Twenty-five years of selection for improved leg health in purebred broiler lines and underlying genetic parameters

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ABSTRACT Leg health is an important component of broiler welfare and the economics of broiler production. This study presents the development of leg health in 3 purebred commercial broiler lines during 25 yr of selection and investigates the genetic background of leg health traits in current populations of these lines. The leg health traits were deformities of the long bones (LD) and crooked toes (CT), recorded since 1985, and tibial dyschondroplasia (TD) and hock burn (HB), recorded since 1990. The prevalence of CT and HB decreased mainly in the first decade (range among lines −1.2 to −2.3% and −1.3 to −1.5% per year, respectively), after which it stabilized at low levels. The prevalence of LD and TD decreased by −0.6 to −0.9% and −0.4 to −1.2% per year, respectively. Genetic parameters were estimated using data from 4 recent generations. The BW ranged from 2.0 to 2.4 kg at 5 wk of age; the prevalences of LD, CT, TD, and HB from 8.6 to 12.9%, 0.6 to 2.6%, 4.6 to 8.0%, and 4.0 to 12.2%, respectively. Estimates of heritability were 0.04 to 0.07 for LD, 0.01 to 0.10 for CT, 0.10 to 0.27 for TD, and 0.06 to 0.09 for HB (all SE ≤0.01). Estimates of the genetic correlations between LD and CT were 0.11 to 0.43 (all SE ≤0.09), between these traits and HB were negligible, and of TD with LD, CT, and HB were −0.26 to 0.16 (all SE ≤0.11). Estimates of genetic correlations between the leg health traits and BW were lowly to moderately unfavorable, ranging from 0.09 to 0.37 (all SE ≤0.06). The differences between the lines suggest that strategies for simultaneous improvement of all traits tailored for each line individually have been effective. This research demonstrates the long-term effectiveness of selection for improving leg health in broilers and highlights that, despite somewhat unfavorable genetic correlations with BW, these traits can be improved simultaneously in a balanced breeding program.

Key words: heritability, leg defect, genetic correlation, welfare, long-term trend

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INTRODUCTION

Leg health has been an important component of broiler welfare and of the economy of broiler production for many decades—it encompasses a wide range of leg disorders leading to locomotion problems (e.g., reviews by Thorp, 1994; Scientific Committee on Animal Health and Animal Welfare, 2000; Bradshaw et al., 2002). The present study focuses on 3 skeletal disorders, namely (1) deformities of the long bones (**LD**), which includes valgus or varus deformation and bowed legs, (2) crooked toes (**CT**), and (3) tibial dyschondroplasia (**TD**), and a form of contact dermatitis, namely hock burn (**HB**). A second form of contact dermatitis, foot pad dermatitis (**FPD**), was the subject of a separate study (Kapell et al., 2012).

Angular or rotational deformities of the long bones in the leg are among the most common forms of leg weakness of developmental origin, and dyschondroplasia is the most common lesion in bones of broiler legs (Scientific Committee on Animal Health and Animal Welfare, 2000). These leg disorders are associated with a range of welfare issues, including pain, reduced activity, and restricted feeding as a result of pain (Julian, 1998). Improper incubation conditions (Oviedo-Rondón et al., 2009) or deficiencies or excesses in nutrition (review by Waldenstedt, 2006) may negatively affect leg health. High weight-bearing, low activity, and genotype (Bradshaw et al., 2002), as well as housing conditions (Sanotra et al., 2003), have all been linked to the development of deformities.

There are substantial differences among broiler strains in the prevalence of leg disorders. In a trial study using 4 commercial broiler hybrids, considerable differences in TD and valgus/varus angulations at slaughter were found among the crosses (Kestin et al., 1999). For TD, one hybrid showed a significantly lower prevalence

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than the others, whereas for valgus/varus angulations, the pair with a high prevalence of TD showed significantly lower angulations than the others. Sanotra et al. (2003) reported significant differences in the prevalence of valgus/varus deformities and TD between 2 commercial broiler hybrids on commercial farms, ranging from 37 to 53% in Sweden and 45 to 57% in Denmark, although the prevalence was confounded with differences in housing and BW between the countries.

