Genetic parameters of foot-pad dermatitis and body weight in purebred broiler lines in 2 contrasting environments

D. N. R. G. Kapell,*[1] W. G. Hill,† A.-M. Neeteson,* J. McAdam,* A. N. M. Koerhuis,* and S. Avendaño*

*Aviagen Ltd., Newbridge, Midlothian EH28 8SZ, UK; and †Institute of Evolutionary Biology, School of Biological Sciences, University of Edinburgh, West Mains Road, Edinburgh EH9 3JT, UK

ABSTRACT The aims of this study were to investigate the genetic background of foot-pad dermatitis (FPD) in 4 different broiler lines reared in 2 contrasting environments (pedigree or sib-test) and to evaluate the performance of simultaneous genetic selection for improved FPD and BW. Data were available for 4 generations from 4 broiler lines, bred with varying intensities of selection for growth. The average BW ranged from 1.7 to 2.4 kg at 5 wk of age. In the pedigree environment, the prevalence of FPD ranged from 14 to 37%, with 3 to 9% being severely affected; in the sib-test environment, these values were correspondingly 45 to 79% and 35 to 70%. Both traits showed re-ranking of the 4 lines in terms of phenotype across the 2 environments, indicating the existence of a genotype-by-environment interaction. In both environments, females showed higher prevalences of FPD than males. In line with their higher prevalence, heritabilities of FPD in the sib-test environment ranged from 0.22 to 0.32, compared with 0.18 to 0.24 for FPD in the pedigree environment (all SE $\leq$0.02). Estimates of the genetic correlation between FPD in the pedigree and in the sib-test environments were high (0.78–0.82), which suggests that selection against FPD in a highly biosecure environment can improve the genetic merit for birds reared under commercial conditions. Estimates of the genetic associations between FPD and BW were small and varied in sign. Predicted responses to selection showed a yearly reduction in average score of −3.4 to −7.5% for FPD in the pedigree environment and −0.5 to −6.6% for FPD in the sib-test environment, while maintaining improvement of BW of 2.6 to 3.2% and 2.6 to 3.8% of the average BW per year, respectively. This research indicates that balanced genetic selection for both BW and FPD in contrasting environments is an effective strategy to reduce the genetic disposition to develop FPD in broilers.

Key words: broiler, heritability, foot-pad dermatitis, genotype-by-environment interaction, welfare

2012 Poultry Science 91:565–574
http://dx.doi.org/10.3382/ps.2011-01934

INTRODUCTION

Foot-pad dermatitis (**FPD**), a form of contact dermatitis, is an ulceration of the skin of the foot in chickens and turkeys (Martland, 1984; Greene et al., 1985; Mayne, 2005). Affected areas show a dark discoloration and an inflammation and necrosis of the skin (Greene et al., 1985). It is associated with a range of welfare issues (e.g., Martland, 1984, 1985; Kestin et al., 1999), and the Council of the European Union determined that monitoring of the levels of contact dermatitis at postmortem inspections should be used as an indicator of poor welfare conditions (Council of the European Union, 2007).

The mean prevalence of FPD in European countries ranged from 11 to 49% in standard commercial systems (Ekstrand et al., 1997; Sanotra et al., 2003; Haslam et al., 2007). Trial studies in the Netherlands and Denmark found prevalences ranging from 19 to 93% (Kjaer et al., 2006; Ask, 2010). The broad range reflects the large differences in management, environment, and genotypes among these studies. Ekstrand et al. (1997) found no significant difference in prevalence of FPD between 2 commercial broiler hybrids in Sweden, but they did find significant effects of environmental factors, such as litter quality, litter depth, and drinker type. A trial study using 4 commercial broiler hybrids found significant differences in prevalence of FPD at slaughter among the crosses, with one strain showing significantly higher scores than the others (Kestin et al., 1999). A survey of commercial broiler farms in Sweden and Denmark found significant differences in prevalence of FPD at slaughter between 2 commercial broiler hybrids, but this was confounded with large

©2012 Poultry Science Association Inc.
Received October 11, 2011.
Accepted December 4, 2011.
[1]Corresponding author: dkapell@aviagen.com
Open access under CC BY-NC-ND license.

differences in housing and BW between the countries (Sanotra et al., 2003).

Estimates of heritabilities for FPD and genetic correlations with BW were first reported by Kjaer et al. (2006). The authors evaluated FPD in a dual-purpose strain and a commercial broiler hybrid. Foot-pad dermatitis was only present in the latter (17% at 4 wk of age and 44% at 6 wk of age). The commercial hybrids were produced from parent stock in a fully pedigreed system and a heritability of 0.31 ± 0.12 was estimated, with a favorable genetic correlation with BW of −0.08 ± 0.26. Ask (2010) reported prevalences and heritabilities of FPD in 8 female and 2 male purebred commercial lines. The total prevalence (57–93%) and the probability of being more severely affected (45–76%) differed significantly among the 10 lines. The estimates of heritabilities, estimated in the 2 male lines at 0.21 ± 0.03 and 0.08 ± 0.02, were lower than those found by Kjaer et al. (2006), which may be due to the more elaborate scoring system and the higher prevalence in the latter study. The favorable genetic correlations with BW (−0.51 ± 0.12 and 0.08 ± 0.19) showed high standard errors but may indicate that the relationship between FPD and BW is line-dependent (Ask, 2010).

Differences in the prevalence and estimated heritabilities of FPD have been found between strains within the same environment (Kestin et al., 1999; Kjaer et al., 2006; Ask, 2010). However, none estimated genetic parameters for broilers sharing a common genetic background but reared in different environments. The effect of an environment on the phenotype can vary depending on the genotype of an individual (genotype-by-environment interaction; **G×E**; Kruuk et al., 2008) and responds to natural or artificial selection (Scheiner, 1993). Long-term selection on traits in a specific environment may be accompanied by an increased environmental sensitivity (van der Waaij, 2004). Genotype-by-environment interactions have been found for a range of performance traits in broilers (Ye et al., 2006; Long et al., 2008), and similar interactions may exist for FPD.

The main aim of this study was to estimate heritabilities for FPD and genetic correlations with BW in 4 purebred broiler lines, reared in 2 contrasting environments, and to examine the presence of a G×E interaction. Furthermore, the study aims to investigate the effectiveness of combined selection for BW and FPD and the potential to increase the genetic merit for a trait across environments in the presence of a G×E interaction, through the examination of the recent genetic trends for both traits.

