
TV	10	23 cM	MCW067 - MCW035	1.52	*
MORT-TOT	10	59 cM	ADL158 - LEI112	1.69	**
PCO_2	10	6 cM	MCW194 - ADL038	1.6	*
HCO_3	10	34 cM	MCW035 – ADL102	1.28	ns
TCO_2	10	35 cM	MCW035 – ADL102	1.29	ns
PH	10	35 cM	MCW035 – ADL102	1.49	ns

[1] BW5 = BW at 5 wk of age; RV = right ventricular weight; RV:TV = ratio of right ventricular weight to total ventricular weight; PO_2 = partial pressure of oxygen; sO_2 = Oxygen saturation in arterial blood; BW2 = BW at 2 wk of age; TV = total ventricular weight; MORT-TOT = Total mortality; PCO_2 = Partial pressure of carbon dioxide; HCO_3 = Blood bicarbonate concentration; TCO_2 = Total carbon dioxide content; PH = Blood pH

[2] Accounting for the multiple testing over the 3 chromosomes regions: *** = P<0.05, ** = P<0.10, * = P<0.20 and ns = non significant.

DISCUSSION

This article aims at confirming QTLs controlling ascites resistance in broilers. A full sib regression interval mapping approach was applied, because it includes the segregation of alleles from both parents. This research has resulted in the identification and confirmation of several regions on two different chromosomes that may involved in susceptibility of chicken to develop ascites. Twelve ascites-related traits and more than 1500 individuals where analyzed in the current study. Compared to the previous work (Rabie et al., 2004), both experiments were conducted under cold stress conditions which can stimulate metabolic rates and increase oxygen requirements, adversely affecting the incidence of ascites (Lubritz et al.,1995). Some of the ascites-related traits like BW, RV, TV, RV:TV and MORT-TOT were common in both experiments. However, in the previous study some score traits related to ascites syndrome (e.g. fluid accumulation in the abdominal cavity, heart and liver abnormality and etc.) were

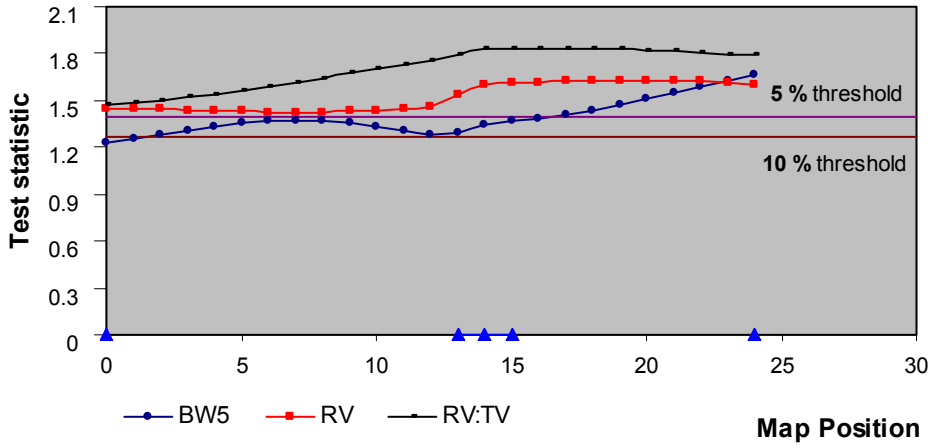

FIGURE 2. Test statistic values from the analysis of traits BW5, RV and RV:TV for quantitative trait loci on chromosome 8. 5 and 10 % thresholds for trait RV:TV are included. Map positions are given using Haldane scale. The triangulars indicate the position of markers on chromosome.

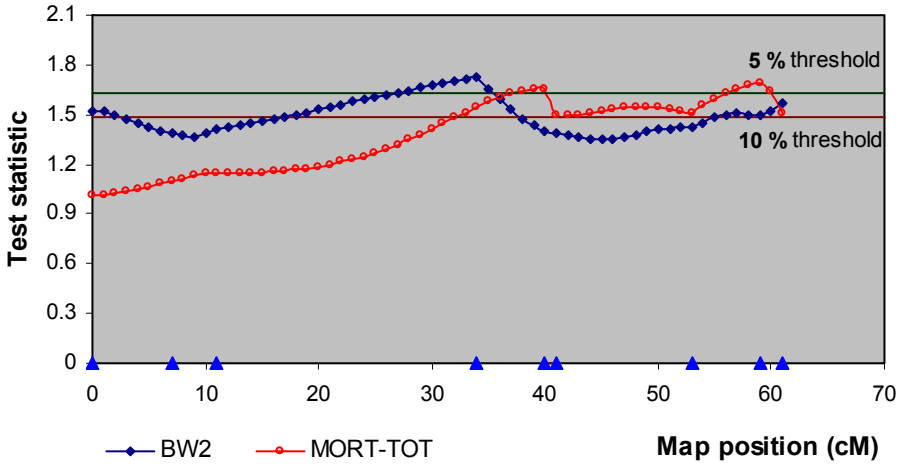

FIGURE 3. Test statistic values from the analysis of traits BW2 and MORT-TOT for quantitative trait loci on chromosome 10. 5 and 10 % thresholds for trait BW2 are included. Map positions are given using Haldane scale. The triangulars indicate the position of markers on chromosome.

measured, whereas these traits were not measured in the current study and blood gas traits were investigated in its place.

The most significant results in the present study were found on chromosome 8 for the traits BW at five weeks of age and RV:TV and on chromosome 10 for the traits BW at two weeks of age and total mortality. These QTLs explain 5.7% and 5% of the total phenotypic variance for the traits BW5 and RV:TV respectively, and 6.8% and 5.7% of the total phenotypic variance for the traits BW2 and MORT-TOT respectively.

Weight ratio of the right ventricle wall relative to both ventricles and septum (RV:TV) that quantifies the degree of hypertrophy of the heart, is a good indicator for ascites syndrome (Huchzermeyer and de Ruyck, 1986; Pakdel et al., 2004a). It is generally agreed that birds susceptible to the ascites syndrome are expected to have higher RV:TV than resistant birds. The QTL results of current study show that there are QTLs on chromosome 8 associated with traits BW5, RV and RV:TV. These results suggest that there are genes in this region which regulate growth rate at 5 wk of age, the weight of right ventricular of the heart and ratio of RV:TV and therefore susceptibility of birds to ascites syndrome.

Among the factors causing ascites syndrome, inadequate oxygen supply relative to metabolic demand of tissues is a main factor. Low oxygen accessibility (high altitude) or high oxygen consumption (high performance or low ambient temperature) can increase the incidence of ascites (Julian, 1993. and Odum, 1993). The traits that indicate such oxygen deficiency in susceptible birds are partial pressure of oxygen (PO2) and/or oxygen saturation in arterial blood (sO_2). The results of current study showed suggestive linkage on chromosome 8 for PO_2 and sO_2. Because these two traits are genetically highly correlated (0.78, data not shown) and the most likely location of the QTL were the same in the current study, it seems reasonable to assume that the same QTL affected these traits.

In the present study two significant loci were detected for the growth traits (BW2 and BW5). The two QTL affecting growth rate in chickens were identified on chromosome 8 and 10. The QTL detected for BW at 2 wk (BW2) on chromosome 10 did not significantly affect weight at 5 wk of age. This result suggest that the gene or genes involved in early growth and are responsible for skeletal growth and digestive organs are different with that affect the later growth of muscle tissue. Cheverud et al. (1996) indicated that QTLs affecting early and late growth in mice were generally distinct, which was explained by different physiological mechanisms at different life stages. The QTL reported in this paper for later growth trait (BW5) on chromosome 8 is in agreement with that of Sewalem et al. (2002). Sewalem et al. (2002) reported a QTL for BW at 6 wk of age on chromosome 8. The flanking markers in reported study were ADL179 and ROS075.

The present research has resulted in the identification and confirmation of five regions on two chromosomes which contain genes that are involved in susceptibility of chicken to develop ascites. To identify the genes involved in the ascites syndrome, additional microsatellite markers need to be mapped in these regions. Once the susceptible alleles or closely linked markers are identified, marker-assisted selection can be applied to select birds against ascites syndrome.

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APPENDIX

PO_2, PCO_2 and Calculated Values for HCO_3, TCO_2, sO_2:

PCO_2 is measured by direct potentiometry. In the calculation of results for PCO_2, concentration is related to potential through the Nernst equation. When a cartridge includes sensors for both pH and PCO_2, bicarbonate (HCO_3), total carbon dioxide (TCO_2) are calculated.

Log HCO_3 = pH + log PCO_2 – 7.608

$TCO_2 = HCO_3 + 0.03\ PCO_2$

PO2 is measured ampermetrically. sO_2 (oxygen saturation) is the amount of oxyhemoglobin expressed as a fraction of the total amount of hemoglobin able to bind oxygen (oxyhemoglobin plus deoxyhemoglobin).

$$sO_2 = 100\frac{X^3 + 150X}{X^3 + 150X + 23400}$$

where $X = PO_2 \times 10^{(0.48(pH-7.4)-0.0013(HCO3-25))}$

Chapter 6

Selection Strategies for Body Weight and Reduced Ascites Susceptibility in Broilers

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ABSTRACT Ascites syndrome is a metabolic disorder in broilers. Mortality due to ascites especially in later ages results in significant economic losses and has a negative impact on animal welfare. The aim of the present study was to evaluate the consequences of alternative selection strategies for BW and resistance to ascites syndrome using deterministic simulation. Besides the consequences of current selection, i.e. selection for BW, alternative selection strategies including information on different ascites-related traits measured under normal and/or cold conditions were quantified. Five different schemes were compared based on the selection response for BW, ascites susceptibility and the rate of inbreeding. Traits investigated in the index as indicator traits for ascites were hematocrit value (HCT) and ratio of right ventricle to the total ventricular weight of the heart (RV:TV). The results of base and alternative selection strategies indicated that by ignoring ascites susceptibility in the breeding goal, although achieved gain for BW is relatively high (130 gr), the genetic response for ascites susceptibility is 0.025 unit and rate of inbreeding is 3% per generation. Including information of ascites related traits (HCT and RV:TV) measured under normal and cold conditions makes it possible to achieve relatively high gain for BW (111.4 gr) with constant level of ascites susceptibility (zero) at lower rate of inbreeding (2.4% per generation).

(*Key word:* broiler, ascites, body weight, breeding program, deterministic simulation)

INTRODUCTION

Ascites syndrome is a metabolic disorder of fast-growing meat-type chickens. It has been suggested that this syndrome is the consequence of allomorphic differences in heart and lung growth relative to the size of the animal (Siegel and Dunnington, 1997). Ascites results in significant economic losses to the broiler industry due to high mortality especially at later ages and has a negative impact on animal welfare. The incidence of ascites is influenced by both environmental and genetic factors. The most important environmental factors causing the development of ascites in broilers are high altitudes and cold temperatures (Smith et al., 1954; Siller and Hemsley, 1966; Bendheim et al., 1992; Shlosberg et al., 1992). Several studies have shown that traits related to ascites syndrome have a relatively high heritability (Lubritz et al., 1995; Maxwell and Robertson, 1997; De Greef et al., 2001; Pakdel et al., 2002). This indicates that genetic factors play a considerable role in susceptibility of birds to ascites and this offers perspectives for selection against this syndrome.

In practice selection will be for a combination of production traits like BW and ascites susceptibility. A few studies have reported genetic correlations between BW and ascites-related traits (Moghadam et al., 2001; De Greef at al., 2001; and Pakdel et al., 2004a). Under normal climatic conditions, Moghadam et al. (2001) found a positive genetic correlation between ascites and BW. Under cold conditions, however, De Greef et al. (2001) and Pakdel et al. (2004a) reported a negative genetic correlation between traits related to ascites and BW. In addition Pakdel et al. (2004b) estimated a weak but positive genetic correlation among ascites-related traits measured under cold conditions and BW measured under normal conditions. These results indicate that there is considerable scope for simultaneous selection of birds for increased BW while controlling susceptibility to ascites. However, it is not obvious which selection strategy is optimal to achieve this goal.