There is genetic variation in leg health traits and their correlations with BW within broiler strains. In many scoring systems, a higher value indicates the presence of a leg defect; therefore we will discuss correlations such that a positive correlation between BW and a leg defect trait is unfavorable. Mercer and Hill (1984) estimated genetic parameters for BW and a range of skeletal health traits, including crooked toes, splay leg, and bowed leg, in 3 purebred commercial broiler lines. The prevalence of the leg defects at 6 wk of age was between 1 and 5%. When analyzed on the observed scale and subsequently transformed, the estimates of heritability were 0.29 to 0.62 and of their genetic correlations with BW were generally low but unfavorable, 0.00 to 0.27. Le Bihan-Duval et al. (1996, 1997) estimated genetic parameters for valgus and varus deformities at 6 wk of age in 2 commercial broiler strains. Data were analyzed using a multinomial logit model, and the heritability estimates ranged from 0.15 to 0.39 for valgus and varus deformities. Their estimates of genetic correlations with BW were also low, ranging from −0.06 to 0.12. Chen et al. (2011) estimated heritabilities of 0.11 and 0.09 on the observed scale for leg angle in a purebred broiler sire line and dam line, respectively.

Wong-Valle et al. (1993) showed that the prevalence of TD can be decreased by selection in an experiment in broiler lines selected high or low, and obtained a realized heritability of 0.44 in the high line. More recently, prevalences were 5% in the low line and 98% in the high line, with intermediate prevalences in high-low and low-high crosses and a contemporary control line of 42, 39, and 30%, respectively (Yalçin et al., 2000).

Hock burn is a form of contact dermatitis: an ulceration of the skin whereby affected areas show brown or black discoloration as well as inflammation and necrosis (Greene et al., 1985). Haslam et al. (2007) found a mean prevalence of 1.3% for HB in 149 UK broiler flocks reared in standard systems. In a study of 12 farms in the UK, the prevalence of HB ranged from 0 to 75% (Department for Environment Food and Rural Affairs, 2010) and in studies in Denmark and the Netherlands from 67 to 89% (Kjaer et al., 2006; Ask, 2010). The large range reflects a broad array of environmental, management, and genetic factors affecting the prevalence of HB. Contact dermatitis is associated with a range of welfare issues, including reduced walking ability and reduced growth, which may be a consequence of pain-induced lack of appetite (Martland, 1985; Kestin et al., 1999). The prevalence varies considerably depending on factors such as feed, season, litter quality, or broiler genotype (Haslam et al., 2007; Department for Environment Food and Rural Affairs, 2010; Hepworth et al., 2010).

Kestin et al. (1999) found significant differences in the prevalence of HB between 4 commercial broiler hybrids, ranging from 0.45 to 0.68 on a scale from 0 to 3. In a comparison of 4 commercial broiler lines, significant differences were found in the prevalence of HB between the lines, and by mixing different lines within a pen, these differences were shown to be due to differences both in susceptibility and in their predisposition to generate wet litter (Department for Environment Food and Rural Affairs, 2010). Kjaer et al. (2006) were the first to report estimates of heritability for HB (0.08 on the observed scale) and its genetic correlation with BW (0.44) in a fast-growing commercial broiler hybrid strain, produced from parent stock in a fully pedigreed system in which 88% of the birds showed signs of HB at 6 wk of age. Ask (2010) examined the prevalence of HB in 10 purebred commercial broiler lines that differed in total prevalence (67 to 89%) and the probability of being more severely affected (4 to 37%). Neither the heritabilities of HB, estimated in 2 male lines at 0.10 for both on the observed scale, nor the genetic correlations of HB with BW (0.14 and 0.16), differed significantly from those found by Kjaer et al. (2006).

As shown in the previous paragraphs, leg disorders have been studied for many decades. McKay et al. (2000) described the effectiveness of expanding breeding goals to achieve simultaneous improvements in production, fitness, and welfare-related traits. However, little has been published about the long-term improvements that have been achieved in broiler breeding for leg health.

Following the publication by Mercer and Hill (1984), selection for improved leg health was intensified in the Aviagen UK breeding program. The aims of this study were therefore 3-fold: (1) to document the changes of leg health in 3 purebred commercial broiler lines (contributing significantly to the Ross 308 and the Ross 708 crossbred) in the Aviagen UK breeding program following a quarter of a century of selection, and in contemporary populations of these lines to estimate (2) heritabilities for a range of different leg health traits under selection: LD, CT, TD, and HB, and (3) genetic correlations among these 4 traits and with BW.