MATERIALS AND METHODS

Birds, Housing, and Management

The data for this study originate from the ongoing recording of dermal traits within the Aviagen Ltd. (Newbridge, UK) breeding program. For this study, data collected between October 2007 and September 2010, comprising 4 generations, were used. In total, records for 910,737 birds across 4 purebred commercial broiler lines (A to D) were available (Table 1). The difference in selection emphasis has led to large differences in BW between the lines, with line A having the highest average BW at 2.4 kg, lines B and C having intermediate weights at 2.0 kg, and line D having the lowest BW at 1.7 kg at 5 wk of age. An additional generation of pedigree was added for the estimation of genetic parameters. The birds were housed on farms in southern Scotland in 2 different environments: (1) a high bio-secure environment referred to as pedigree (**P**) environment where breeding-program selection candidates are recorded and selected, and (2) a non-bio-secure environment referred to as sib-test (**S**) environment aimed to resemble broader commercial conditions and where full-sibs and half-sibs of selection candidates are placed.

Table 2 provides a detailed overview of the environmental parameters for the 2 environments. Water and a high-quality diet were provided ad libitum throughout the growing period. Litter was supplied in the form of a layer of wood shavings, which was topped up as required. From April 2010 onwards, the amount of wood shavings per top up was reduced to allow for the further expression of the trait. In the P environment, the litter was removed completely at the end of each cycle, after which pens were disinfected and filled with fresh wood shavings. In the S environment, half of the litter was retained at the end of each cycle, mechanically conditioned, and subsequently topped up with fresh wood shavings.

The average stocking density in the P environment between October 2007 and September 2010 ranged from 29 kg of bird weight per m^2 in line C to 32 kg of bird weight per m^2 in line D. In the same period, the

Table 1. Records for birds across 4 purebred commercial broiler lines (A to D)[1]

Line	Phenotype (P)	Phenotype (S)	Pedigree	c^2	Batch
A	132,813	15,339	193,081	4,938	3,594
B	217,943	40,371	327,192	5,393	3,236
C	248,096	45,942	384,668	6,372	3,159
D	181,783	28,450	262,034	4,216	1,988

[1]Number of birds with phenotypic information (Phenotypes) in the pedigree (P) and sib-test (S) environments, number of birds in the pedigree (Pedigree), number of levels for the permanent environmental effect of the dam (c^2), and number of levels for the fixed effect accounting for the interaction between the hatchweek, pen, contributing mating group, and sex of the individual (Batch).

Table 2. Description of the environmental parameters of the pedigree and sib-test environment

Parameter	Pedigree environment	Sib-test environment
Feed d 0–10	Starter (240 g of CP/kg; 12.6 MJ of ME/kg)	Starter (195 g of CP/kg; 12.0 MJ of ME/kg)
Feed d 11–25	Grower (210 g of CP/kg; 13.3 MJ of ME/kg)	Grower (170 g of CP/kg; 12.7 MJ of ME/kg)
Feed d 25–final weighing	Finisher (205 g of CP/kg; 13.5 MJ of ME/kg)	Grower (170 g of CP/kg; 12.7 MJ of ME/kg)
Stocking density	29 to 32 kg of bird weight per m^2	26 to 27 kg of bird weight per m^2
Temperature	Gradually reduced from 29 to 20°C	Gradually reduced from 35 to 24°C
Photoperiod d 0–7	23L:1D	23L:1D
Photoperiod d 8–final weighing	20L:4D (18L:6D from October 2009)	20L:4D (18L:6D from September 2010)
Light intensity d 0–7	40 lx	40 lx
Light intensity d 8–final weighing	Gradually reduced to 10 to 20 lx	Gradually reduced to 10 to 20 lx

average stocking density in the S environment ranged from 26 kg of bird weight per m^2 in line D to 27 kg of bird weight per m^2 in line B, in accordance with the maximum stocking density of 33 kg per m^2 as laid down in the EU Council Directive 2007/43/EC (Council of the European Union, 2007). All birds hatched in the same hatchery, where they were sexed and tagged with a barcoded wing band. Birds were subsequently moved to the growing farms, where they were distributed over pens according to line.

Assessment of Traits

Birds were individually weighed and visually assessed for dermatitis by a trained team at 5 wk of age (line D in the P environment at 6 wk of age starting in October 2008). The team of scorers was regularly assessed for consistency using correlations between and within selectors and was the same across the whole data set. The trait FPD was analyzed using a scale with 3 levels according to absence or severity of the lesion (Figure 1). These scores ranged from no lesions (score 0), over mild lesions (up to 50% of the plantar surface affected—score 50), to severe lesions (more than 50% of the plantar surface affected—score 100). A stringent approach was used, whereby both feet were evaluated and the higher-scoring foot determined the final score. Following the start of recording of FPD in 2006, active selection against this trait commenced in 2008. Hereby, information from birds in the S environment was used for the evaluation of selection candidates in the P environment.

Statistical Analyses

The trait FPD was recorded on a multinomial scale, and differences in prevalence between lines, as well as between sexes within line, were tested using the Wilcoxon nonparametric rank sum test, as implemented in the software R (R Development Core Team, 2010).

Both BW and FPD were treated as separate traits depending on the environment, resulting in a total of 4 traits: BW-P, BW-S, FPD-P, and FPD-S. For the genetic analysis, the following multivariate animal model including 4 traits was used to estimate genetic parameters per line:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Za} + \mathbf{Wc} + \mathbf{e},$$

where **y** is the vector of observations of the traits; **b** the vector of the fixed effect accounting for the interaction between the hatchweek, pen, contributing mating group, and sex of the individual; **a** the vector of additive genetic effects; **c** the vector of permanent environmental effects of the dam; and **e** the vector of residuals. In the equation, **X**, **Z**, and **W** are incidence matrices relating the vectors **b**, **a**, and **c** with **y**. The assumed (co)variance structure was:

$$\mathrm{V}\begin{bmatrix}\mathbf{a}\\\mathbf{c}\\\mathbf{e}\end{bmatrix} = \begin{bmatrix}\mathbf{A}\otimes\mathbf{G} & \mathbf{0} & \mathbf{0}\\ \mathbf{0} & \mathbf{I}\otimes\mathbf{C} & \mathbf{0}\\ \mathbf{0} & \mathbf{0} & \mathbf{I}\otimes\mathbf{R}\end{bmatrix},$$

where **A** and **I** are the additive genetic relationship matrix and identity matrix, respectively. The matrices **G**, **C**, and **R** represent the variance and covariance matrices of additive genetic effects, permanent environmental effects of the dam, and residual effects, respectively. Numbers of levels per effect for the bird, permanent environmental of the dam, and batch are given in Table 1. All variance component analyses were performed by restricted maximum likelihood using the software VCE (Groeneveld et al., 2008). The estimates for variance components obtained with the software VCE were subsequently used to estimate breeding values and predict long-term genetic trends using the software PEST (Groeneveld, 2006).