Designing effective selection strategies for ascites resistance not only has to deal with the identification of good indicator traits, but also concerns the choice of the selection environment. Indicator traits like hematocrit value (HCT) or ratio of right ventricle to the total ventricular weight of the heart (RV:TV) differ not only with respect to their correlations to ascites susceptibility but also differ in a sense that HCT can be measured on the live bird whereas RV:TV can not. Further, measuring birds under cold-stressed conditions is expected to reveal to a larger extend the genetic differences that exist in ascites susceptibility between birds as compared to the testing birds under normal temperature conditions.

The aim of the present study was to evaluate the consequences of alternative selection strategies for BW and resistance to ascites syndrome using deterministic

simulation. Besides the consequences of current selection, i.e. selection for BW, alternative selection strategies including information on different ascites-related traits measured under normal and/or cold conditions will be qualified. Schemes will be compared based on the selection response for BW and ascites susceptibility and the rate of inbreeding.

MATERIAL AND METHODS

Population Structure

A population with discrete generations was simulated, in which 50 males are randomly mated to 350 females with a mating ratio of one male to 7 females. Each female produces 32 progeny, 16 males and 16 females and each male has 112 progeny of each sex. The total number of progeny of each sex is 350 × 16 = 5600. Among the progeny, the best males and females are selected as parents of the next generation. In the starting situation 50 male parents out of 5600 available males are selected (selected proportion≈ 0.009) and 350 females are selected out of the available 5600 (selected proportion ≈ 0.063). Base generation individuals were assumed to originate from a large population in Hardy-Weinberg and genetic phase equilibrium.

Breeding Goal and Index

The breeding goal was a combination of two traits: body weight (BW) and ascites susceptibility (AS),

$$H = V_{BW} * A_{BW} + V_{AS} * A_{AS}$$

Where H is a weighted sum of the true breeding values, V_{BW} is the economic value of BW and A_{BW} is the true breeding value for BW, V_{AS} is the economic value of AS and A_{AS} is the true breeding value for Ascites Susceptibility. In practice an index I is used to predict value for the breeding goal H of each selection candidate. The index I is the estimated breeding value (EBV) of the breeding goal:,

$$I = V_{BW} * EBV_{BW} + V_{AS} * EBV_{AS}$$

The breeding goal applies to normal husbandry conditions.

The most apparent sign of ascites is the accumulation of fluid in the abdominal cavity of the bird. Fluid accumulation in the abdominal cavity appears in the latest stages of ascites that is before death occurs. Two different breeding goals were used: 1) base situation where selection is only for BW and with no emphasis on ascites susceptibility (V_{AS} = 0) and 2) the economic value of ascites susceptibility in the breeding goal (V_{AS}) is changed in order to obtain a zero response in AS. The base situation reflects selection for BW based on the breeding values estimated from an

animal model BLUP procedure. In this situation information on BW measured under normal temperature conditions is available on all the birds. Alternative selection strategies considered differ with respect to the type of ascites indicator and the environmental conditions they were measured in: indicator traits that can be measured on the live bird like hematocrit value (HCT) and indicator traits for which the bird has to be slaughtered like ratio of right ventricle to the total ventricular weight of the heart (RV:TV). It is assumed that the birds on which RV:TV was recorded, were not available as selection candidates. Four different scenarios were considered:

A-1) Measurement of BW and HCT on all the birds and under normal conditions [100% (BW_N + HCT_N)].

A-2) Measurement of BW and HCT on all the birds and the measurement of RV:TV on 50% of the birds. All birds are kept under normal conditions and birds on which RV:TV was measured were not available for selection [100% (BW_N + HCT_N) + 50% ($RV:TV_N$)].

A-3) 50% of the birds are tested under cold-stress conditions. In this scenario the traits BW and HCT were measured under normal and cold conditions, whereas the trait RV:TV was measured only under cold conditions. Birds on which RV:TV was measured were not available for selection [50% (BW_N + HCT_N) + 50% (BW_C + HCT_C + $RV:TV_C$)].

A-4) All the birds were tested under cold-stress conditions. In this scenario the traits BW and HCT were measured on all the birds. 50% of the birds were sacrificed to measure the trait RV:TV [100% (BW_C + HCT_C) + 50% ($RV:TV_C$)].

TABLE 1. The selected proportion per sex and the number of half-sib and full-sib birds on which phenotypic information was available under different selection strategies

Scheme	Selected proportion Per sex	Normal conditions (N)						Cold conditions (C)					
		BW_N		HCT_N[1]		$RV:TV_N$		BW_C		HCT_C		$RV:TV_C$	
		FS[2]	HS	FS	HS	FS	HS	FS	HS	FS	HS	FS	HS
Base	5600	31	192	-	-	-	-	-	-	-	-	-	-
A-1	5600	31	192	31	192	-	-	-	-	-	-	-	-
A-2	2800	31	192	31	192	16	96	-	-	-	-	-	-
A-3	2800	15	96	15	96	-	-	16	96	16	96	16	96
A-4	2800	-	-	-	-	-	-	31	192	31	192	16	96

[1] HCT = hematocrit value; RV:TV = ratio of right ventricular weight to total ventricular weight where subscript C indicates that the trait was measured under cold conditions and subscript N indicates that the trait was measured under normal temperature conditions.

[2] FS = number of full-sib birds; HS = number of half-sib birds.

Table 1 summarises the traits recorded, and the number of half-sibs and full-sibs in the different breeding schemes. For BW and HCT, besides the average phenotypic

performance of the full sibs and the half sibs, the birds own performance was available. RV:TV was not available for the selection candidate.

The Genetic Parameters

The genetic parameters used in the simulation were based on an actual experiment, including 4200 birds kept under cold conditions and 790 birds kept under normal conditions (Pakdel et, 2002 and 2004a). The genetic parameters for BW under normal conditions (BW_N) were based on 1999 observation (Pakdel et al, 2004b). Results of Pakdel et al. (2002) indicated that there is a significant maternal genetic effect for traits BW and RV:TV. In the current study, the estimated heritabilities of these traits were based on a model including maternal genetic effects, i.e. direct heritabilities were used. Maternal genetic effects were not accounted for when predicting selection response. The genetic parameters for ascites susceptibility were based on those for the trait fluid accumulation in the abdominal cavity that were scored as 0, 1 or 2. The variation for susceptibility to ascites is only partly expressed under normal conditions. Under cold conditions, however, more accurate estimates for ascites susceptibility can be obtained. Therefore, parameters for ascites susceptibility were based on fluid accumulation in the abdomen under cold conditions.

TABLE 2. The genetic parameters used in the simulation study

Traits [1]	σ^2_p [2]	The genetic parameters [3]						
		BW_N	AS	HCT_N [3]	$RV:TV_N$	BW_C [4]	HCT_C	$RV:TV_C$
BW_N	60000	**0.20**	0.18	0.55	0.46	0.46	0.27	0.37
AS	0.14	-	**0.10**	0.46	0.55	-0.01	0.64	0.73
HCT_N	5	-0.10	-	**0.20**	0.64	0.14	0.82	0.46
$RV:TV_N$	20	0.11	-	0.10	**0.10**	-0.06	0.73	0.82
BW_C	60000	-	-0.30	-	-	**0.20**	-0.21	-0.25
HCT_C	15	-	0.30	-	-	-0.40	**0.40**	0.55
$RV:TV_C$	60	-	0.50	-	-	-0.30	0.50	**0.25**

[1] AS = ascites susceptibility trait; HCT = hematocrit value; RV:TV = ratio of right ventricular weight to total ventricular weight where subscript C indicates that the trait was measured under cold conditions and subscript N indicates that the trait was measured under normal temperature conditions.

[2] σ^2_p = Phenotypic variance

[3] The genetic correlation above, phenotypic correlation below and heritabilities are on the diagonal.

Analytical Comparison of Breeding Strategies

Prediction of the rate of genetic change and the rate of inbreeding were performed by deterministic simulation of single-stage selection schemes with discrete generation, using the program SelAction (Rutten et al., 2002). This program predicts the rate of genetic gain using multi-trait pseudo-BLUP (Villanueva et al, 1993). The program accounts for reduction in variance due to selection (Bulmer, 1971), and corrects selection intensities for finite population size and for the correlation between index values of family members (Meuwissen, 1991). The program is an accurate approximation of stochastic simulation with selection on animal model BLUP, because full pedigree information is accounted for (Wray and Hill, 1989). Pedigree information consists of the estimated breeding values (EBV) of the sire and dam and the mean EBV of the dams of each half-sib group. The mating structure is assumed to be hierarchical and random and selection response is predicted for the Bulmer equilibrium situation (Rutten et al., 2002). Prediction of the rate of inbreeding was based on the long-term genetic contribution theory (Wray and Thompson, 1990).

The genetic correlation matrix was tested for being singular. The results indicated that the correlation matrix was singular. A bending routine was used to make the genetic correlation matrix non-singular. This resulted in small changes as compared to the original parameters estimated by Pakdel (2002, 2004a, 2004b)(Table 2).

RESULTS

Base Situation

Table 3 gives the response for body weight (BW), ascites susceptibility (AS) and the rate of inbreeding for the base and alternative scenarios. In the base situation where AS is ignored in the breeding goal and selection is for BW only resulted in a selection response of 130 gr. In this situation the correlated selection response for AS was +0.025 units. AS is a score trait that is categorized as 0, 1 or 2. The mean of this score trait was 0.08 with phenotypic standard deviation of 0.38 (Pakdel et al., 2002). The value of 0.025 is therefore equal to 0.2 additive genetic standard deviation. The distribution of this underlying continuous variable can be assumed normal. The percentage of birds under cold conditions with score 1 or 2 in the base situation was equal to 4.2%. A selection response of 0.025 corresponds to an increase of the number of birds with score 1 or 2 to 4.8% under cold conditions. Therefore under this scenario the fraction of ascites susceptible birds increases gradually.

Use of Ascites-Indicator Traits Measured under Normal Temperature Conditions

When including information on a non-destructive indicator trait (HCT) for ascites measured on all the birds kept under normal conditions (scheme A-1), the response for BW decreased by 11.4% as compared to the base situation. The rate of inbreeding increased from 3% under base situation to 4.3% per generation under scheme A-1 (Table 3). By including information on RV:TV measured on 50% of the birds under normal conditions (scheme A-2), the number of selection candidates reduced to 2800 birds per sex. In this scheme, as compared to the base situation, response for BW reduced 17.3%. Scheme A-2 also showed a 6.7% lower selection response for BW as compared to scheme A-1. The predicted rate of inbreeding for this scheme was 2.3% per generation (Table 3).

TABLE 3. The effect alternative scenarios on BW, AS and rate of inbreeding

Scheme	Traits in the index	# of Sel.Can.	e.v. of AS [1]	Res. for BW [2]	Res. for AS [3]	ΔF [4] (%)
Base	100%(BW_N)	5600	0	130	0.025	3.0
A-1	100%(BW_N +HCT_N)	5600	-1050	115.2	0	4.3
A-2	100%(BW_N +HCT_N)+50%($RV{:}TV_N$)	2800	-775	107.5	0	2.3
A-3	50%(BW_N +HCT_N)+50%(BW_C+HCT_C+$RV{:}TV_C$)	2800	-400	111.4	0	1.7
A-4	100%(BW_C+HCT_C)+50%($RV{:}TV_C$)	2800	-580	54.1	0	2.1

[1] The economic value of ascites susceptibility (AS) in the breeding goal. The economic value of BW in each scheme was equal to 1.

[2] Response on BW, the unit of BW is gram. The additive genetic standard deviation (σ_a) for BW is equal to 109.5 gr. Therefore 130 gr = 1.2 σ_a

[3] The accumulation of fluid in the abdomen is a score trait as 0, 1 or 2. The additive genetic standard deviation for AS is equal to 0.12 unit. Therefore 0.025 = 0.21 σ_a

[4] ΔF = Rate of inbreeding per generation.

Use of Ascites-Indicator Traits Measured under Cold Temperature Conditions

In scenario's A-3 and A-4, information of traits measured under cold conditions were used in the index. In scheme A-3, half of the birds were kept under normal temperature conditions and the other half was kept under cold conditions. In this scheme, information was available on BW and HCT under both cold and normal conditions and the trait RV:TV was only measured under cold conditions. The gain achieved for trait BW in this scheme was higher (111.4) than that of scheme A-2. In addition, the rate of inbreeding in this scheme was reduced to 1.7% per generation which was the lowest inbreeding rate among the different scenarios that were

considered. Moreover the economic value that was required to keep ascites susceptibility at the same level was lower than that required for the other scenarios.