MATERIALS AND METHODS

Trait Description and Scoring

The data for this study originate from the ongoing recording of skeletal leg traits within the Aviagen UK breeding program. Birds were individually weighed and visually assessed for leg health by a trained team at 5 wk of age (6 wk between 1987 and 1998) to maintain commercial relevance. The team of scorers was regularly assessed for consistency using correlations between and within selectors. Scorers were not allowed to assess

Table 1. Trait description and scale of measurement

Abbreviation	Description	Variable type
BW	Body weight (g)	Continuous
LD	Long bone deformity: either a valgus or a varus deformity of the tarsometatarsi and, to a lesser extent, the tibiotarsi or a bending of the tarsometatarsi, sometimes continued in the middle forward digit	Binary
CT	Crooked toes: curling of one or more of the toes due to a deviation of the phalanges, giving the foot a crab-like appearance	Binary
TD	Tibial dyschondroplasia: (a) no lesions, (b) moderate lesions, or (c) severe lesions	Ordinal, 3 scores
HB	Hock burn: (a) 0%, (b) 25% or less, (c) between 25 and 50%, or (d) more than 50% of the plantar surface of the hock affected	Ordinal, 4 scores

selection candidates until they completed a training period of at least 2 yr, after which they were regularly assessed for satisfactory repeatability scores. One scorer remained in the team from 1965 till 2012. Table 1 gives an overview of the traits included in this study.

Long bone deformity was defined as a bird displaying either a valgus or a varus deformity of the tarsometatarsi and, to a lesser extent, the tibiotarsi or a bending of the tarsometatarsi, sometimes continued in the middle forward digit (Figures 1b and 1c). Crooked toes were defined as curling of one or more of the toes due to a deviation of the phalanges, giving the foot a crab-like appearance (Figure 1d). Both traits were binomially scored as (0) unaffected or (100) affected.

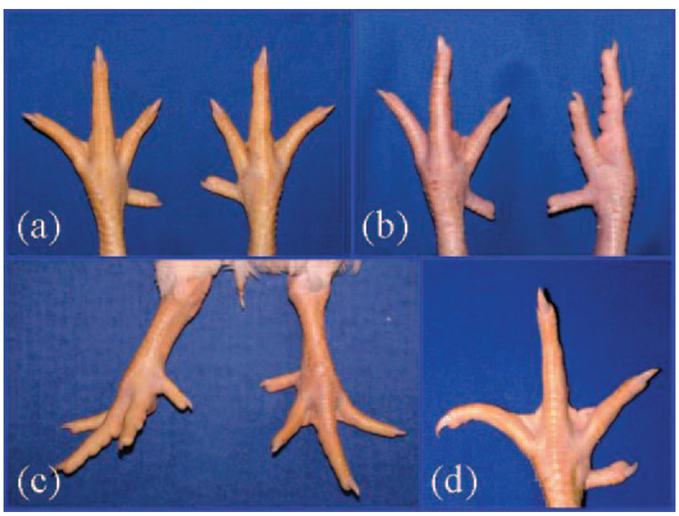

Figure 1. Illustrations of (a) healthy legs (score 0) compared with (b) and (c) long bone deformities (score 100) and (d) crooked toes (score 100).

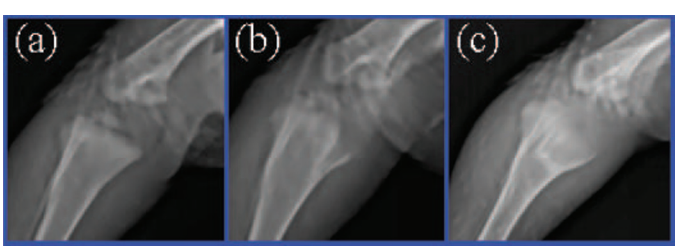

Figure 2. Illustrations of the scores for tibial dyschondroplasia: (a) no lesions (score 0), (b) moderate lesions (score 100), and (c) severe lesions (score 100).

Tibial dyschondroplasia was assessed using a low-intensity x-ray imaging scope (lixiscope) and scored on a 3-point scale, depending on the extent to which abnormal cartilage developed in the tibia: no lesions (score 0), moderate lesions, or severe lesions (Figures 2a to 2c). For subsequent analyses, moderate and severe lesions were combined into one category (score 100). Two different lixiscope devices were used during this time: a first generation device from 1990 till 2006, and a newer and more accurate version since 2007. The trait TD was measured only in males identified as selection candidates, based on a selection step that combined breeding values for performance traits and a thorough physical assessment including no clinical prevalence of leg defects. As a consequence, only subclinical TD was scored because birds showing LD or CT were excluded at the previous selection step. In line A, from 2010 onward, TD was measured on all males. The 3 traits LD, CT, and TD were considered to be major disorders, and any bird showing either one of them was discarded for breeding and culled using a zero tolerance policy.

Figure 3. Illustrations of the scores for hock burn: (a) no lesions (score 0), (b) mild lesions (score 50), (c) moderate lesions (score 50), and (d) severe lesions (score 100).