RESULTS

Phenotypic Trend and Descriptive Statistics

Recording of FPD started in 2006, coinciding with the publication of the first study to present genetic parameters for this trait (Kjaer et al., 2006). Figure 2 shows the frequency of the different scores since the start of recording in the P environment (top row) and in the S environment (bottom row). In the P environment, the proportion of birds without lesions decreased between 2006 and 2010. At the same time, the proportion of birds that showed mild lesions increased at first, but then stabilized, to be replaced by an increased pro-

Figure 1. Illustrations of the scores for foot-pad dermatitis. The scores range from (a) no lesions (score 0), over (b) mild lesions (up to 50% of the plantar surface affected—score 50), to (c) severe lesions (more than 50% of the plantar surface affected—score 100).

portion of birds with severe lesions. In the S environment, no clear phenotypic trend was visible. The birds showed more variation between measuring points and a higher proportion of the 2 extreme phenotypes (no lesions or severe lesions). The proportion of birds showing mild lesions was generally below 25%.

The number of observations, means of BW, and prevalence of FPD, per sex and in total, in the 4 lines and the 2 environments are given in Table 3. The values in this table describe the data used for the genetic analysis but may not be representative of the average prevalence at a specific point in time. Line A showed the highest BW in both environments (2,373 and 1,804 g, respectively, for P and S) compared with the other lines, whereas line D showed the lowest BW (1,740 and 1,416 g, respectively, for P and S; Figure 3a). The ratio of BW-S to BW-P was fairly consistent across lines at on average 3 quarters, though in the S environment, lines B and C showed a re-ranking with a higher BW in line C.

Line D was the least affected by FPD across both environments (Figure 3b). Whereas line A had the highest proportion of affected birds in the P environment, lines B and C showed higher proportions of affected birds in the S environment, mainly due to the high prevalence of FPD among females in these lines. Differences between the sexes were more pronounced in the P environment, where the total prevalence was between 1.7 and 2.3 times higher in females than in males compared with between 1.0 and 1.3 times in the S environment. In the P environment, severe prevalence affected less than 10% of the birds across all lines; it accounted for on average 25% of the total prevalence. In the S environment, 35 to 70% of the birds showed severe FPD, which accounted for on average 85% of the total prevalence.

Heritabilities

Table 4 shows the estimates of heritabilities, genetic correlations, and phenotypic correlations for the 4 traits and lines. Estimates of heritabilities for BW-P ranged from 0.32 to 0.40. Heritabilities for the same

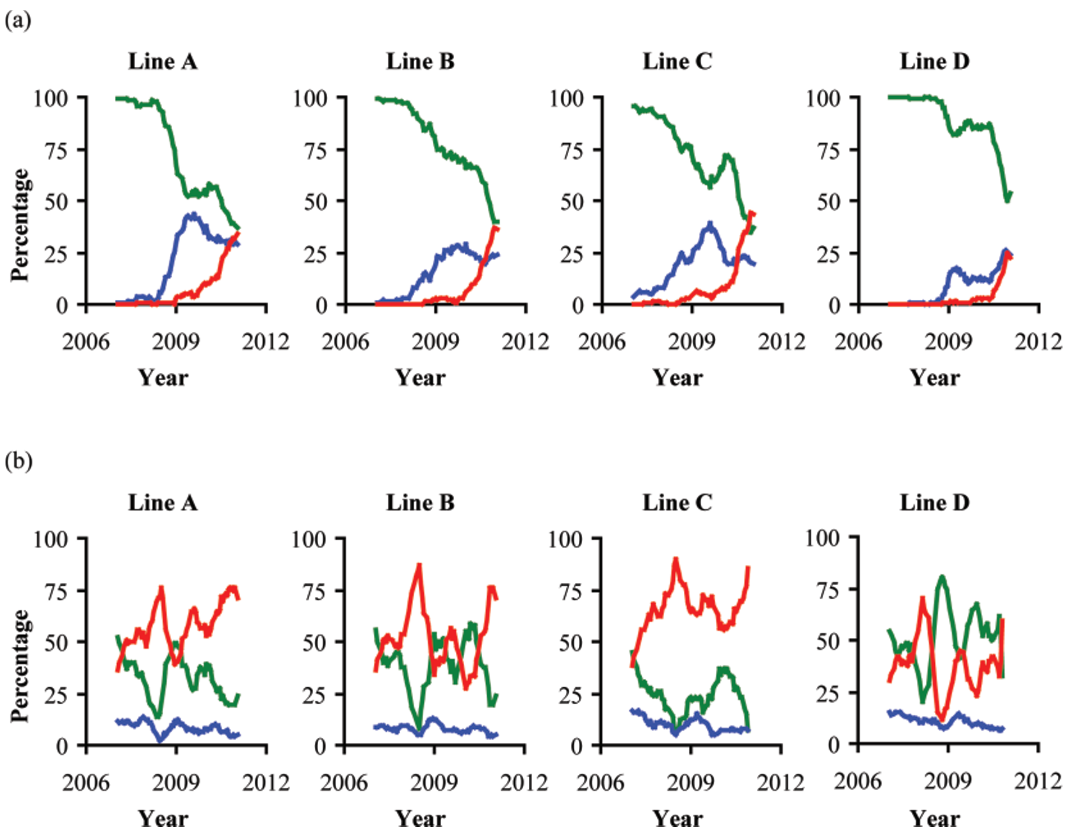

Figure 2. Distribution of the scores: 0 (green line), 50 (blue line), and 100 (red line) for foot-pad dermatitis in (a) the pedigree and (b) the sib-test environments from 2006 until 2010. The data are presented as the 6-mo moving average.