The last scenario considered was one in which all the birds were kept under cold conditions (scheme A-4). In this scheme traits BW and HCT were measured on all the birds. To measure the trait RV:TV, half of the birds were sacrificed. The number of selection candidates in this scheme was equal to the number of selection candidates in the schemes A-2 and A-3. The selection response for BW in this scheme was 54.1 gr, i.e. it was clearly lower than the response under the other schemes.

The Effects of Proportion of Birds that are Sacrificed

To investigate the effect of the proportion of birds that is sacrificed for measuring the trait RV:TV, this proportion was changed from 50% to 25% or 75%. In each scheme response for AS was kept constant and response in BW and the inbreeding rate are presented in Table 4. The results indicate that by increasing the number of sacrificed birds, response on BW and the rate of inbreeding per generation decreased. However, in scheme A-4, where all the birds kept under cold conditions, the proportion of birds that is sacrificed has a relatively small effect on the results.

TABLE 4. The effects of the proportion of birds that is sacrificed on scenarios *A-2, A-3,* and *A-4* [1]

Scheme [2]	25%			50%			75%		
	e.v. of AS [3]	Res. for BW	ΔF[4] (%)	e.v. of AS	Res. for BW	ΔF (%)	e.v. of AS	Res. for BW	ΔF (%)
A-2	-825	114.6	3.2	-775	107.5	2.3	-750	92.3	1.4
A-3	-425	120.9	2.4	-400	111.4	1.7	-410	92.6	1.0
A-4	-575	58.4	2.8	-580	54.1	2.1	-580	46.5	1.2

[1] For each alternative, the response for ascites susceptibility is fixed at zero.

[2] scheme ***A-2*** including traits BW_N, HCT_N and $RV{:}TV_N$, scheme ***A-3*** including traits BW_N, HCT_N , BW_C, HCT_C and $RV{:}TV_C$ and scheme ***A-4*** including traits BW_C, HCT_C and $RV{:}TV_C$

[3] The economic value of ascites susceptibility (AS) in the breeding goal. The economic value of BW in each scheme was equal to 1.

[4] ΔF = Rate of Inbreeding

Comparing Schemes at Equal Rate of Inbreeding (ΔF)

The scheme A-1 showed higher response for BW than scheme A-3 when the number of sacrificed birds was 2800 or 4200, but the inbreeding rate in scheme A-1 was relatively high. Ideally, schemes should be compared at equal rates of inbreeding. To make scheme A-1 comparable to schemes A-2 and A-3, the rate of inbreeding was reduced by increasing the number of selected sires (Table 5). When the number of sires increased from 50 to 90 or 140, the inbreeding rate in scheme A-1 reduced to 2.4% and

1.7% respectively which was equal to the rate of inbreeding in the schemes A-2 and A-3. At equal rates of inbreeding the gain achieved for BW in scheme A-1 was higher than that in scheme A-2 (110.1 versus 107.5) but was lower than that in scheme A-3 (105.8 versus 111.4). Therefore, when comparing selection response at the same rate of inbreeding, scheme A-3, i.e. including information of BW_N, HCT_N, BW_C, HCT_C and $RV{:}TV_C$ in the index, is the best among alternative breeding schemes considered. In this scheme the genetic progress in BW is reduced by around 18.4 gr as compared to the base situation.

TABLE 5. The effect of changing the number of sires used in scheme A-1.

Number of Sires	e.v. of AS [1]	Res. For BW [2]	ΔF (%) [3]
50	-1050	115.2	4.3
90	-1075	110.1	2.4
140	-1090	105.8	1.7

[1] The economic value of ascites susceptibility (AS) in the breeding goal. The economic value of BW in each scheme was equal to 1.

[2] Response for BW in gr. Response for AS was fixed at zero level in each scheme.

[3] ΔF = Rate of Inbreeding

DISCUSSION

In order to combine selection for BW and resistance to AS in broilers five different schemes were compared by deterministic simulation. In the alternative schemes the traits HCT and/or RV:TV measured under normal and /or cold conditions were used as index information. It has been accepted that as an adaptation to hypoxia, hematocrit value (HCT) increases, so the direct measurement of HCT is useful in accessing ascites progression (Maxwell, 1991, Mirsalimi and Julian, 1991, Lubritz and McPherson, 1994, Shlosberg et al., 1996). Moreover, the ratio of right ventricle to the total ventricular weight of the heart (RV:TV) is a pathological trait that has value as a predictive indicator of ascites (Maxwell, 1991; Enkvetchakul et al.,1995; Wideman et al., 1998). However because of high non-ascites mortality in the experimental groups with low hematocrit value (Shlosberg et al., 1996), selection against HCT needs more attention and scruple than selection against RV:TV.

The results of the current study indicate that by using information of ascites-related traits measured under normal conditions, the gain achieved for BW is reduced. This

reduction in BW was higher in scheme A-2, where RV:TV was measured on a proportion of the birds kept under normal temperature conditions. However, when ascites-related traits were measured on a proportion of the birds kept under cold conditions (scheme A-3), the gain achieved for BW was higher, when results are compared at the same level of inbreeding. If all information is collected on birds kept under cold conditions (scheme A-4), the selection response for BW reduced considerable. This can be ascribed to the low genetic correlation between BW_N and BW_C (0.49). Therefore, we can conclude that the best scheme for improving BW while controlling ascites susceptibility is scheme A-3 in which ascites related traits were measured under cold and normal conditions.

Inbreeding

It has been generally recommended that the rate of inbreeding in broiler lines should kept at a level lower than 1% (Morris and Pollott, 1997). In all our simulations the rate of inbreeding (ΔF) was greater than this critical level. SelAction calculates the rate of inbreeding for a Bulmer equilibrium situation accounting for the effect of selection (Rutten et al., 2002). Prediction of the rate of inbreeding is based on the long-term genetic contribution theory (Wray and Thompson, 1 990; Woolliams and Bijma, 2000). In the current simulation we assumed that selection is for BW and AS only. However, in a practical poultry breeding program selection will be for several other traits. Therefore, in practice the number of selection candidates will be lower than what has been assumed in the current study. If the number of available selection candidates is reduced by 50% to allow for selection on other traits not correlated to the breeding goal traits, on average the rate of inbreeding reduced by about 40% in each scheme, e.g. in the base scheme ΔF reduced from 3% to 1.9% or in scheme A-3 ΔF reduced from 1.7% to 1.1%.

In addition to the number of parents, there are two other mechanisms that affect the rate of inbreeding (ΔF). Higher selection intensity and more sib information in the index both increase the probability of coselection of relatives, which in turn increases ΔF. By changing the number of sires used in scheme A-1, the ΔF of that scheme was made equal to that of scheme A-2 and A-3. The results indicated that at equal rate of inbreeding the gain achieved for BW in this scheme still is lower than the gain achieved for BW in scheme A-3.

There are however, more efficient ways of maximizing gain while restricting inbreeding i.e. by using stochastic simulation rather than deterministic simulation. Meuwissen, (1997) introduced a dynamic selection tool to maximize genetic gain while restricting the rate of inbreeding. In this method the number of parents and the number of offspring per parent may vary, depending on the candidates available in a particular

generation which results in a dynamic breeding program. Dynamic selection tools are likely to reduce the variance of the rate of inbreeding as well (Meuwissen, 1997).

Genotype by Environment Interaction

Breeding for improved adaptation to a particular stressful environment might be the strategy of choice when genotype by environment interactions significantly affects economically important traits (Cahaner, 1990; Hartmann, 1990; Leenstra and Cahaner, 1991). Pakdel et al. (2004a) reported that broilers with high genetic values for BW under normal conditions do not necessarily have high genetic value for BW under cold conditions as indicated by genetic correlation of 0.46. Deeb et al. (2002) found that birds that have a higher potential for growth rate under normal temperature conditions are more likely to suffer from ascites under cold-stress conditions as compared to birds with a lower potential for growth rate. Therefore, it is important to measure performance of birds under cold and normal conditions. In the current study and in scheme A-3, the trait BW measured under cold and normal conditions were used in the index. Therefore genotype by environment interaction was accounted for in this breeding program. This strategy provided genetically adapted birds that are capable of maintaining acceptable production performance under cold and normal conditions. The results showed that apart from the cost, this scheme gives relatively high gain with low inbreeding rate. However by excluding genotype by environment interaction in scheme A-4 where all the birds kept under unfavorable environmental conditions (cold-stress), the gain achieved for BW considerably reduced.

Literature

The result of current study showed that selection for BW and resistance to ascites syndrome is possible in broilers. This result is in agreement with the previous results. In a theoretical study, McMillan and Quinton (2002) investigated the effects of selecting for a production trait, such as growth rate on a fitness trait such as ascites through stochastic simulation. They reported that the use of sib information and an indicator trait for ascites reduced the genetic level for ascites susceptibility. The rate of inbreeding in that study was unaffected by culling on sib information and the level of correlation between two index traits, but it was strongly affected by the number of sires. However in the current study, the results demonstrated that the rate of inbreeding is related to the sib information as well as the number of sires chosen.

In experimental studies several researchers have chosen a strategy to test the animals's ability to withstand severe stress and not succumb to ascites (Wideman and French, 2000; Anthony et al., 2001; Balog et al., 2001). Wideman and French, (2000) demonstrated improvement in ascites resistance of progeny from broiler breeders that,

for two consecutive generations, have survived the rigorous selection pressure imposed by unilateral pulmonary artery occlusion. Chronic unilateral pulmonary artery occlusion triggers a pathophysiological progression that terminates with a high incidence of mortality diagnosed as ascites. Wideman and French, (2000) concluded that by using this technique genetic selection for ascites resistance can be accomplished. However the final BW in nonascitic broilers in one experiment was lighter than for nonascitic base population birds, but in the second experiment there was no difference for final BW among nonascitic birds. Anthony et al. (2001) made sire-family selections from siblings in broilers based on mortality data obtained in a hypobaric chamber. They reported success at selecting an ascites-resistant and an ascites-susceptible population of broilers. Balog et al. (2001) reported that the selection for ascites resistance or susceptibility did not affect weight gain.

Conclusion

In the present study, we have considered alternative selection schemes for simultaneous selection on BW as well as reduction of ascites susceptibility traits. The alternative selection strategies indicate that by ignoring ascites susceptibility in the breeding goal, although achieved gain for BW is relatively high (130 gr), the genetic response for ascites susceptibility is 0.025 unit and rate of inbreeding is 3% per generation. Including information of ascites related traits (HCT and RV:TV) measured under normal and cold conditions makes it possible to achieve relatively high gain for BW (111.4 gr) with constant level of ascites susceptibility (zero) at lower rate of inbreeding (2.4% per generation).

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Chapter 7

General Discussion

INTRODUCTION

Breeding companies have been very successful in their effort to populate the poultry production industry in a logistically efficient manner with increasing numbers of increasingly efficient stock of increasingly high health status (Arthur et al., 2003). The efficiency of commercial broilers has shown a dramatic increase since the 1950s. The modern broiler grows more than three times faster, with greater meat yield and with better feed conversion reaching market weight on less than ½ the feed required by the vintage broiler. The role of breeding in this success has been dominant, as has been elegantly shown by Havenstein et al. (1994a, b). Some 80% of progress over time has been made possible by improvement of the genetic potential of the birds used. However, selection of broilers for growth and yield has been accompanied by a number of undesirable side effects and physiological changes like ascites syndrome (Julian, 1998, Rauw et al., 1998). Ascites syndrome is of major international concern to the broiler industry because it has serious effects on the health, welfare and profitability of broiler flocks. In recent years mortality due to ascites syndrome has increased and is especially a problem under circumstances such as high altitude, cold-stress or any other extreme stress (Julian, 1993). It seems that the modern commercial broilers are close to the limit at which their cardiopulmonary system can provide oxygen for growth. Therefore, any external stress that increases their oxygen requirement or decreases their ability to supply oxygen can tip them over this limit. The breeding companies are aware of this and are investigating ways to improve their selection schemes and they changed breeding goals. In order to design optimal selection strategies that take into account ascites, knowledge is needed about the genetic background of this syndrome. Although the physiology of this syndrome has been studied extensively, only a limited number of studies have investigated the genetic basis of this syndrome. This thesis focused on the genetic analysis of traits related to ascites syndrome in an experimental broiler population at sea level and under cold conditions. This general discussion starts with a description of traits related to ascites susceptibility by using statistical and biological approaches. Subsequently the relationship of ascites-related traits with productivity traits and the environmental sensitivity of the genetic parameters are discussed. Furthermore, the consequences of alternative selection schemes for ascites resistance as well as the opportunities for marker assisted selection are discussed. Finally some topics for further research are presented.