Table 2. Description of the environmental parameters in the contemporary population

Parameter	Pedigree environment
Feed d 0 to 10	Starter (240 g of CP/kg; 12.6 MJ of ME/kg)
Feed d 11 to 25	Grower (210 g of CP/kg; 13.3 MJ of ME/kg)
Feed d 25 to final weighing	Finisher (205 g of CP/kg; 13.5 MJ of ME/kg)
Stocking density	29 to 31 kg of bird weight per m^2
Temperature	Gradually reduced from 29 to 20°C
Photoperiod d 0 to 7	23L:1D
Photoperiod d 8 to final weighing	20L:4D (18L:6D from October 2009)
Light intensity d 0 to 7	40 lx
Light intensity d 8 to final weighing	Gradually reduced to 10 to 20 lx

Hock burn was scored on a 4-point scale, depending on the percentage of the surface affected by lesions: 0%, no lesions; up to 25%, slight lesions; between 25 and 50%, moderate lesions; or more than 50%, severe lesions (Figures 3a to 3d). For subsequent analyses, slight and moderate lesions were combined into one category; thus, the trait was analyzed on a 3-point scale as unaffected (0), slight to moderate lesions (50), or severe lesions (100). For all traits, a stringent approach was used, whereby both legs were evaluated and the higher scoring leg determined the final score.

Birds, Housing, and Management

All birds were hatched in the same hatchery, where they were sexed and tagged with a barcoded wing band. Birds were subsequently moved to the growing farms and distributed over pens according to line. They were housed on farms in southern Scotland in a highly biosecure pedigree environment where breeding program selection candidates are recorded and selected. Table 2 provides a detailed overview of the environmental parameters for the contemporary population that was used for genetic parameter estimation. 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 supplemented with fresh litter as required. From April 2010 onward, the amount of wood shavings per top up was reduced to enhance the expression of contact dermatitis traits, including HB. The average stocking density ranged from 29 kg of bird weight per m^2 in line C to 31 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).

Long-Term Phenotypic Trends

Historical data for this study were available from January 1986 onward for 3 purebred commercial broiler lines (line A ~1.0 million birds, line B ~1.5 million birds, and line C ~2.3 million birds), thus comprising more than 25 yr of selection for leg-health-related traits. These lines were previously analyzed by Mercer and Hill (1984) to determine genetic parameters for a range of leg health traits. The mean prevalence of skeletal disorders per week and sex was available from January 1986 onward for LD and CT, from December 1990 onward for TD, and from July 1990 onward for HB. The trends are based on the weekly prevalence, calculated as the average of both sexes, and are given as raw phenotypic trends; due to the categorical nature of the traits, no corrections for environmental changes were made. Minor changes in selection age occurred over the years: the average age at selection was 5 wk at the start of the period, increased to 6 wk around 1987, but decreased again to 5 wk in 1998. In addition, changes took place in environmental factors such as feed, lighting program, and litter management. All broilers were managed according to the specifications in the contemporary Aviagen Broiler Manual (1982, 1995, 1996, 1999, 2002, 2005, and 2009) and the corresponding nutritional recommendations.

Statistical Analyses

For the estimation of genetic parameters, the data were restricted to a contemporary population, comprising 4 generations collected between October 2007 and September 2010, with an extra generation of pedigree (Table 3). All skeletal leg traits were recorded on a binomial or multinomial scale. For the genetic analysis, the following multiple trait model including 5 traits (BW, LD, CT, TD, and HB) was used to estimate genetic parameters:

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

where $\mathbf{y}$ is the vector of observations of the traits, $\mathbf{b}$ the vector of the fixed effect accounting for the interaction between the hatchweek, pen, contributing mating group and sex of the individual ("batch"), $\mathbf{a}$ the vector of additive genetic effects, $\mathbf{c}$ the vector of maternal permanent environmental effects (**PEm**), and $\mathbf{e}$ the vector of residuals. $\mathbf{X}$, $\mathbf{Z}$, and $\mathbf{W}$ are incidence matrices relating the vectors $\mathbf{b}$, $\mathbf{a}$, and $\mathbf{c}$ with $\mathbf{y}$. The assumed (co) variance structure was

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

Table 3. Statistics for the genetic parameter estimation: number of birds with phenotypic information (phenotypes), number of birds in the pedigree (pedigree), number of levels for the maternal permanent environmental effect (PEm), 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)

	Numbers of levels of			
Line	Phenotypes	Pedigree	PEm	Batch
A	132,813	177,741	4,765	3,342
B	217,943	286,819	5,291	2,938
C	248,096	338,726	6,259	2,861

where **A** is the additive genetic relationship matrix, **I** is the identity matrix, and **G**, **C**, and **R** represent the variance and covariance matrices of additive genetic effects, PEm effects, and residual effects, respectively. Numbers of levels per effect for the bird, PEm effect, and batch effect are given in Table 3. All variance component analyses were performed by restricted maximum likelihood using the software VCE (Groeneveld et al., 2008). The inclusion of BW in the multivariate analysis ensures that estimates for leg health traits are not biased due to weight-associated effects and selection.