Table 3. Mean values for BW and prevalence of foot-pad dermatitis (FPD), per sex and in total, in the pedigree (P) and sib-test (S) environments for October 2007 until September 2010[1,2]

		P			S		
			BW (g)	FPD		BW (g)	FPD
Line	Sex	n	Mean (SD)	P_{tot} (P_{sev})[3,4]	n	Mean (SD)	P_{tot} (P_{sev})[3,4]
A	Male	65,464	2,521 (231)	0.279 (0.036)	7,761	1,857 (373)	0.625 (0.535)
	Female	67,349	2,230 (216)	0.461 (0.146)	7,578	1,750 (356)	0.650 (0.548)
	Total	132,813	2,373 (267)	0.371 (0.092)	15,339	1,804 (369)	0.637 (0.542)
B	Male	106,079	2,200 (182)	0.159 (0.040)	18,669	1,585 (299)	0.598 (0.516)
	Female	111,864	1,888 (167)	0.358 (0.091)	21,702	1,448 (289)	0.702 (0.616)
	Total	217,943	2,040 (234)	0.261 (0.066)	40,371	1,511 (302)	0.654 (0.569)
C	Male	122,055	2,100 (190)	0.234 (0.069)	22,062	1,658 (299)	0.770 (0.691)
	Female	126,041	1,807 (174)	0.425 (0.110)	23,880	1,499 (279)	0.813 (0.715)
	Total	248,096	1,951 (234)	0.331 (0.090)	45,942	1,576 (300)	0.792 (0.703)
D[5]	Male	87,644	1,869 (183)	0.100 (0.026)	13,724	1,481 (293)	0.394 (0.295)
	Female	94,139	1,621 (153)	0.179 (0.037)	14,726	1,355 (272)	0.507 (0.401)
	Total	181,783	1,740 (209)	0.141 (0.032)	28,450	1,416 (289)	0.453 (0.350)

[1]All differences in BW and FPD between lines (in total and per sex) and within lines between sexes are significantly different at $P < 0.001$, except FPD-S between males and females in line A ($P < 0.05$).

[2]In the P environment, all birds were scored for FPD. In the S environment, the proportion of birds scored for FPD exceeded 98%.

[3]P_{tot} = total prevalence (scores 1 and 2); P_{sev} = severe prevalence (score 2).

[4]The values in this table describe the data used for the genetic analysis, but may not be representative of the average prevalence at a specific point in time.

[5]Measurements for BW-P from October 2008 onwards corrected to 5-wk weight.

trait in the S environment were slightly lower in lines A, B, and D. In contrast, line C showed a higher heritability (0.32 vs. 0.36 for P and S, respectively). The heritabilities for FPD were low to moderate, ranging from 0.18 to 0.32. No difference in heritability between the 2 environments was found for line A, but lines B, C, and D showed increased heritabilities in the S environment, ranging from 0.22 to 0.32. Overall, despite minor differences, the estimated heritabilities for both traits showed a remarkable concordance across all lines.

A combined linear-threshold model was performed for line B. In this analysis, a Bayesian approach was used, with Gibbs sampling and MCMC methods using flat priors, as implemented in the software of THRGIBBS1F90 (Misztal et al., 2002), and heritabilities were estimated at 0.44 for FPD-P and 0.45 for FPD-S. Conversion of the heritabilities obtained with the software VCE to the underlying liability scale resulted in heritabilities of 0.37 when combining scores 50 and 100 and 0.76 when combining scores 0 and 50 for FPD-P; for FPD-S, it resulted in heritabilities of 0.42 and 0.40, respectively.

Genetic Correlations

The estimates of the genetic correlation between FPD-P and FPD-S were similar for all 4 lines, ranging from 0.78 to 0.82. The genetic correlation between BW-P and BW-S showed more variation, ranging from 0.46 to 0.69. Within the P environment, the estimated genetic correlations between BW and FPD were typically negative (and thus favorable), but they tended to be positive in the S environment. Across environments, the estimated genetic correlations between BW and FPD were generally small and were on either side of zero.

Long-Term Genetic Predictions

Figure 4 shows the predicted genetic trend since the start of recording in the P environment (top row) and in the S environment (bottom row). It should be noted that both BW and FPD, the only traits used in this prediction, are part of a much larger index for selection in the Aviagen Ltd. program, which includes a broad range of traits, including growth, lifetime performance, reproduction, livability, and health. These traits, however, were not considered for the prediction of the genetic trends, because this would be outside the scope of this research. Line A showed a steady improvement of the predicted breeding value in the P environment, followed in more recent years by lines B, C, and D. In the S environment, all lines showed a tendency toward more favorable breeding values. Since the start of recording FPD, the predicted yearly genetic trend showed a reduction of −0.5 to −7.5% of the average FPD score (Table 5). The predicted genetic trend for BW increased steadily at 2.6 to 3.8% of the average BW per year in both environments.

DISCUSSION

Foot-pad dermatitis is associated with a range of welfare issues (Martland, 1984, 1985; Kestin et al., 1999) and high prevalences may be indicators for poor welfare conditions (Haslam et al., 2007). Studies have shown that a genetic background for FPD in broilers exists (Kjaer et al., 2006; Ask, 2010); therefore, genetic selec-