Development of an Aggregate Trait Describing Ascites

The aim of this section is to develop a trait that describes the degree of ascites susceptibility for each bird by combining the information from different ascites-related traits. For this purpose two approaches will be used: a statistical approach using

principal component analysis and an approach were we will utilize biological knowledge on the trait.

1. Statistical Approach

For the statistical procedure a set of principal components (SAS, procedure Princomp) were fitted to the traits BW, HCT, RV, TV, RV:TV; %RV, %TV, ABDOMEN, BREAST, LIVER and HEART which were measured under cold stress conditions (n=3,394). The purpose of a principal component analysis is to derive a small number of independent linear combinations (principal components) of a set of variables, that retain as much of the information in the original variables as possible. Principal components are by definition uncorrelated. Results of the analysis showed that the first principal component explained 40% of total variance in the ascites-related traits and the second principal component explained 19%. The eigenvectors for the first and the second principal components are in Table 1. The first component has a high positive loading on the variables that are more related to ascites like %RV, RV:TV, ABDOMEN and LIVER and a negative loadings on the variable BW. The second component has high positive loadings on the variables BW and TV and negative loading for traits like ABDOMEN, LIVER and HCT.

The genetic correlation among ascites-related traits and the first two principal components were estimated using an animal model:

$$Y_{ijklm} = \mu + Sex_i + Feather_j + Batch_k + Group_l + a_m + e_{ijklm}$$

where: Y_{ijklm} = the dependent variable on chicken m of sex i, feathering class j from batch k in group l; Sex_i = fixed effect of sex i (i=1,2 female or male); $Feather_j$ = fixed effect of feathering j (j = 1,2 fast or slow); $Batch_k$ = fixed effect of batch k of the birds (k = 1,2…9), classes were formed based on a combination of hatching day and pen; $Group_l$ = Fixed effect of group (l=1,2…46), classes were formed based on the age of the dam and the hatching day of the experimental birds ; a_m= random direct genetic effect of individual m; e_{ijklm} = random residual effect. The fixed and random effects were identical for all the traits under study. Bivariate analyses were performed to compute correlations between principal components and the ascites-related traits. Estimates of variance components were obtained using the ASREML software (Gilmour et al., 2000) and shows in Table 1.

The estimated heritability for the first principal component was equal to 0.47 and for the second principal component the heritability was 0.31. The genetic correlation between the two principal components was 0.29. The genetic correlation among the principal components and the ascites indicator traits shows that the first principal component is highly correlated with traits that indicate the presence of (subclinical) ascites such as %RV, RV:TV, HEART, LIVER and ABDOMEN, whereas the second

component is more related to the performance traits such as TV and BW. Therefore, these results suggest that the first component is closely related to the ascites susceptibility and can be used as an indicator trait for ascites. The heritability of this principal component (Prin 1) is much higher than the heritability of fluid accumulation in the abdominal cavity (ABDOMEN, heritability is 0.1) which was used previously as ascites susceptibility trait (Chapter 6). However, ABDOMEN is a categorical trait (scores of 0, 1 or 2) which was analyzed using a linear model. When the heritability of ABDOMEN was transformed from a linear model to the underlying scale (Lynch and Walsh, 1998), the heritability was 0.40 which is close to the estimated heritability for principal component 1. These results suggest that the heritability for the underlying ascites susceptibility trait is in the order of 0.4 and therefore relatively high.

De Greef et al. (2001a) also used principal component analysis to develop an aggregate trait. The first principal component from the traits RV:TV, HCT, ABDOMEN, HEART and LIVER in their research showed highest correlation (Spearman's rank correlation) with the trait HEART. Therefore, De Greef et al. (2001a) conclude that HEART is the best first predictor for ascites syndrome.

TABLE 1. The eigenvectors (contribution) of the traits and the genetic correlation among ascites-related traits with the first two principal components (PRIN1 and PRIN 2)

Traits [1]	Eigenvectors		Genetic correlations	
	PRIN 1	PRIN 2	PRIN 1	PRIN 2
BW	-0.16	0.55	-0.28	0.76
HCT	0.27	-0.10	0.72	0.05
RV	0.37	0.39	0.93	0.57
TV	0.09	0.62	0.36	0.95
RV:TV	0.41	0.09	0.93	0.14
% RV	0.45	0.06	0.99	0.15
% TV	0.32	0.04	0.74	0.16
MORT-TOT	-	-	0.74	-0.02
ABDOMEN	0.32	-0.24	0.84	0.26
BREAST	0.11	-0.13	0.63	-0.18
LIVER	0.30	-0.24	0.86	0.22
HEART	0.26	-0.01	0.92	0.43

[1] HCT = hematocrit value; RV = right ventricular weight; TV = total ventricular weight; RV:TV = ratio of right ventricular weight to total ventricular weight; %RV= right ventricular weight as percentage of BW; %TV = total ventricular weight as percentage of BW; MORT-TOT = Total mortality; ABDOMEN = Fluid in the abdomen; BREAST = Color of the breast; LIVER = Liver abnormalities; and HEART = Fluid in the heart sac.

2. Utilizing Biological Knowledge

Instead of using a statistical approach, we could also use biological knowledge about the development of the ascites syndrome for constructing an aggregate trait. For this purpose we need a clear understanding about ascites development and it is important to know the order in which events occur that indicate ascites. Grevenhof (2004) indicated the most likely order of occurrence of the categorical traits is fluid accumulation in the heart (HEART), followed by liver abnormalities (LIVER) and finally fluid accumulation in the abdominal cavity (ABDOMEN). The number of birds in each of the categories for ABDOMEN, BREAST, LIVER and HEART are shown in Table 2.

TABLE 2. The number of birds in each category (0, 1 or2) for score traits [1]

Category [2]	ABDOMEN	BREAST	LIVER	HEART
0	3542	3585	3488	1781
1	23	110	170	1653
2	132	2	39	262

[1] ABDOMEN = Fluid in the abdomen; BREAST = Color of the breast; LIVER = Liver abnormalities; and HEART = Fluid in the heart sac.

[2] 0 represented no abnormality (healthy bird), 1 represented an abnormal and 2 represented serious abnormality.

Figure 1 shows the mean values for HCT and RV:TV for each of the categorical traits. The figure suggests two groups of birds. The first group of birds has lower values for HCT and RV:TV and no severe signs of ascites, i.e. a score of 0 for ABDOMEN, BREAST, LIVER and HEART. Birds with a score of 1 for HEART and BREAST also seem to belong to group 1. The second group of birds has increased values for HCT and RV:TV with clear signs of ascites, i.e. a score of 1 for the traits LIVER and HEART or a score of 2 for all categorical traits. Results show that birds with score 1 and 2 for ABDOMEN have almost the same value for HCT and RV:TV. Further, a little fluid accumulation in the HEART (HEART=1) is not accompanied by increased values for HCT or ratio of RV:TV. Only 2 out of 4202 birds had dark breast meat (BREAST=2) suggesting that this classification does not provide much additional information regarding the susceptibility status of the birds. Based on these results, categorical traits can be redefined in order to get a better characterization of the ascites susceptibility of the birds: susceptible birds are birds with a score for LIVER of 1 or 2, a score for ABDOMEN of 1 or 2 or a score of 2 for HEART. Therefore, each of the categorical traits can be redefined to a 0/1 trait. By adding the values for each of the redefined traits HEART, LIVER, and ABDOMEN for each bird an aggregate trait can be constructed. Based on this aggregate trait, each bird can be scored on a scale from 0 to 3 where a

score of 3 indicates that the bird has gone through all the stages of ascites and has the highest ascites susceptibility. This aggregate trait can be further developed by including the birds which died due to ascites and assigning them the highest susceptibility score.

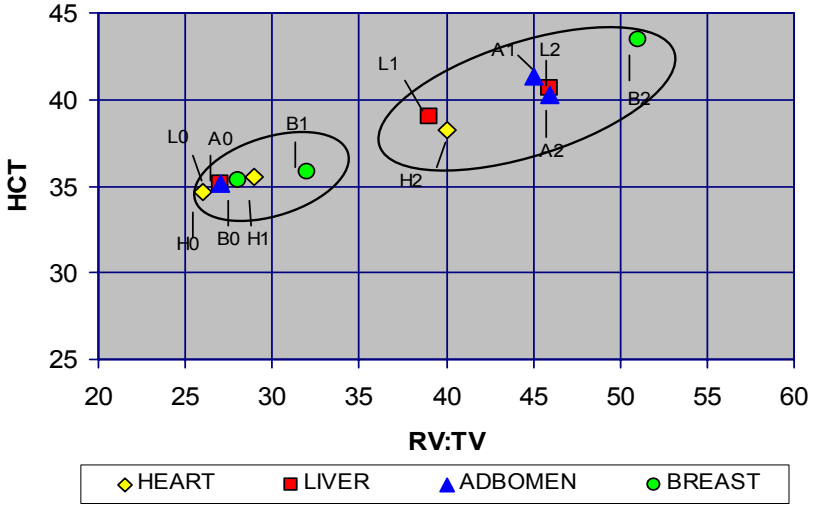

FIGURE 1 Hematocrit value (HCT) and ratio of right to total ventricular weight (RV:TV) for birds with a score of 0, 1 or 2 for each categorical trait

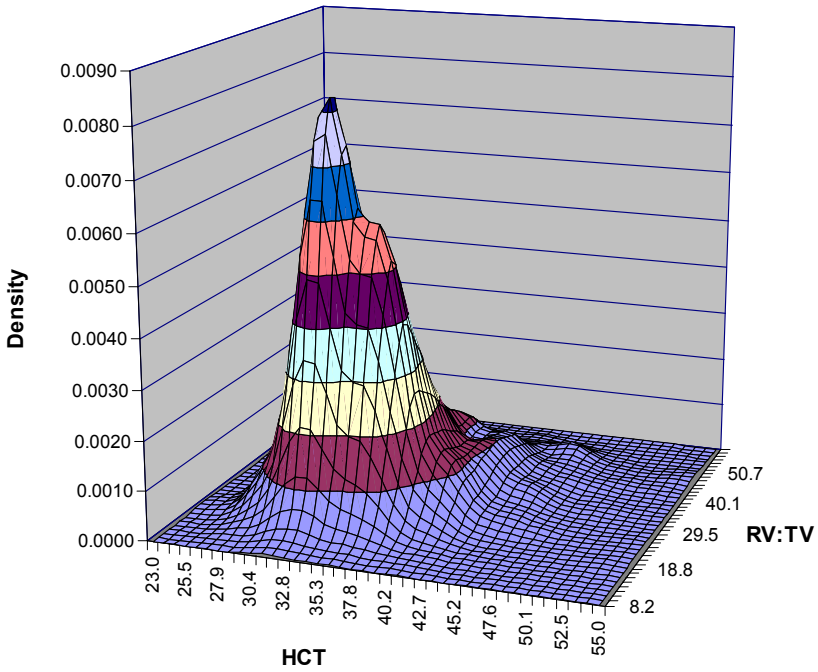

FIGURE 2. Surface plot of traits hematocrit value (HCT) and ratio of right ventricular weight to total ventricular weight (RV:TV) measured under cold conditions.

Figure 1 suggests that there are two groups of birds; birds showing clear signs of ascites and therefore might be qualified as “affected” and the “healthy” birds. Figure 2 shows the joint distribution of HCT and RV:TV. This distribution does not clearly show

a bimodal pattern, however, the distribution is clearly skewed which might indicate a mixture of two distributions representing the healthy and the affected birds.

In summary these results suggest that an improved ascites indicator trait can be constructed by combining information from different traits. Combining traits resulted in an increased heritability and therefore gives better scope for improvement of the trait. The optimal way of combining information must be based on integration of biologic and statistical approach.