RESULTS

Phenotypic Trend and Descriptive Statistics

Figures 4 to 7 show the phenotypic trend for LD, CT, TD, and HB. Following the analyses of these lines by Mercer and Hill (1984), the focus on selection for improved leg health increased in the breeding program. Between 1986 and 1996, LD decreased on average by −1.4 to −1.6% per year, whereas CT decreased by −1.2 to −2.3% per year. The trait CT stabilized at low levels, whereas LD has continued to decrease by −0.7 to −1.2% per year. Between 1990 and 2006, TD steadily decreased by −0.6 to −1.8% per year. Its prevalence increased after 2007, linked with the change to a more accurate device, but declined rapidly from 2008 onward in all 3 lines at a rate of −1.0 to −5.2% per year. Similar to CT, HB showed a large decrease, at a rate of −1.3 to −1.5% per year, in the first 10 yr after initiating recording of this trait, after which its prevalence stabilized at very low levels. From April 2010 onward, the expressed prevalence of HB has increased, as expected from management changes made to target expression of the contact dermatitis traits HB and FPD (Kapell et al., 2012).

The number of observations, means of BW, and prevalence of leg disorders in each line from October 2007 to September 2010 are given in Table 4. Consequent on their different origins and emphases given to weight and growth traits, the average BW were 2.4 kg for line A, 2.0 kg for line B, and 2.0 kg for line C at 5 wk of age in the contemporary populations. The trait LD showed the highest prevalence of the leg health traits, ranging from 8.6% (line C) to 12.9% (line A). In contrast, CT showed a much lower prevalence, ranging from 0.6% in lines A and C to 2.6% in line B. Combining the prevalence of these 2 skeletal leg health traits, line C was lower (9.2%) than lines A and B (both 13.4%). Males were significantly more affected by skeletal leg disorders than females, the difference being more pronounced for LD (2.2- to 2.3-fold higher in males) than for CT (1.6- to 1.9-fold). Overall, the proportion of male birds showing at least one of these skeletal leg disorders was more than double that of females.

The trait TD reflects subclinical prevalence and is recorded only on preselected males with no clinical leg defects. In these birds, the average prevalence of TD ranged from 4.6% in line B to 8.0% in line C. The prevalence of HB ranged from 4.0 to 12.2%. In lines B and C, the prevalence of HB was up to 2.5 times higher in males than in females. In contrast to the other leg health traits, however, males did not show consistently higher prevalences for HB than females, for in line A it was slightly lower (9.5 vs. 10.2%). Severe HB affected less than 1% of the birds across all lines and sexes, and accounted for less than 5% of the total prevalence.

Heritabilities

Table 5 shows the heritabilities, genetic correlations, and phenotypic correlations for the traits and Table 6 shows the phenotypic SD and proportion of variance attributed to the PEm effect. Heritability estimates for BW ranged from 0.33 in line C to 0.40 in line B. Those for both LD (0.04 to 0.07) and HB (0.06 to 0.09) varied little between the 3 lines. A small difference between lines was seen for CT, where estimates of heritability for lines A and C (0.01 to 0.02) were lower than for line B (0.10). A larger difference between lines was found for TD, with heritability estimates of 0.10 and 0.15 for lines B and C, respectively, and 0.27 for line A. The PEm effect accounted for 3.0 to 4.3% of the phenotypic variance for BW and 0.5 to 3.8% for the leg traits. Overall, heritability estimates across leg health traits and lines ranged from 0.01 to 0.27, and despite minor and significant differences, the estimates showed a good concordance across the lines.