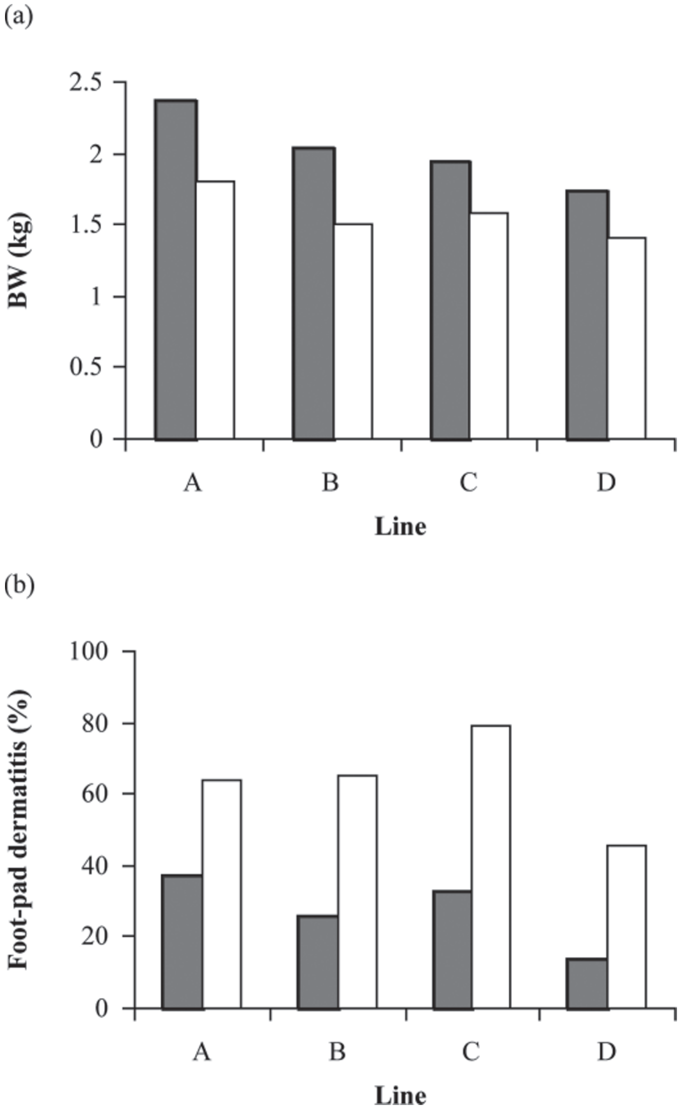

Figure 3. Comparison of (a) the mean BW and (b) the total prevalence of foot-pad dermatitis in the pedigree (gray bar) or the sib-test (white bar) environments.

tion against the disposition to develop FPD may contribute to the reduction of the prevalence. However, purebred commercial broilers are selected in a different environment from the one in which commercial production takes place. An important aspect to consider is that a G × E interaction may develop as a result of long-term selection on traits in a specific environment (van der Waaij, 2004). In this study, we have not only analyzed the genetic background of FPD, but we have also shown that continuous improvement of a live performance (BW) and a welfare-related (FPD) trait can be achieved simultaneously across contrasting environments. We have compared the heritabilities of FPD, as well as the genetic correlations with their corresponding BW in each environment, to show how these traits differ depending on the environment in which the bird is reared and how selection in a highly biosecure environment can lead to improvement of the genetic merit under commercial conditions.

Table 4. Estimates of heritabilities (bold, diagonal), genetic correlations (above diagonal), and phenotypic correlations (below diagonal) for BW and foot-pad dermatitis (FPD) in the pedigree (P) and the sib-test (S) environments with SE in parentheses below

	Line A				Line B				Line C				Line D			
Trait	BWT-P	BWT-S	FPD-P	FPD-S	BWT-P	BWT-S	FPD-P	FPD-S	BWT-P	BWT-S	FPD-P	FPD-S	BWT-P	BWT-S	FPD-P	FPD-S
BWT-P	**0.36**	0.46	−0.14	−0.07	**0.39**	0.54	−0.03	0.03	**0.32**	0.56	0.05	0.03	**0.40**	0.69	0.00	−0.03
SE	**(0.010)**	(0.04)	(0.02)	(0.03)	**(0.007)**	(0.03)	(0.01)	(0.02)	**(0.006)**	(0.03)	(0.01)	(0.01)	**(0.019)**	(0.04)	(0.03)	(0.02)
BWT-S	0.18	**0.32**	0.08	0.19	0.23	**0.34**	0.02	0.07	0.21	**0.36**	0.08	−0.02	0.27	**0.32**	0.11	0.04
SE		**(0.015)**	(0.03)	(0.03)		**(0.013)**	(0.04)	(0.03)		**(0.006)**	(0.02)	(0.01)		**(0.016)**	(0.04)	(0.05)
FPD-P	−0.05	0.02	**0.24**	0.82	−0.02	0.01	**0.20**	0.78	0.01	0.02	**0.18**	0.80	−0.01	0.02	**0.19**	0.82
SE			**(0.009)**	(0.03)			**(0.008)**	(0.03)			**(0.006)**	(0.02)			**(0.010)**	(0.03)
FPD-S	−0.03	0.05	0.20	**0.24**	0.01	0.07	0.19	**0.25**	0.01	0.05	0.17	**0.22**	−0.01	0.02	0.21	**0.32**
SE				**(0.016)**				**(0.010)**				**(0.006)**				**(0.016)**

Table 5. Predicted yearly genetic trend for BW and foot-pad dermatitis (FPD) in the pedigree (P) and the sib-test (S) environments for August 2006 until September 2010

	P (%)		S (%)	
Line	BW	FPD	BW	FPD
A	+3.2	−4.1	+2.6	−1.3
B	+2.6	−7.5	+3.0	−1.6
C	+2.6	−3.4	+3.8	−0.5
D	+3.2	−7.1	+2.9	−6.6

FPD

The total prevalence of FPD across the 4 lines and 2 environments (12–79%) was within the range previously found in standard rearing systems in the UK and other European countries (11–93%; Sanotra et al., 2003; Kjaer et al., 2006; Pagazaurtundua and Warriss, 2006; Haslam et al., 2007; Ask, 2010). The large differences in prevalence between these studies may in part be due to the scoring systems that were used—the present study used a 3-point scale; other studies recorded up to 9 different categories (e.g., Kjaer et al., 2006; Pagazaurtundua and Warriss, 2006; Haslam et al., 2007; Ask, 2010). The prevalence of FPD increases steadily with age up to 7 wk, after which it remains relatively steady or declines (Martland, 1985; Bilgili et al., 2006; Kjaer et al., 2006)—this is supported by findings in the P environment. At 5 wk of age, the total prevalence of FPD-P in line D was less than 1%. The change in age of recording from 5 to 6 wk in 2008 led to an increased proportion of mildly affected birds, which is also seen in Figure 2 in the decrease of scores 0 and the increase of scores 50 from this point onwards. The recent increase in severe FPD in the P environment coincides with a change in litter management policy from April 2010, whereby litter was topped up with fewer shavings on a routine basis, leading to a reduction in litter quality through an increase in moisture, thereby increasing the prevalence and the variation that can be used in selection.