Genetic Parameters of Traits Related to Ascites

Heritabilities of ascites-related traits were estimated using an animal model. Values obtained for ascites-related traits indicated that there is a moderate to high heritability for ascites; therefore it seems reasonable to expect that a genetic selection program could be successful in reversing the current trend towards an increase of the ascites incidence (Chapter 6). However, the heritability is a property not only of the trait but also of the population and the environmental conditions surrounding the animals (Falconer, 1989). Due to the fact that genetic differences in ascites susceptibility of birds become more evident under cold conditions, the heritability of the traits measured under cold conditions was higher than the heritability of the traits measured under normal conditions.

Furthermore, in order to determine the importance of maternal genetic effects, models with or without maternal genetic effects were compared. The model including direct and maternal genetic effects gave a significantly better fit for BW, RV:TV and some other ascites-related traits than a model with only direct genetic effects. This indicates that maternal genetic effects play a role in the development of the ascites syndrome. Further, a large increase in the direct heritability was found for traits with a significant maternal genetic effect when this factor was ignored in the analysis. For instance for BW, the heritability of the direct genetic effect increased from 0.21 to 0.42 when ignoring maternal genetic effects in the analysis. These results are in line with the results of Clément et al. (2001) who demonstrated that when maternal genetic effects exist but are neglected in the model, the direct heritability is overestimated. The maternal (genetic) environment affects the growth of birds during two periods, the preovopositional period and the postovipositional period. The postovipositional effect can be divided into the prehatch (incubation) and the posthatch effects where the effect of posthatch period on growth is not important, because the birds were raised independently of the dams. Therefore, the effects that may possibly affect chick growth are preovipositional maternal components, such as egg size, egg weight, shell quality and yolk composition (Aggrey and Cheng, 1993). The maternal effect seems to influence BW in young birds (Tullett and Burton, 1982; Pinchasov, 1993). This may contribute to the imbalance between the demand tissues and the mass, form and

function of the support tissues. Recent observations indicate that early growth restriction increase the fitness of poultry (Currie.,1999; Balog et al., 2000) and therefore Currie (1999) recommends feeding birds with a low protein / low energy diet during the first 14 days in order to reduce the oxygen demand and therewith to control susceptibility to ascites. Balog et al. (2000) showed that birds under food restriction regimes had significantly lower ascites incidence compared to the unrestricted controls. These results suggest that ascites susceptibility can be reduced by choosing birds with lower hatching weight and by changing the diet regimes at the beginning of rearing period. From a genetic point of view, exploiting maternal genetic effects and selection for alternative growth curves might result in a period of slow-growth at earlier ages and with that reduce ascites susceptibility.

The Effect of Environment Sensitivity on Estimated Genetic Correlations

The estimated genetic correlation among ascites-related traits measured under cold conditions showed that broilers that have a higher genetic potential for growth, have a lower genetic potential for ascites indicator traits. Under normal conditions, however the genetic correlations between BW and ascites indicator traits shifted to positive values. This indicates that the genetic parameters for these traits are sensitive to the applied temperature schedule. Knap and Bishop (2000) pointed out, by referring to the study by De Greef et al. (2001b), how environmental sensitivity may have important effects on estimates of genetic parameters. De Greef et al. (2001b) indicated that susceptibility to ascites is only expressed in a challenging environment and growth rate becomes depressed when ascites actually occurs. As a result, birds with the highest genetic potential for growth rate under normal conditions show below-average growth under cold conditions due to ascites. Environmental sensitivity of high-production genotypes is an important issue for genetic improvement and it will be a major topic for fundamental research and simulation modeling during the coming decade (Knap and Bishop, 2000).

The unique set up of our experiments, where parents had offspring under cold and normal conditions, enabled the estimation of genetic correlations between traits measured under both conditions. Those results indicated that except for BW, the genetic correlation between the same trait measured under cold and normal temperatures were high. This indicates that mainly the same genes affect ascites-indicator traits in both environments. In contrast the low genetic correlation for BW in different environments (0.49) indicates genotype by environment interaction. The problem of genotype by environment interaction might become an important issue in case the breeding stocks are developed in one environment but are used under a wide range of conditions. Therefore, in case of ascites, where temperature affects the incidence of the syndrome,

it is important to know whether superior animals in one environment would remain superior when they are used in another environment.

Evaluation of the Alternative Selection Schemes to Improve Resistance to Ascites

The desired direction of genetic change of pure line chickens is determined by customer demands and the economics of broiler production. Primary breeders must be careful in identifying the characteristics of greatest importance, finding methods of selecting for these traits and setting progress goals. Broiler selection has focused on traits such as growth rate, feed efficiency, livability, and carcass quality. In Chapter 6 five alternative schemes were compared by deterministic simulation using the program SelAction (Rutten et al., 2002). In the alternative selection strategies a constant economic value was used for BW, whereas the economic value for ascites susceptibility (AS) was changed in order to obtain zero response for AS. At a zero level for ascites, maximum response for BW is obtained when testing birds under both cold and normal conditions.

In order to see whether the results for the different schemes were sensitive to the condition of "no change in ascites susceptibility (AS)", two other situations were investigated. In the first situation the economic value of BW in the breeding goal was set equal to zero. This will give the maximum response that can be obtained for AS. The results are presented in Table 3.

TABLE 3. The effect alternative scenarios on BW, AS and rate of inbreeding when all emphasis was on AS [1]

Scheme	Traits in the index [2]	# of Sel.Can.	Res. for BW	Res. for AS	Inb. %
Base	100%(BW_N)	5600	-132.3	-0.025	2.7
A-1	100%(BW_N +HCT_N)	5600	-70.79	-0.066	2.9
A-2	100%(BW_N +HCT_N)+50%$RV{:}TV_N$	2800	-53.6	-0.068	2.2
A-3	50%(BW_N +HCT_N)+50%(BW_C+HCT_C+$RV{:}TV_C$)	2800	-40.1	-0.096	2.7
A-4	100%(BW_C+HCT_C)+50%$RV{:}TV_C$	2800	-61.2	-0.106	1.7

[1] The economic value of AS was equal to -1 in each scheme

[2] HCT = hematocrit value; RV:TV = ratio of right ventricular weight to total ventricular weight where subscript C indicates that the trait was measured under cold conditions and subscript N indicates that the trait was measured under normal temperature conditions.

In the base situation with index information on BW only, the absolute level of response for AS was the same as with BW in the breeding goal only, but as expected, opposite in direction (negative sign). In the alternative schemes which included

information on ascites-indicator traits, response in AS increased. In scheme A-1 the reduction in AS was increased by 164% as compared to the base situation. Including information on RV:TV measured under normal conditions (scheme A-2) only resulted in a small further improvement. However, by using information of traits related to ascites measured under cold condition (scheme A-3), the gain achieved for AS considerably increased. Further, this scheme gave the lowest level of reduction in response for BW among the alternative schemes. The maximum gain for AS was achieved in scheme A-4 where all the birds are kept under cold conditions (324% as compared to the base situation). Based on these results we can conclude that selection to reduce AS can benefit considerably from testing birds under cold conditions.

In the second situation, alternative schemes were compared for a situation where the aim is not only to control AS, but also to reduce it by -0.025 units per generation. Table 4 gives the results for the base situation and for the alternative scenarios. In scheme A-1, the rate of inbreeding increased with 70% and response for BW decreased with 39% as compared to the base scheme. For scheme A-2, response for BW was similar to that for scheme A-1, but the rate of inbreeding decreased considerably. By including information on traits measured under cold conditions (scheme A-3) response for BW increased with 13.7 % as compared to scheme A-1 and the rate of inbreeding decreased by 51%. The gain for BW in this scheme (scheme A-3) was highest among the alternative schemes. The last scheme (scheme A-4) where birds are kept only under cold conditions resulted in a low selection response for BW. These results indicate that it is possible to reduce ascites susceptibility and to achieve an acceptable level of gain for BW. The best scheme, i.e. a scheme that has substantial improvement in AS as well as BW is scheme A-3. This is in agreement with results obtained in Chapter 6.

TABLE 4. The effect alternative scenarios on BW, AS and the rate of inbreeding (AS fixed at -0.025 unit in the alternative schemes)

Scheme	Traits in the index [2]	# of Sel.Can.	e.v. of AS [1]	Res. for BW	Res. for AS	Inb. %
Base	$100\%(BW_N)$	5600	-	130	0.025	3.0
A-1	$100\%(BW_N + HCT_N)$	5600	-1775	79.1	-0.025	5.1
A-2	$100\%(BW_N + HCT_N)+50\%RV:TV_N$	2800	-1400	79.8	-0.025	2.9
A-3	$50\%(BW_N + HCT_N)+50\%(BW_C+HCT_C+RV:TV_C)$	2800	-940	89.9	-0.025	2.5
A-4	$100\%(BW_C+HCT_C)+50\%RV:TV_C$	2800	-705	38.1	-0.025	2.1

[1] The economic value of BW was equal to 1 in all schemes.

[2] HCT = hematocrit value; RV:TV = ratio of right ventricular weight to total ventricular weight where subscript C indicates that the trait was measured under cold conditions and subscript N indicates that the trait was measured under normal temperature conditions.

Genetic Progress in Breeding Schemes Using Genetic Markers

Finding and developing genetic markers linked to ascites susceptibility and ascites resistance offers new opportunities for breeding. Groenen et al., (2001) performed a whole genome scan aimed at the mapping of quantitative trait loci (QTL) for ascites. Three significant QTL affecting ascites-related traits were detected, whereas two QTL reached the genome-wise suggestive threshold. In this thesis QTLs controlling ascites resistance in broilers on chromosomes 8 and 10 were confirmed in a population originating from the original mapping population. Markers linked to genes involved in susceptibility to ascites may be used by breeders for selecting ascites resistant birds, i.e. marker-assisted selection (MAS).

The use of MAS can especially usefull for traits that have a low heritability or are dificult to measure. Both of these charactersitics apply to ascites suscebtibility and therefore it is expected that MAS can make an important contribution. To quantify the contribution of QTL information on the genetic progress in BW as well as resistance to ascites a breeding scheme was simulated. The breeding goal consisted of two traits, BW and ascites susceptibility (AS). Details on the calculations are given in Box 1.

BOX 1: The heritability of BW was 0.2 and the phenotypic variance was 60000. The heritability of AS was 0.10 and phenotypic variance was 0.14. The economic value of BW was set equal to 1 and the economic value of AS was changed in order to obtain zero response for AS. The information source for the genetic evaluation of BW were the animal's own record, pedigree information, average phenotypic performance of full sibs and average phenotypic performance of half sibs. The information sources for the genetic evaluation of AS was the QTL information. All the birds were kept under normal conditions and no birds were sacrificed. We considered QTLs that explain 5, 10, 20 or 50% of the genetic variance of AS. These situations will be referred to as Q05, Q10, Q20 and Q50, respectively. Variance can be explained by one or number of genes. The remaining genetic variation for AS results from polygenes (i.e. not marked). The QTL information is modeled as a trait that is correlated to AS in the breeding goal and has a heritability of 1. We assumed that the QTL has no pleiotropic effects on BW and therefore the genetic correlation between the QTL and BW is equal to zero. Further, it was assumed that the correlation between the QTL and the polygenic component is 0 in the base generation. (i.e. prior to selection). The correlation between the QTL and the breeding goal trait AS depends on the amount of variation that is explained by the QTL. The genetic correlations of AS with the QTL and the polygenic component are $\sqrt{q}$ and $\sqrt{1-q}$ respectively and the phenotypic correlation of AS with QTL and polygenic component are $\sqrt{q \times h^2_{AS}}$ and $\sqrt{(1-q) \times h^2_{AS}}$ respectively where q is the fraction of the genetic variance in AS trait explained by the QTL. The genetic correlation between polygenic component and BW is equal to $\frac{rg_{AS,BW}}{\sqrt{1-q}}$ so that for any q, the total genetic correlation of BW and AS is equal to 0.18. The heritability of the polygenic component is $\frac{1-q}{\frac{1}{h^2_{AS}}-q}$. The phenotypic variance of QTL is equal to additive genetic variance of QTL which is equal to $q \times \sigma^2_{A_{AS}}$ and the phenotypic variance of polygenic component is equal to $\sigma^2_{P_{AS}} - \sigma^2_{QTL}$.