Genetic Correlations

Leg health traits were generally negligibly correlated at the phenotypic level. The estimated genetic correlations of HB with LD, CT, or TD were generally small and not significantly different from zero, except

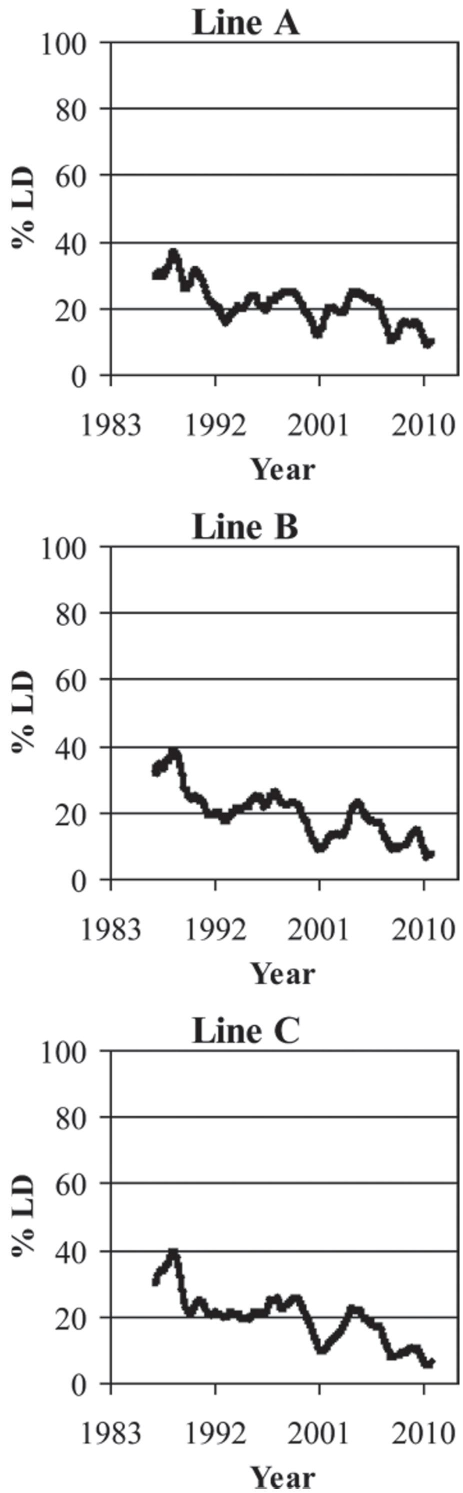

Figure 4. Prevalence of long bone deformity (LD) between October 1985 and September 2010 (1-yr moving average).

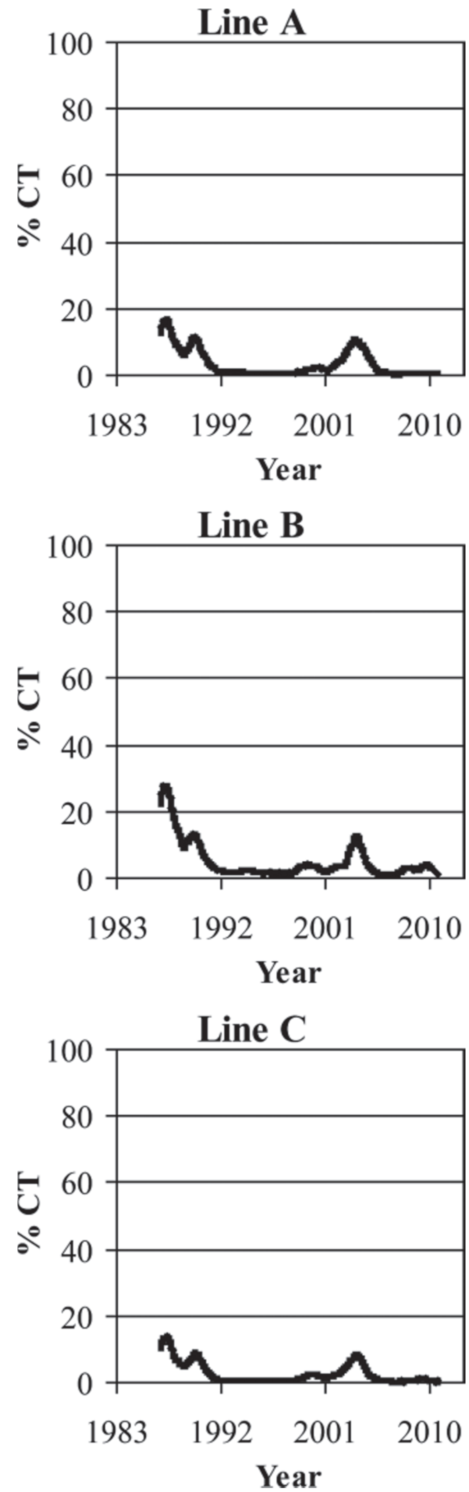

Figure 5. Prevalence of crooked toes (CT) between October 1985 and September 2010 (1-yr moving average).

between HB and TD in lines B and C. The genetic correlations between LD and CT were consistently positive, but differed between the lines: weak for lines A and C (0.11 and 0.13), but much higher for line B (0.43). Those between LD and TD were weak in all lines (−0.06 to 0.11). Genetic correlations of CT with TD were of similar, moderate magnitude but in opposite direction in lines B (0.25) and C (−0.26), and weak in line A (−0.12).