Heritability estimates of FPD in this study (0.18–0.32) are within the range of the heritabilities found in other studies in purebred (0.08 and 0.21 in Ask, 2010) and crossbred birds (0.31 in Kjaer et al., 2006). However, neither of these studies included a permanent environmental effect of the dam in their analysis, which may have lead to an inflation of the heritabilities, as illustrated by other analyses in which models with and without maternal effects were compared (e.g., Koerhuis and Thompson, 1997; Clément et al., 2001; Grosso et al., 2010). In our study, the permanent environmental effect of the dam accounted for 3.0 to 4.9% of the phenotypic variance for BW and 1.5 to 2.8% for FPD across all lines. To evaluate the effect of not fitting this effect, line B was analyzed additionally with a model including only the random additive genetic effect of the bird and the fixed effect of batch. This resulted in higher heritability estimates at 0.29 and 0.33 for FPD-P and FPD-S, respectively, and at 0.57 and 0.55 for BW-P and BW-S, respectively.

The prevalence of FPD is scored on a 3-point scale. Although more categories would allow increased discrimination, those used in this study (no FPD, less than 50% covered, or more than 50% covered) are easy to distinguish and score repeatably. Heritabilities on the observed scale depend on the choice of categories and their frequencies and are lower than on a continuous underlying scale (e.g., Dempster and Lerner, 1950; Gianola, 1982). In our restricted maximum likelihood approach, distances between the categories are assumed to be equal, so other methods, such as a threshold model, may have higher expected heritabilities (e.g., Giano-

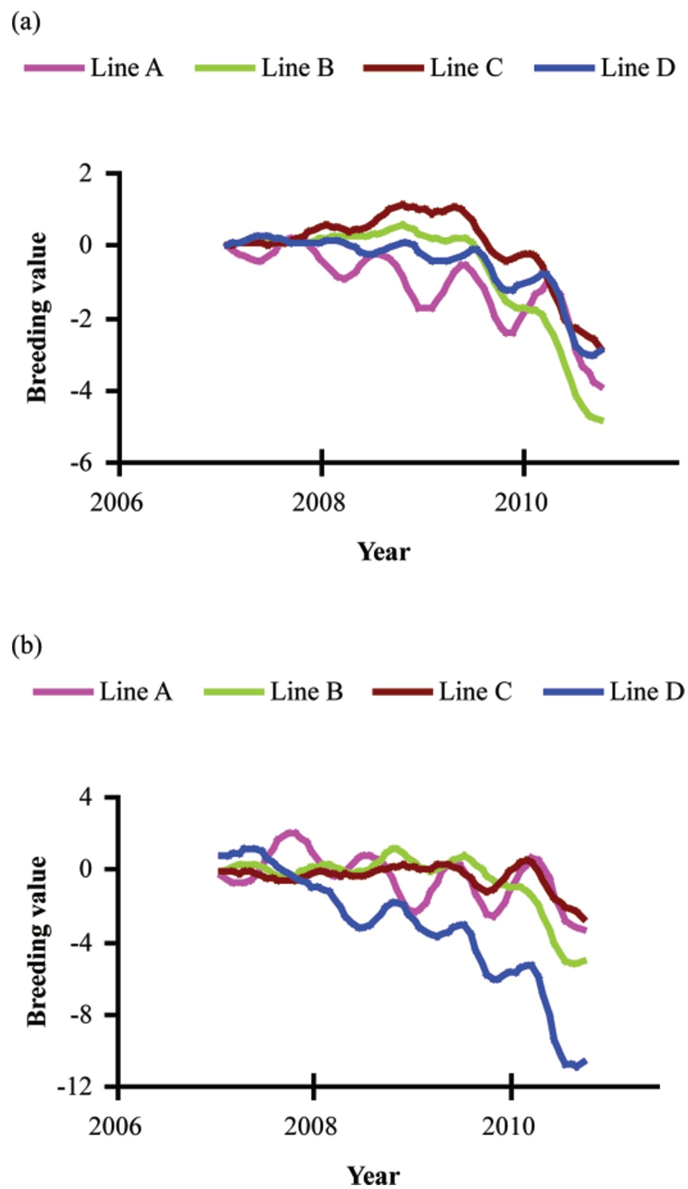

Figure 4. Genetic predictions for foot-pad dermatitis in (a) the pedigree and (b) the sib-test environments. The data are presented as the 6-mo moving average. Note the difference in scale of the y-axis between the 2 traits. Breeding values for foot-pad dermatitis were predicted on a scale of 0 to 100.

la, 1982; Sorensen et al., 1995). Indeed, in the analysis of line B with a threshold model, higher heritability estimates were obtained. For practical implementation in a routine breeding program, however, it is appealing to use genetic parameter and breeding value estimates on the observed scale.

Ask (2010) attributed the significant difference in heritability between the 2 lines for which they estimated genetic parameters in part to a much higher prevalence in one line compared with the other. This probably played a part in the current study as well when comparing lines A, B, and D within environment. An exception was line C, which had a high prevalence of FPD in both environments but the lowest heritabilities of all lines.

Historically, the prevalence of FPD in the pedigree lines has been very low. However, to enable effective selection at the breeding-program level, FPD needs to be expressed sufficiently in selection candidates through a higher prevalence and variation. For this reason, both the P and the S environments have been adjusted to attain, and subsequently maintain, a higher level of expression of FPD. Consequently, this has resulted in an obvious contrast between the genetic prediction and the actual phenotypic trend. The predicted genetic trend for FPD in both environments, resulting from continuous selection of candidates with an average prevalence below the average population prevalence, shows that selection against FPD can be expected to be successful, while the phenotypic trend has remained stable or increased. The achievement of a trend that reduces the genetic propensity of commercial broilers to develop FPD in a wide range of environments is what will ultimately benefit the industry and the welfare of the animals as a whole.

Effect of the Interaction Between Genotype and Environment on FPD and BW

The prevalence of FPD differed markedly between the 2 environments. Dawkins et al. (2004) concluded that not only stocking density, but also a broad range of housing conditions, including factors like temperature, humidity, and litter moisture, play a major role in leg health and overall welfare of broilers. The 2 environments in this study differed substantially in feed, litter management, and temperature, which together are likely the main factors that contributed to the differences in prevalence. A recent study into the effect of, among others, diet on the prevalence of FPD found a significantly higher prevalence when broilers were fed a low-energy content diet. This may have been due to the poorer litter quality on this diet, as a result of increased nitrogen excretion (Zuowei et al., 2011).