Results of schemes with different fractions of variance explained by the QTL were compared with the base scheme and scheme A-3. The results are summarized in Table 5. By using information on QTL that describe only 5% of the genetic variance (scheme Q05) ascites can be controlled while selection response for BW was 122.3 gram. This is only 6% lower than the achieved gain for BW in the base scheme (130 gram) and 10% higher than the gain obtained for BW in the optimal scheme (scheme A-3). Inbreeding for the MAS schemes was at a similar level as that of the base scheme. It is good to keep in mind that in the MAS schemes, similar as in the base scheme, all the birds are available as selection candidates and they are kept under normal circumstances. However, in scheme A-3 a proportion of the birds has to be kept under cold conditions and they have to be sacrificed in order to measure ascites-related traits. By using QTL that describe a higher proportion of the genetic variance of AS (scheme Q10, Q20 and Q50), the gain for BW was higher.

The results show that QTL information can be used very effectively in controlling ascites susceptibility. Even if the QTL explains only 5% of the genetic variance the reduction in gain for BW is limited as compared to a scheme where selection is for BW only (Base). This illustrates that MAS can make an important contribution in selection for birds which are resistant to ascites.

Whether implementation of MAS in a breding scheme is economically beneficial, depends upon the cost of the breeding program and the benefits from increased genetic progress. Monetary cost and benefit from changes to the breeding program need to be tailored towards the particular breeding program. Economic evaluation of the MAS-scheme has therefore not been carried out in the current study.

TABLE 5. The effect of amount of variance explained by the QTL on the breeding goal traits.

Scheme	# of selection candidates	e.v. of AS [1]	ΔG for BW	ΔG for *AS*	Inb. (%)
Base [2]	5600	-	130.0	0.025	3.0
A-3 [3]	2800	-400	111.4	0	1.7
Q05 [4]	5600	-550	122.3	0	3.0
Q10	5600	-450	123.8	0	2.9
Q20	5600	-320	125.9	0	2.9
Q50	5600	-165	128.0	0	2.9

[1] The economic value of BW in the breeding goal was equal to 1 in all schemes.
[2] Base scheme including information on BW only.
[3] Scheme A-3 including information of BW and HCT measured on 50% of birds under normal conditions and BW, HCT and RV:TV measured on the rest of birds under cold conditions.
[4] Q refers to the amount of variance explained by the QTL. This is 5%, 10%, 20% or 50%.

Derivation of Economic Value for Ascites Susceptibility

When evaluating alternative selection schemes to improve resistance to ascites in chapter 6, the economic value of BW in the breeding goal was fixed at 1 and the economic value of ascites susceptibility (AS) was changed to obtain zero response in AS. In this section we will derive an approximate economic value for ascites susceptibility. For this purpose birds are categorized in four different groups:

1. Healthy birds that take score 0.
2. Birds with reduced growth but no severe signs of ascites. These are birds take score 1 and have an increased value for HCT and RV:RV: HCT>38 and RV:TV>30.
3. Birds with severe signs of ascites; ABDOMEN = 1 or 2, LIVER = 1 or 2 and HEART = 2: it is assumed that this meat is not suitable for human consumption and has a value of 0. These group of birds take score 2
4. Dead birds that take score 3.

The percentage of birds in each category under cold conditions and their average value for BW are in Table 6. Based on Table 6 the mean and the standard deviation of AS can be calculated, i.e. a mean of 0.977 and a standard deviation of 1.072 units. Further, liabilities for each category can be determined.

TABLE 6. The frequency of birds under cold, normal and normal +1 conditions and the mean value of BW in each category under cold conditions

Category	% of birds under			The mean value of BW under cold conditions
	Cold	Normal	Normal+1	
0	0.426	0.679	0.319	1658
1	0.331	0.232	0.341	1604
2	0.083	0.039	0.101	-
3	0.160	0.050	0.238	-

The economic value of a trait is defined as “the change in profitability of an enterprise expressed per unit product output as a consequence of one unit of change in performance of the trait considered, without changing performance of other traits”. The unit of change in body weight is defined as gram per marketable bird. Suppose that the rate of mortality (category 3) under normal condition is 5% and that the underlying distribution is normal and has a standard deviation of 1.072. Based on these assumptions we can calculate the percentage of birds in each category under normal conditions (Table 6). The mean value of AS under normal conditions is equal to 0.28. Economic values in principle are derived by computing profit margin or cost price for the base level of the trait concerned and for a level that is marginally higher. If the mean

value of AS increased from 0.28 to 1.28, the frequency of birds in each category will change. These frequencies are shown in Table 6 as "normal + 1".

The value of an average bird under normal conditions is equal to:

$$0.679 \times X + 0.233 \times (X - 54) + 0.039 \times 0 + 0.05 \times 0$$

Where X = weight of the commercial broiler in gram. If X = 2200 g, then the value of an average bird under normal conditions is 1992 g. When ascites susceptibility would be increased with one unit the value of an average bird would become 1434 g. Therefore, the economic value of ascites susceptibility is -558 time the value of one gram improvement of BW. Note that in chapter 6 the trait ABDOMEN was used as a breeding goal trait and this trait has a different standard deviation than the trait we defined here.

Perspectives for Further Research

Further research in breeding against ascites susceptibility must be based on combination of the traits related to ascites. In this chapter it is shown that combining the traits resulted in higher heritability and gives better scope for improvement of the trait. The optimal way of combining the information should be based on integration of a biologic and statistical approach.

Upcoming developments in the breeding of meat-type chickens will no doubt be governed by the same factors that have determined developments in the past, but with one important difference: the 'chicken itself' is likely to play its own role because its biological capabilities sets the limits to improvements (Arthur et al., 2003). There is a need for an investigation for better understanding of the biological basis of balance between health and welfare and production efficiency in the modern broilers. Understanding this biological basis will direct researchers and breeders to design selection approaches aimed at well balanced improvement in animal health and welfare and production efficiency. Genomics could well play a role in this, both in unraveling the biological mechanisms and in supporting the breeders in selection programmes. However the ethical soundness and acceptability of breeding goals needs to be kept continuously under review.

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Summary

Ascites, also known as water belly, is a growth-related disorder of broilers that occurs more often in fast growing birds, at high altitudes and low temperature conditions. This dissertation deals with the estimation of genetic parameters for traits related to the ascites syndrome and the relationship between ascites-related traits and performance traits. Further, the possibilities to genetically change the incidence of this metabolic disorder in broilers were investigated.

The objective of *Chapter 2* was to estimate heritabilities for ascites-related traits and to investigate the importance of maternal genetic effects for these traits. Several traits related to ascites were measured on more than 4,000 broilers kept under cold temperature conditions. In addition, traits related to ascites from 795 birds kept under a normal temperature schedule were measured. These observations were used to describe the distribution of traits under normal temperature conditions. The results indicated that cold stress had a marked effect on the mean values for hematocrit value and ratio of right ventricular weight to the total ventricular weight (RV:TV) as well as on the variance of these traits. Heritabilities of traits related to ascites measured under cold temperature conditions were estimated using an animal model with a direct genetic effect and a model with direct and maternal genetic effects. Estimated heritabilities from the direct genetic effects model were 0.46 for hematocrit value, 0.42 for body weight, 0.47 for right ventricular weight, 0.46 for total ventricular weight, 0.45 for RV:TV, 0.32 for total mortality, and 0.18 for fluid accumulation in the heart sac. Maternal genetic effects significantly influenced the traits body weight, total ventricular weight, RV:TV and total mortality. Direct and maternal heritabilities, respectively, for body weight were 0.21 and 0.04, for total ventricular weight were 0.29 and 0.03, for RV:TV were 0.28 and 0.02 and for total mortality were 0.16 and 0.05. The results indicate that both direct and maternal genetic effects play a role in the development of the ascites syndrome.

In *Chapter 3* the genetic and phenotypic correlations among ascites-related traits measured under cold and normal temperature conditions were estimated. Under cold temperature conditions the genetic correlation between body weight and hematocrit value was -0.23 and between body weight and RV:TV -0.27. But under normal temperature conditions these genetic correlations were 0.55 and 0.50 respectively. These results demonstrate that the genetic correlations between ascites-related traits and body weight depend on the temperature conditions under which animals are kept. Under cold temperature conditions strong positive genetic correlations (around 0.8) were observed between total mortality, fluid accumulation in the abdominal cavity and

RV:TV. Except for body weight, the genetic correlations between the same traits measured under cold and normal temperatures conditions were high, e.g. 0.93 for hematocrit value, 0.89 for right ventricular weight, 0.80 for total ventricular weight and 0.91 for RV:TV. These results indicate that mainly the same genes affect these traits in both environments. In addition, ratio of RV:TV measured under normal temperature conditions might serve as a good indicator trait for ascites. In contrast the low genetic correlation for body weight measured in different environments (0.29) suggests that the genetic factors involved in body weight are very sensitive to the applied temperature schedule.

The knowledge of the genetic relationships among ascites-related traits and performance traits like carcass traits or feed efficiency are required to design breeding programs that aim to improve the degree of resistance to ascites syndrome as well as production traits. The objective of *Chapter 4* was to estimate these genetic correlations. Three different experiments were set up to measure ascites-related traits (4202 birds), feed efficiency traits (2166 birds) and carcass traits (2036 birds). Birds in the ascites experiment were kept under cold temperature conditions, whereas birds in feed efficiency or carcass experiment were kept under normal temperature conditions. All the birds in three different experiments originated from the same group of parents, which enabled the estimation of genetic correlations among traits measured in each experiment. The genetic correlation of body weight measured under normal temperature conditions in carcass experiment with RV:TV measured under cold temperature conditions was 0.30. The estimated genetic correlation indicated that single-trait selecting for body weight leads to an increased incidence of the ascites syndrome but also there are good opportunities of multi-trait selection of birds for improved body weight and resistance to ascites. Weak but positive genetic relationships were found between feed efficiency and ascites-related traits suggesting that more efficient birds tend to be slightly more susceptible towards ascites. However these results did not strongly supported our expectation that more efficient birds are more susceptible to ascites. The relatively low genetic correlation between body weight measured in the carcass or in the feed efficiency experiments and body weight measured in the ascites experiment (around 0.51) showed considerable genotype by environment interaction. These results indicate that birds with high genetic potential for growth rate under normal temperature conditions can not fully express their potential growth rate under cold stress conditions due to ascites.

Using DNA marker techniques, Quantitative Trait Loci (QTL) controlling ascites susceptibility can be identified and used in marker assisted selection. Moreover knowledge about QTL for such traits may contribute to a better understanding of the physiological and biological background of ascites. *Chapter 5* aims at confirming QTLs

affecting ascites-related traits. A population consisting of 19 full sib families has been created. In total 14 microsatellite markers were analyzed on all individuals. Twelve ascites-related traits measured on more than 1500 individuals. Significant results were found for the traits body weight at 2 and 5 weeks of age, right ventricular weight, RV:TV, and total mortality. The most significant QTL were located on chromosome 8 for traits body weight at 5 wk of age at 24 cM, right ventricular weight at 19 cM and RV:TV at 15 cM and on chromosome 10 for traits body weight at 2 wk of age at 34 cM and total mortality at 59 cM. This research has resulted in the confirmation two chromosomes which contain genes that are involved in susceptibility of chickens to develop ascites. Once these genes or closely linked markers are identified, marker assisted selection can be use to select birds against this syndrome.

The aim of *Chapter 6* was to evaluate the consequences of alternative selection strategies for body weight and resistance to ascites syndrome using deterministic simulation. Besides the consequences of current selection, i.e. selection for body weight, alternative selection strategies including information on different ascites-related traits measured under normal and/or cold temperature conditions were quantified. Traits investigated in the index as indicator traits for ascites were hematocrit value (HCT) and ratio of RV:TV. Five different schemes were compared based on the selection response for body weight (BW), ascites susceptibility (AS) and the rate of inbreeding. The index information used in the base and four alternative schemes was as follow:

Base) 100% (BW_N)

A-1) 100% ($BW_N + HCT_N$)

A-2) 100% ($BW_N + HCT_N$) + 50% ($RV{:}TV_N$)

A-3) 100% ($BW_N + HCT_N$) + 50% ($BW_C + HCT_C + RV{:}TV_C$)

A-4) 100% ($BW_C + HCT_C$) + 50% ($RV{:}TV_C$)

where the percentage indicates the proportion of birds that are used to measure the corresponding trait, subscript N indicate that traits are measured under normal temperature conditions and subscript C indicate that traits are measured under cold temperature conditions. In all alternative schemes ascites susceptibility kept at zero level.