The genetic correlations between skeletal leg health traits and BW were all unfavorable but generally low to moderate. All lines showed similar genetic correlations between CT and BW (0.14 to 0.16) and TD and BW (0.16 to 0.22). Line A showed a much lower genetic correlation (0.09) between LD and BW than lines B and C (0.20 to 0.25). The genetic correlation between BW and HB ranged from 0.24 to 0.37.

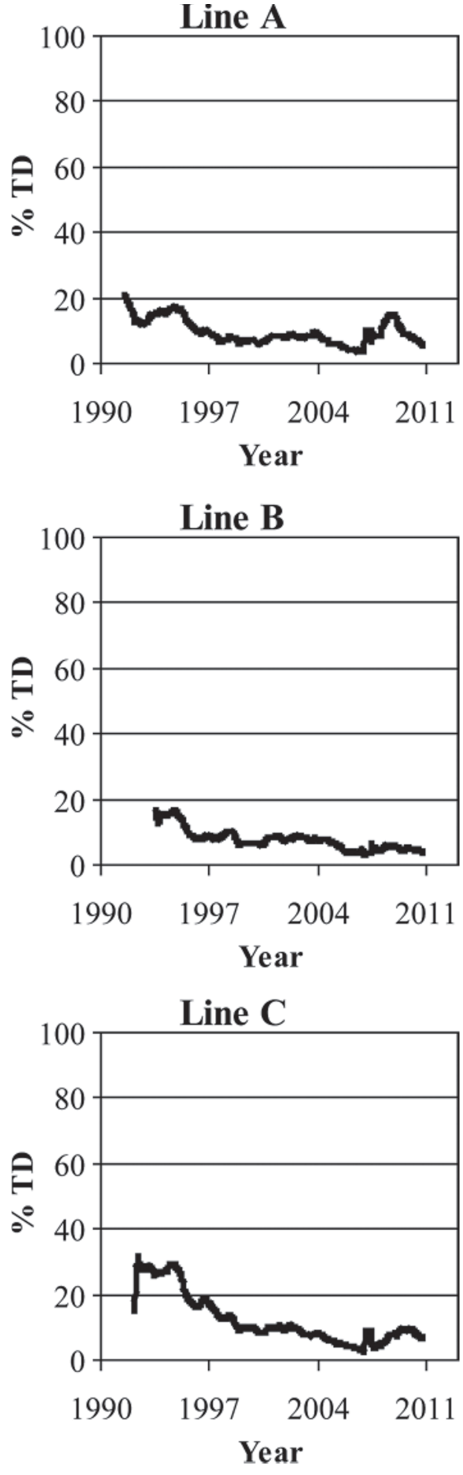

Figure 6. Prevalence of tibial dyschondroplasia (TD) between December 1990 and September 2010 (1-yr moving average).