Long-term selection on production traits in a specific environment will lead to increased productivity under those circumstances. However, in the presence of a G × E interaction this may cause problems when animals are placed in poorer environments (van der Waaij, 2004). This has been shown in selection experiments; for example, in mice (Rauw et al., 2003) and in broilers (Deeb and Cahaner, 2002; Deeb et al., 2002). Using deterministic predictions, Mulder and Bijma (2005) concluded that in dairy cattle breeding schemes, recording relatives of selection candidates in the production environment minimizes the loss in gain due to a G×E interaction when the genetic correlation between environments is below 0.8. There is substantial G×E interaction for BW in the present study, as the genetic correlation between BW-P and BW-S is much less than 1 (0.46–0.69). Although in broiler breeding it is not logistically feasible to record relatives of selection candidates directly in the commercial conditions, the use of farms replicating a range of commercial-like conditions (e.g., the S environment) to rear full-sibs and half-sibs of selection candidates is an appealing strategy to address the effects of a G×E interaction.

Contrary to what was observed for BW, the high genetic correlations between FPD-P and FPD-S indicate that the effects of a G×E interaction would be much less pronounced than for BW. Therefore, a reduction of the disposition to develop FPD under commercial conditions can be achieved through direct selection in the P environment and through a correlated response from recording in the S environment.

Correlations Between FPD and BW

Genetic correlations between BW and FPD were either favorable or, if unfavorable, small, as was found by Ask (2010) and Kjaer et al. (2006). This indicates that, from a genetic stand point, there is no evidence that selection for BW has led and would lead to appreciable increases in the disposition to develop FPD. Moreover, balanced selection, including both traits in a selection index, is an effective way of achieving continuous improvement in both traits. Indeed, the genetic trend predicted that in both environments, genetic selection for FPD in recent years improved the average FPD score steadily at −3.4 to −7.5% in the P environment and −0.5 to −6.6% in the S environment, while at the same time maintaining progress in BW. The yearly genetic progress in BW at 2.6 to 3.8% is in line with the progress in meat production that has been reported in earlier publications; for example, 2.4% for BW (McKay et al., 2000; Hill, 2010) and 2 to 3% for the overall efficiency of meat production (McKay, 2009).

Differences Between Sexes

The effect of sex on FPD is unclear, with studies finding a higher prevalence of FPD in males (e.g., Greene et al., 1985; Nagaraj et al., 2007a; Zuowei et al., 2011), a higher prevalence in females (e.g., Kjaer et al., 2006; Nagaraj et al., 2007b), or no difference between the sexes (Martland, 1985). In our study, females showed consistently higher prevalences of FPD than males in both the P and the S environments. A separate analysis of BW-P and FPD-P, whereby FPD-P was split into a male and a female trait depending on the sex of the bird, showed a high genetic correlation between FPD in males and females (ranging from 0.86 ± 0.02 to 0.93 ± 0.01), indicating that the difference in prevalence between the sexes is mainly due to a differential of the sexes to a common environment. Studies in which females showed higher prevalences of FPD suggested that a lower content of collagen and protein in the skin may predispose females to skin injuries (Nagaraj et al., 2007b). Although the greater prevalence of FPD in females held across both P and S environments, both the absolute and the relative difference between sexes was less in the S environment. Similarly, the difference in BW between the sexes decreased in the S environment—on average, the ratio of BW-S to BW-P was ~5% lower in males than in females, leading to a decreased difference between the sexes in the S environment. Studies looking into the interaction between heat stress and performance traits in males and females found significant interactions between the effect of the environment and the sex on several performance traits, indicating a higher sensitivity of males to their environment than females (e.g., Deeb and Cahaner, 2002; N'Dri et al., 2007). For example, BW, weight gain, and feed consumption were higher in males under normal temperatures, but under high temperatures, males showed a higher decrease in these traits than females, leading to similar performance levels for both sexes in the suboptimal environment (Deeb and Cahaner, 2002).

To conclude, this study has shown that genetic selection against FPD can be incorporated effectively in a breeding goal that focuses simultaneously on welfare traits and production traits. The heritabilities for FPD were of moderate magnitude and the genetic correlations with BW were generally low. The genetic predictions for BW and FPD show that simultaneous improvement of the genetic merit for both traits is possible. The estimates of genetic parameters varied considerably, depending on the line and the environment, and inclusion of selection against FPD should be considered for each line individually. However, the genetic correlation between FPD measured in different environments was high, which suggests that selection against FPD in a highly biosecure environment can reduce the prevalence of FPD under commercial conditions.

REFERENCES

Ask, B. 2010. Genetic variation of contact dermatitis in broilers. Poult. Sci. 89:866–875.

Bilgili, S. F., M. A. Alley, J. B. Hess, and M. Nagaraj. 2006. Influence of age and sex on footpad quality and yield in broiler chickens reared on low and high density diets. J. Appl. Poult. Res. 15:433–441.

Clément, V., B. Bibé, E. Verrier, J. M. Elsen, E. Manfredi, J. Bouix, and E. Hanocq. 2001. Simulation analysis to test the influence of model adequacy and data structure on the estimation of genetic parameters for traits with direct and maternal effects. Genet. Sel. Evol. 33:369–395.

Council of the European Union. 2007. Council Directive 2007/43/EC of June 28, 2007, laying down minimum rules for the protection of chickens kept for meat production. L182:19–28.

Dawkins, M. S., C. Donnelly, and T. Jones. 2004. Chicken welfare is influenced more by housing conditions than by stocking density. Nature 427:342–344.

Deeb, N., and A. Cahaner. 2002. Genotype-by-environment interaction with broiler genotypes differing in growth rate. 3. Growth rate and water consumption of broiler progeny from weight-selected versus nonselected parents under normal and high ambient temperatures. Poult. Sci. 81:293–301.

Deeb, N., A. Shlosberg, and A. Cahaner. 2002. Genotype-by-environment interaction with broiler genotypes differing in growth rate. 4. Association between responses to heat stress and to cold-induced ascites. Poult. Sci. 81:1454–1462.

Dempster, E. R., and I. M. Lerner. 1950. Heritability of threshold characters. Genetics 35:212–236.

Ekstrand, C., B. Algers, and J. Svedberg. 1997. Rearing conditions and foot-pad dermatitis in Swedish broiler chickens. Prev. Vet. Med. 31:167–174.