The results for the base scheme indicated that by ignoring AS in the breeding goal the genetic response for ascites susceptibility is 0.025 unit indicating an increase in the ascites incidence. In this scheme the gain for body weight was 130 gr. Including information of ascites-related traits measured under normal temperature conditions, the gain achieved for body weight is reduced. The gain for body weight was lower (107.5 g) in scheme A-2, where RV:TV was measured on a proportion of the birds kept under

normal temperature conditions. However, when ascites-related traits were measured on a proportion of the birds kept under cold temperature conditions (scheme A-3), the gain achieved for body weight was higher (120.9 g) at the same level of inbreeding. If all the birds were kept under cold temperature conditions (scheme A-4), the selection response for body weight reduced considerable (54.1 g). This can be ascribed to the low genetic correlation between body weight measured under cold and normal temperature conditions (0.49). Therefore, we can conclude that the best scheme for improving body weight while controlling ascites susceptibility is scheme A-3 in which ascites-related traits were measured under cold and normal temperature conditions.

In the general discussion (*Chapter 7*) an aggregate trait describing ascites susceptibility was developed by using statistical and biological approaches. The results suggested that an improved ascites-indicator trait can be constructed by combining information from different traits. The aggregate trait has a higher heritability and therefore gives better scope for improvement of the trait. The optimal way of combining information must be based on integration of biological and statistical approach.

In order to see whether the alternative selection schemes were sensitive to the condition of "no change in ascites susceptibility", two other situations were investigated. In the first situation the economic value of body weight in the breeding goal was set equal to zero. The results indicated that selection to reduce ascites susceptibility can benefit considerably from testing birds under cold temperature conditions. In the second situation, alternative schemes were compared for a situation where the aim is not only to control AS, but also to reduce it. The results indicated that it is possible to reduce AS and to achieve an acceptable level of gain for body weight. The best scheme, i.e. a scheme that has substantial improvement in ascites susceptibility as well as body weight is scheme A-3. This is in agreement with the results obtained in *Chapter 6*.

To quantify the contribution of the QTL information on the genetic progress in body weight as well as resistance to ascites, results of schemes with different fractions of variance explained by the QTL were compared with the base scheme and scheme A-3. The results showed that QTL information can be used very effectively in controlling ascites susceptibility. Even if the QTL explains only 5% of the genetic variance in ascites susceptibility the reduction in gain for body weight is limited as compared to a scheme where selection is for body weight only (base). This illustrates that marker assisted selection can make an important contribution in selection for birds which are resistant to ascites.

Samenvatting

Ascites, ook wel bekend onder de naam waterbuik, is een aan groei gerelateerde aandoening in vleeskuikens. De aandoening komt vooral voor bij snel groeiende vleeskuikens en bij vleeskuikens die worden gehouden op hoogte of bij lage temperaturen. Dit proefschrift geeft schattingen voor genetische parameters van kenmerken die gerelateerd zijn aan ascites. Ook worden verbanden gegeven tussen aan ascites gerelateerde kenmerken en productiekenmerken. Verder is in dit proefschrift onderzocht welke mogelijkheden er zijn om de incidentie van ascites bij vleeskuikens genetisch te beïnvloeden.

Het doel van *hoofdstuk 2* was om erfelijkheidsgraden van aan ascites gerelateerde kenmerken te schatten en te onderzoeken in hoeverre maternaal genetische effecten deze kenmerken beïnvloeden. Verschillende kenmerken gerelateerd aan ascites zijn gemeten aan meer dan 4000 vleeskuikens die werden gehouden onder koude omstandigheden. Verder zijn er ook metingen verricht aan 795 kuikens die werden gehouden bij een normale omgevingstemperatuur. Deze laatste waarnemingen zijn gebruikt om de verdeling van de kenmerken onder normale temperatuursomstandigheden te beschrijven. De resultaten geven aan dat koudestress een duidelijk effect heeft op zowel het gemiddelde als op de spreiding van de hematocriet waarde en RV:TV (ratio van het gewicht van de rechter hartkamer en het totale gewicht van beide hartkamers). Erfelijkheidsgraden voor aan ascites gerelateerde kenmerken gemeten onder koude omstandigheden zijn geschat met behulp van een diermodel met alleen een direct genetisch effect en een diermodel met een direct en een maternaal genetisch effect. Bij gebruik van een model met alleen een direct genetisch effect waren de geschatte erfelijkheidsgraden 0,46 voor hematocriet waarde; 0,42 voor lichaamsgewicht; 0,47 voor gewicht van de rechter hartkamer; 0,46 voor totaal hartkamergewicht; 0,45 voor RV:TV; 0,32 voor totale uitval en 0,18 voor ophoping van vocht in het hartzakje. Maternaal genetische effecten hebben een significant effect op de kenmerken lichaamsgewicht, totale hartgewicht, RV:TV en totale uitval. De erfelijkheidsgraden voor de direct en maternaal genetische effecten waren respectievelijk 0,21 en 0,04 voor lichaamsgewicht; 0,29 en 0,03 voor totaal hartkamer gewicht; 0,28 en 0,02 voor RV:TV en 0,16 en 0,05 voor totale uitval. De resultaten laten zien dat zowel directe alsook maternaal genetische effecten een rol spelen in de ontwikkeling van het ascites syndroom.

In *hoofdstuk 3* zijn genetische en fenotypische correlaties geschat tussen aan ascites gerelateerde kenmerken die gemeten zijn bij een koude en een normale omgevingstemperatuur. Onder koude omstandigheden was de genetische correlatie

tussen lichaamsgewicht en hematocriet waarde -0,23 en tussen lichaamsgewicht en RV:TV -0,27. Bij een normale temperatuur waren deze correlaties echter respectievelijk 0,55 en 0,50. Deze resultaten laten zien dat de genetische correlaties tussen aan ascites gerelateerde kenmerken en lichaamsgewicht afhankelijk zijn van de temperatuur waarbij de dieren zijn gehuisvest. Bij lage temperaturen werden er sterke positieve correlaties (rond 0,8) waargenomen tussen totale uitval, ophoping van vloeistof in het abdomen en RV:TV. Behalve voor lichaamsgewicht waren de correlaties hoog tussen dezelfde kenmerken die gemeten werden bij koude en normale temperaturen, bijvoorbeeld 0,93 voor hematocriet waarde, 0,89 voor het gewicht van de rechter hartkamer, 0,80 voor het totale hartkamergewicht en 0,91 voor RV:TV. Deze resultaten geven aan dat deze kenmerken in beide milieus door voornamelijk dezelfde genen worden beïnvloed. Verder blijkt dat RV:TV gemeten bij normale temperaturen zou kunnen dienen als een goede indicator voor ascites. De lage genetische correlatie tussen lichaamsgewichten gemeten in verschillende milieus (0,29) geeft aan dat de genetische achtergrond van lichaamsgewicht erg gevoelig is voor de omgevingstemperatuur.

Kennis over de genetische relatie tussen aan ascites gerelateerde kenmerken en productiekenmerken zoals karkaseigenschappen en voorefficiëntie is nodig om fokprogramma's te ontwerpen die tot doelstelling hebben zowel productie als de ascites gevoeligheid te verbeteren. Het doel van *hoofdstuk 4* was om deze relaties te schatten. Drie verschillende experimenten zijn opgezet om aan ascites gerelateerde kenmerken (4202 vleeskuikens), voorefficiëntie (2166 vleeskuikens) en karkaseigenschappen (2036 vleeskuikens) te meten. De vleeskuikens in het ascites experiment werden gehouden onder koude omstandigheden terwijl de vleeskuikens in beide andere experimenten werden gehouden onder normale temperatuursomstandigheden. Alle vleeskuikens in de drie verschillende experimenten stammen af van dezelfde groep ouderdieren. Dit maakt het mogelijk om genetische correlaties tussen kenmerken in de verschillende experimenten te schatten. De genetische correlatie tussen lichaamsgewicht gemeten in het karkasexperiment, en bij een normale temperatuur en RV:TV gemeten onder koude omstandigheden was 0,30. Deze geschatte genetische correlatie geeft aan dat selectie op uitsluitend lichaamsgewicht zal leiden tot een toename van de ascitesincidentie. De correlatie geeft echter ook aan dat er voldoende mogelijkheden zijn om gelijktijdig te selecteren op lichaamsgewicht en ascites incidentie. Zwakke, maar positieve, genetische relaties werden gevonden tussen voorefficiëntie en aan ascites gerelateerde kenmerken wat suggereert dat de efficiëntere vleeskuikens iets gevoeliger zijn voor ascites. Deze resultaten geven echter weinig steun aan onze voorveronderstelling dat efficiëntere kuikens gevoeliger zijn voor ascites. De relatief lage correlatie tussen lichaamsgewicht gemeten in het karkasexperiment en lichaamsgewicht gemeten in het ascites experiment (0,51) geeft aan dat er sprake is van aanzienlijke genotype*milieu interactie. De

resultaten laten zien dat vleeskuikens met een groot genetisch potentieel voor groei onder normale temperatuursomstandigheden hun genetisch potentieel voor groei in een koude omgeving niet ten volle kunnen benutten ten gevolge van het optreden van ascites.

Door gebruik te maken van genetische merkers kunnen genen met een effect op ascitesgevoeligheid (QTL) worden geïdentificeerd. Deze informatie kan vervolgens worden gebruikt voor merker ondersteunde selectie. Verder kan het identificeren van dergelijke genen een bijdrage leveren aan de biologische kennis over ascites. Het doel van hoofdstuk 5 is om eerder aangetoonde QTL met een effect op aan ascites gerelateerde kenmerken te bevestigen. Voor dit doel was een populatie met 19 families van volle broers/zussen beschikbaar. In totaal zijn alle individuen getypeerd voor 14 microsatelliet merkers. Verder zijn aan meer dan 1500 vleeskuikens 12 ascites kenmerken gemeten. Significante QTL effecten zijn gevonden voor de kenmerken lichaamsgewicht op 2 en 5 weken, gewicht van de rechter hartkamer, RV:TV en totale uitval. De meest significante QTL werden gelokaliseerd op chromosoom 8 voor de kenmerken lichaamsgewicht op 5 weken leeftijd op 24 cM, gewicht van de rechter hartkamer op 19 cM en RV:TV op 15 cM, en op chromosoom 10 voor de kenmerken lichaamsgewicht op 2 weken op 34 cM en totale uitval op 59 cM. Dit onderzoek heeft geresulteerd in de bevestiging van QTL op twee chromosomen die een effect hebben op de gevoeligheid van vleeskuikens voor ascites. Als deze genen of nauw gekoppelde merkers zijn geïdentificeerd dan kan deze informatie worden gebruikt voor merker ondersteunde selectie tegen ascites gevoeligheid.

Het doel van *hoofdstuk 6* was om de consequenties van alternatieve selectiestrategieën gericht op het verbeteren van het lichaamsgewicht en de gevoeligheid voor ascites te evalueren door gebruik te maken van deterministische simulatie. Naast de consequenties van de huidige selectiestrategie, gericht op lichaamsgewicht (BW), zijn alternatieve strategieën geëvalueerd waarbij gebruik is gemaakt van verschillende aan ascites gerelateerde kenmerken die gemeten zijn in een normale en/of koude omgevingstemperatuur. Kenmerken die in de selectie-index zijn meegenomen als indicator voor ascites gevoeligheid zijn de hematocriet waarde (HCT) en RV:TV. Vijf verschillende situaties zijn vergeleken op basis van de selectierespons voor lichaamsgewicht en ascitesgevoeligheid en de inteelttoename. De indexinformatie die is gebruikt in de basissituatie en de vier alternatieve situaties was:

Basis) 100% (BW_N)

A-1) 100% (BW_N + HCT_N)

A-2) 100% (BW_N + HCT_N) + 50% ($RV{:}TV_N$)

A-3) 100% (BW_N + HCT_N) + 50% (BW_C + HCT_C + $RV{:}TV_C$)

A-4) 100% (BW_C + HCT_C) + 50% ($RV:TV_C$)

Het percentage is het deel van de vleeskuikens waaraan het desbetreffende kenmerk is gemeten, de letter N geeft aan dat het kenmerk is gemeten bij een normale omgevingstemperatuur en de letter C geeft aan dat het kenmerk is gemeten in een koude omgeving. In alle alternatieve schema's is de economische waarde voor ascitesgevoeligheid in het fokdoel zodanig gevarieerd dat de ascitesgevoeligheid niet verandert als gevolg van de selectie. In de basissituatie is de economische waarde voor ascitesgevoeligheid gelijk gesteld aan nul.