Gianola, D. 1982. Theory and analysis of threshold characters. J. Anim. Sci. 54:1079–1096.

Greene, J. A., R. M. McCracken, and R. T. Evans. 1985. A contact dermatitis of broilers—Clinical and pathological findings. Avian Pathol. 14:23–38.

Groeneveld, E. 2006. PEST User's Manual. Inst. Farm Animal Gen., Neustadt, Germany.

Groeneveld, E., M. Kovač, and N. Mielenz. 2008. VCE User's Guide and Reference Manual Version 6.0. Inst. Farm Animal Gen., Neustadt, Germany.

Grosso, J. L., J. Balieiro, J. Eler, J. Ferraz, E. Mattos, and T. Michelan. 2010. Comparison of different models to estimate genetic parameters for carcass traits in a commercial broiler line. Genet. Mol. Res. 9:908–918.

Haslam, S. M., T. G. Knowles, S. N. Brown, L. J. Wilkins, S. C. Kestin, P. D. Warriss, and C. J. Nicol. 2007. Factors affecting the prevalence of foot-pad dermatitis, hock burn, and breast burn in broiler chicken. Br. Poult. Sci. 48:264–275.

Hill, W. G. 2010. Understanding and using quantitative genetic variation. Philos. Trans. R. Soc. B-Biol. Sci. 365:73–85.

Kestin, S. C., G. Su, and P. Sørensen. 1999. Different commercial broiler crosses have different susceptibilities to leg weakness. Poult. Sci. 78:1085–1090.

Kjaer, J. B., G. Su, B. L. Nielsen, and P. Sørensen. 2006. Foot-pad dermatitis and hock burn in broiler chickens and degree of inheritance. Poult. Sci. 85:1342–1348.

Koerhuis, A. N. M., and R. Thompson. 1997. Models to estimate maternal effects for juvenile body weight in broiler chickens. Genet. Sel. Evol. 29:225–249.

Kruuk, L. E. B., J. Slate, and A. J. Wilson. 2008. New answers for old questions: The evolutionary quantitative genetics of wild animal populations. Annu. Rev. Ecol. Evol. Syst. 39:525–548.

Long, N., D. Gianola, G. J. M. Rosa, K. A. Weigel, and S. Avendaño. 2008. Marker-assisted assessment of genotype-by-environment interaction: A case study of single-nucleotide polymorphism-mortality association in broilers in two hygiene environments. J. Anim. Sci. 86:3358–3366.

Martland, M. F. 1984. Wet litter as a cause of plantar pododermatitis, leading to foot ulceration and lameness in fattening turkeys. Avian Pathol. 13:241–252.

Martland, M. F. 1985. Ulcerative dermatitis in broiler-chickens—The effect of wet litter. Avian Pathol. 14:353–364.

Mayne, R. K. 2005. A review of the aetiology and possible causative factors of foot-pad dermatitis in growing turkeys and broilers. World's Poult. Sci. J. 61:256–267.

McKay, J. C. 2009. The genetics of modern commercial poultry. Pages 3–9 in Biology of Breeding Poultry. P. Hocking, ed. CAB Int., Wallingford, UK.

McKay, J. C., N. F. Barton, A. N. M. Koerhuis, and J. McAdam. 2000. The challenge of genetic change in the broiler chicken. Pages 1–7 in The Challenge of Genetic Change in Animal Production. W. G. Hill, S. C. Bishop, B. J. McGuirk, J. C. McKay, G. Simm, and A. J. Webb, ed. Edinburgh, United Kingdom.

Misztal, I., S. Tsuruta, T. Strabel, B. Auvray, T. Druet, and D. H. Lee. 2002. BLUPF90 and related programs (BGF90). Pages Communication No. 28–07 in Proc. 7th World Congress on Genetics Applied to Livestock Production, Montpellier, France.

Mulder, H. A., and P. Bijma. 2005. Effects of genotype × environment interaction on genetic gain in breeding programs. J. Anim. Sci. 83:49–61.

N'Dri, A. L., S. Mignon-Grasteau, N. Sellier, C. Beaumont, and M. Tixier-Boichard. 2007. Interactions between the naked-neck gene, sex, and fluctuating ambient temperature on heat tolerance, growth, body composition, meat quality, and sensory analysis of slow-growing meat-type broilers. Livest. Sci. 110:33–45.

Nagaraj, M., C. A. P. Wilson, J. B. Hess, and S. F. Bilgili. 2007a. Effect of high-protein and all-vegetable diets on the incidence and severity of pododermatitis in broiler chickens. J. Appl. Poult. Res. 16:304–312.

Nagaraj, M., C. A. P. Wilson, B. Saenmahayak, J. B. Hess, and S. F. Bilgili. 2007b. Efficacy of a litter amendment to reduce pododermatitis in broiler chickens. J. Appl. Poult. Res. 16:255–261.

Pagazaurtundua, A., and P. D. Warriss. 2006. Levels of foot-pad dermatitis in broiler chickens reared in 5 different systems. Br. Poult. Sci. 47:529–532.

R Development Core Team. 2010. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Rauw, W. M., P. W. Knap, L. Gomez-Raya, L. Varona, and J. L. Noguera. 2003. Reallocation of body resources in lactating mice highly selected for litter size. J. Anim. Sci. 81:939–944.

Sanotra, G., C. Berg, and J. Lund. 2003. A comparison between leg problems in Danish and Swedish broiler production. Anim. Welf. 12:677–683.

Scheiner, S. M. 1993. Genetics and evolution of phenotypic plasticity. Annu. Rev. Ecol. Syst. 24:35–68.

Sorensen, D. A., S. Andersen, D. Gianola, and I. Korsgaard. 1995. Bayesian-inference in threshold models using Gibbs sampling. Genet. Sel. Evol. 27:229–249.

van der Waaij, E. H. 2004. A resource allocation model describing consequences of artificial selection under metabolic stress. J. Anim. Sci. 82:973–981.

Ye, X., S. Avendaño, J. C. M. Dekkers, and S. J. Lamont. 2006. Association of twelve immune-related genes with performance of three broiler lines in two different hygiene environments. Poult. Sci. 85:1555–1569.

Zuowei, S., L. Yan, L. Yuan, H. Jiao, Z. Song, Y. Guo, and H. Lin. 2011. Stocking density affects the growth performance of broilers in a sex-dependent fashion. Poult. Sci. 90:1406–1415.