Het resultaat van de basis selectiestrategie geeft aan dat wanneer ascitesgevoeligheid in het fokdoel wordt genegeerd de gecorreleerde genetische response voor ascitesgevoeligheid 0,025 eenheden bedraagt. Dit geeft aan dat de ascitesincidentie zal toenemen. In dit scenario is de respons voor lichaamsgewicht 130 gram. Door ascites gerelateerde kenmerken, gemeten onder normale temperatuuromstandigheden, mee te nemen in de index, vermindert de vooruitgang in lichaamsgewicht. De vooruitgang voor lichaamsgewicht was lager (107,5 g) in scenario A-2 waar RV:TV werd gemeten aan een deel van de vleeskuikens die werden gehouden onder normale temperatuuromstandigheden. Wanneer ascites gerelateerde kenmerken werden gemeten aan een gedeelte van de vleeskuikens die werden gehouden onder koude omstandigheden (A-3) dan was, bij vergelijkbaar niveau voor de inteelttoename, de vooruitgang in lichaamsgewicht groter (120,9 g). Wanneer alle kuikens onder koude omstandigheden werden gehouden dan resulteerde dit in een aanzienlijk lagere vooruitgang in lichaamsgewicht (54,1 g). Dit kan worden toegeschreven aan de lage genetische correlatie tussen lichaamsgewicht gemeten bij een lage en een normale omgevingstemperatuur (0,49). We kunnen dus concluderen dat het beste scenario voor de verbetering van de groei, terwijl ascitesgevoeligheid in de hand wordt gehouden, scenario A-3 is waarin aan ascites gerelateerde kenmerken worden gemeten bij lage en normale omgevingstemperaturen.

In de algemene discussie (*hoofdstuk 7*) is een samengesteld kenmerk ontwikkeld dat ascitesgevoeligheid beschrijft op grond van statistische en biologische benaderingen. De resultaten geven aan dat een verbeterde indicator voor ascitesgevoeligheid kan worden gemaakt door informatie van verschillende kenmerken te combineren. Het samengestelde kenmerk heeft een hogere erfelijkheidsgraad wat aangeeft dat het eenvoudiger is om dit kenmerk door middel van selectie te veranderen. De optimale manier om informatie van verschillende kenmerken te combineren moet gebaseerd zijn op zowel de biologische als de statistische benadering. Om te bezien of de alternatieve selectieprogramma's gevoelig zijn voor de restrictie "geen verandering in ascites gevoeligheid" zijn nog twee andere situaties bekeken. In het eerste alternatief is in het

fokdoel de economische waarde voor lichaamsgewicht gelijk gesteld aan nul. De resultaten voor dit alternatief geven aan dat selectie tegen ascitesgevoeligheid aanzienlijk kan profiteren van het testen van vleeskuikens onder koude omstandigheden. In het tweede alternatief was het doel niet langer om de ascitesgevoeligheid niet te wijzigen door selectie, maar om de ascitesgevoeligheid van de vleeskuikens te verminderen. De resultaten geven aan dat het mogelijk is om de ascitesgevoeligheid te verminderen terwijl er toch een acceptabele vooruitgang in lichaamsgewicht gerealiseerd kan worden. Het beste scenario, dat is een scenario met een aanzienlijke verbetering van zowel ascitesgevoeligheid als lichaamsgewicht, wordt bereikt met alternatief A-3. Dit is in overeenstemming met de resultaten in *hoofdstuk 6*.

Om de mogelijke bijdrage van QTL informatie aan de genetische vooruitgang in lichaamsgewicht en ascitesgevoeligheid te kwantificeren zijn fokprogramma's waarin de door de QTL verklaarde variantie varieerde, vergeleken met scenario A-3. De resultaten geven aan dat QTL informatie zeer effectief kan worden gebruikt voor selectie tegen ascites gevoeligheid. Zelfs als de QTL slechts 5% van de genetische variantie in ascitesgevoeligheid verklaren is de reductie in vooruitgang voor lichaamsgewicht gering in vergelijking tot een fokprogramma waar selectie uitsluitend gericht is op lichaamsgewicht. Dit illustreert dat merker ondersteunde selectie een belangrijke bijdrage kan leveren aan de selectie van vleeskuikens die niet gevoelig zijn voor ascites.

Abbreviation Key

AS	Ascites susceptibility
ABDOMEN	Fluid accumulation in the abdomen
BREAST	Color of the breast
BW2	BW at 2 wk of age
BW5	BW at 5 wk of age
BW_{AS-35}	BW at 35 d of age in ascites experiment
BW_{C-48}	BW at 48 d of age in carcass experiment
BW_{FE-23}	BW at 23 d of age in feed efficiency experiment
BW_{FE-48}	BW at 48 d of age in feed efficiency experiment
CP	Carcass percentage
CW	Carcass weight
FE	Feed efficiency
FI	Feed intake between 23 to 48 d
GAIN	Growth between 23 to 48 d
HCO_3	Blood bicarbonate concentration
HCT	Hematocrit value
HEART	Fluid in the heart sac
LIVER	Liver abnormalities
LS	Leg score
MAS	Marker assisted selection
MC	Meat color
MORT-TOT	Total mortality
PCO_2	Partial pressure of carbon dioxide
pH	Blood pH
PO_2	Partial pressure of oxygen
QTL	Quantitative Trait Locus
RFI	Residual feed intake from 23 to 48 d
RV	Right ventricular weight
RV:TV	Ratio of right ventricular weight to total ventricular weight
sO_2	Oxygen saturation in arterial blood
TCO_2	Total carbon dioxide content
TV	Total ventricular weight
% RV	Right ventricular weight as percentage of BW
% TV	Total ventricular weight as percentage of BW

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Abbas Pakdel

30 June 2004, Wageningen, the Netherlands

Completed PhD Education Plan **Graduate School WIAS**

Name	Abbas Pakdel
Group	Animal Breeding and Genetics Group
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Supervisor(s)	Prof. dr. ir. J. A. M. Van Arendonk
Daily advisor	Dr. ir. H. Bovenhuis

		year	cp *
The Basic Package (minimum 2 cp)			
❍	WIAS Course Philosophy of Science and Ethics (mandatory)	2001	1.0
❍	WIAS Introduction course, 20-24 January (mandatory)	2003	1.0
SUBTOTAL			**2.0**
Scientific Exposure (conferences, seminars and presentations, minimum 5 cp)		year	cp
❍	**International Conferences** (minimum 2 cp)		
	52th Annual Meeting of the EAAP in Budapest, Hungary	2001	0.8
	WCGALP in Montpelier, France	2002	1.0
	54th Annual Meeting of the EAAP in Rome, Italy	2003	0.8
	3rd European poultry genetics Symposium in Wageningen, the NL	2003	0.6
	The XXII World's Poultry Congress in Istanbul, Turkey	2004	1.0
❍	**Seminars and workshops**		
	Studies on Stress and Metabolic Adaptation	2001	0.3
	The Veterinary Science Day, Utrecht university	2001	0.2
	Tropical Animal Health and Production, Utrecht University	2001	0.2
	WIAS Science Day	2002	0.2
	Fine-tuning Animal Breeding (A farewell Seminar for Theo. in ID-Lelystad)	2002	0.2
	Breeding for health in livestock, Wageningen	2003	0.1
	WIAS Science Day	2003	0.2
	Shaping the Embryo; Dynamics of early vertebrate development', Wageningen	2003	0.2
	WIAS Science Day	2004	0.2
❍	**Presentations** (minimum 4 original presentations of which at least 1 oral)		
	Oral presentation in EAAP meeting in Budapest, Hungary	2001	0.5
	Poster presentation in the Veterinary Science Day in Utrecht, the NL	2001	0.5
	Oral presentation in WCGALP in Montpelier, France	2002	0.5
	Poster presentation in WIAS Science Day 2002 in Wageningen, the NL	2002	0.5
	Oral presentation in EAAP meeting in Rome, Italy	2003	0.5
	Oral presentation in WIAS Science Day in Wageningen, the NL	2004	0.5
	Poster presentation in the XXII World's Poultry Congress in Istanbul, Turkey	2004	0.5
SUBTOTAL			**9.5**
In-Depth Studies (minimum 4 cp)		year	cp
❍	**Disciplinary and interdisciplinary courses**		
	Molecular Genetic Applications in Animal Sciences	2001	1.0
	Stable Isotopes in Studies of Nutrient Dynamics; Stress and Metabolic Adaptation	2001	0.6
	Computation of Random and Fixed effects in animal breeding with the Pest	2001	1.4
	Managing diversity in living systems	2001	1.0
	Breeding for Disease Resistance: Uniting Genetics and Epidemiology	2002	0.6
	Genetic Algorithms applied to Animal Breeding	2003	0.2
	Incorporation of competitive effects in breeding programs for improved performance and animal well-being	2004	1.0
❍	**Advanced statistics courses**		
	Design of animal experiments	2002	0.6
❍	**Under graduate courses**		
	Statistical methods	2001	3.0
	Advanced statistics for life scientists (ASLS)	2003	3.0
	Biological aspects of animal breeding	2001	2.0
	Animal genetics	2001	3.0
	Genome analysis	2001	2.0
	Breeding programs	2001	3.0
	Breeding value estimation	2001	3.0
SUBTOTAL			**25.4**
Professional Skills support courses (minimum 2 cp)		year	cp
	WIAS Course Techniques for Scientific Writing	2001	0.8
	END NOTE course	2001	0.1
	Advanced English language course	2001	2.0
SUBTOTAL			**2.9**
Research Skills Training (optional)		year	cp
	Preparing own PhD research proposal	2001	4.0
SUBTOTAL			**4.0**
Didactic Skills Training (optional)		year	cp
	Supervising practical of MSC course (Animal Genetics)	2002	1.0
SUBTOTAL			**1.0**
Education and Training Total			**44.8**

* One credit point (cp) equals a study load of approximately 40 hours.

Curriculum Vitae

Abbas Pakdel was born October 7th , 1967 in Isfahan, Iran. He completed his elementary, intermediate and high school in the same city and in Natural Science in 1986. From 1986-1990 Abbas was undergraduate to obtain his Bachelor of Science (BSC) in animal science in Ferdowsi University of Mashhad and he achieved the title of the distinguished student at that university. The next threshold for him was passing the national entrance examination for Master of Science (MSC) and he became graduate student in the field of Animal breeding and Genetic at Tarbiat Modaress University from 1990-1994 where he became first among 25 graduated students. The title of his thesis was "Genetic study of milking speed of Holstein dairy cattle of Iran". After graduating, Abbas joint the teaching staff members at Ilam University of Iran and he worked there for 6 years. During this period, he was responsible for giving courses on subjects related to Animal Breeding, Genetic and Statistic. In addition at the end of 1994 he passed the national entrance examination for PhD in the abroad universities and he obtained a full scholarship for further studies in animal breeding and genetic. He started his PhD, 7 years later. He joined the Animal Breeding and Genetics Group at Wageningen University in September 2000. His research work was on "Genetic analysis of Ascites and related traits in broiler chickens". He finished his PhD project within 4 years with financial support of "Ministry of Science, Research and Technology (MSRT) of Iran". He is also as a member of world poultry science association. Abbas is now working for the MSRT of Iran.

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این اثر را، اگر ارزشی داشته باشد، پیشکش می کنم به :
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و چگونه زندگی کنم

به نام خداوند جان و خرد

کز این برتر اندیشه بر نگذرد

عباس پاکدل