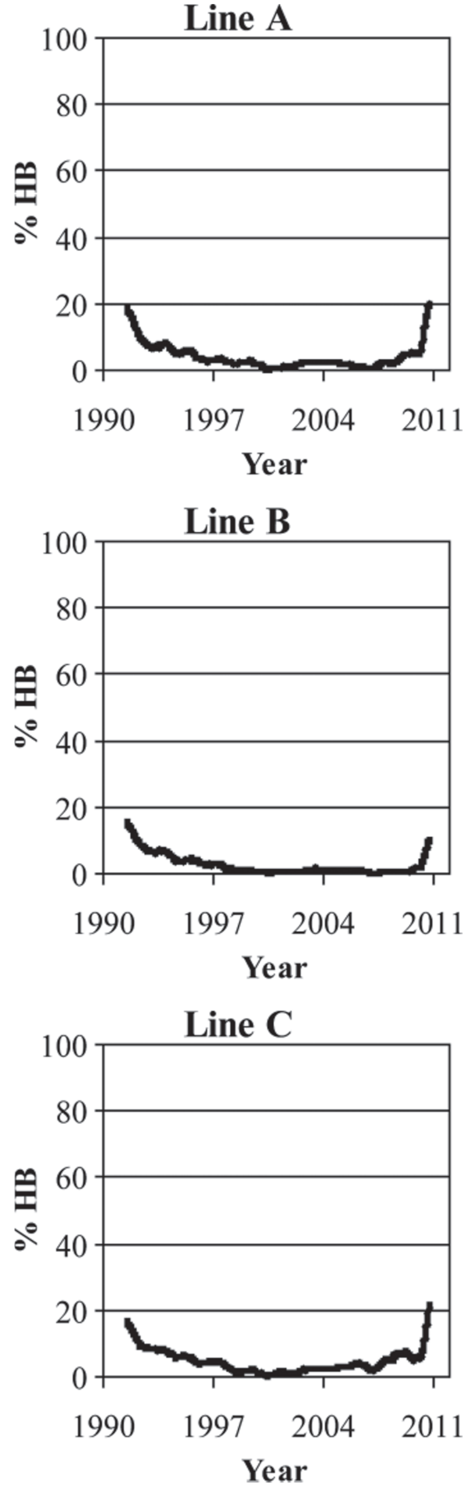

Figure 7. Prevalence of hock burn (HB) between July 1990 and September 2010 (1-yr moving average).

DISCUSSION

Leg disorders have long been associated with a range of economic and welfare issues (e.g., Thorp, 1994; Scientific Committee on Animal Health and Animal Welfare, 2000; Bradshaw et al., 2002). The importance of improving leg health was recognized decades ago and birds showing signs of impaired leg health were culled and excluded from the breeding program as selection candidates. The first estimates of genetic parameters for bowed leg, splay leg, and CT were published in 1984 (Mercer and Hill) and the first for contact dermatitis traits, including HB, in 2006 (Kjaer et al.). Following the publication by Mercer and Hill (1984), selection for improved leg health was intensified. More recently, the Council of the European Union (2007) emphasized the need for good animal health and welfare in broilers

Table 4. Descriptive statistics for BW, long bone deformity (LD), crooked toes (CT), tibial dyschondroplasia (TD), and hock burn (HB) per sex (♂ = male, ♀ = female) and combined (tot.), for October 2007 till September 2010 (n = number of records, mean and SD in grams, P_{tot} = total prevalence, P_{sev} = prevalence of severe lesion for TD and HB)

			BW	LD	CT	TD[1]	HB
Line	Sex	n	Mean (SD)	P_{tot}	P_{tot}	P_{tot} (P_{sev})	P_{tot} (P_{sev})
A	♂	65,464	2,521 (231)	0.176	0.008	0.078 (0.011)	0.095 (0.000)
	♀	67,349	2,230 (216)	0.083	0.005		0.102 (0.002)
	tot.	132,813	2,373 (267)	0.129	0.006		0.098 (0.001)
B	♂	106,079	2,200 (182)	0.152	0.035	0.046 (0.008)	0.058 (0.001)
	♀	111,864	1,888 (167)	0.068	0.018		0.023 (0.000)
	tot.	217,943	2,040 (234)	0.109	0.026		0.040 (0.000)
C	♂	122,055	2,100 (190)	0.120	0.008	0.080 (0.012)	0.151 (0.007)
	♀	126,041	1,807 (174)	0.052	0.005		0.094 (0.001)
	tot.	248,096	1,951 (234)	0.086	0.006		0.122 (0.004)

[1]Only recorded on selected males: 28,566 in line A, 17,999 in line B, and 19,361 in line C.

through regular inspections for health disorders such as difficulties in walking ability. In this study, we have followed the development over the last quarter century of the 3 broiler lines analyzed by Mercer and Hill (1984). We have examined the changes in leg health during 25 years of selection against LD, CT and, more recently, TD and HB, and shown that, despite somewhat unfavorable genetic correlations with BW, simultaneous improvement of all traits has been achieved. This research shows that the suggestion by Dawkins and Layton (2012), regarding the potential for selecting for welfare and production traits simultaneously despite antagonistic correlations, is already routine practice in a commercial breeding program.

Prevalence and Long-Term Phenotypic Trends

The prevalence of LD in this study is lower than that of various long bone deformities in other studies [e.g., 44 to 73% for valgus and varus (Le Bihan-Duval et al., 1996) and 16 to 19% for unacceptable leg angles (Chen et al., 2011)]. A direct comparison between the present study and that of Mercer and Hill (1984) is not straightforward. The only trait common to both is CT, and the prevalence in the contemporary population is much lower than in 1984 (3 to 5%). Reduction of the selection age from 6 to 5 wk in 1998 coincided with a minor decrease of the prevalence of LD, but did not affect CT, TD, and HB, which were then already at very low levels. The phenotypic trends for LD and CT show a peak around 2003, coinciding with 2 changes in management, namely a reduction in digestible phosphorus levels in the feed and in recording procedure for skeletal defects. Subsequently they fell, although the prevalence of CT increased slightly more recently, especially in line B, but only until October 2009. This coincides with the change in lighting program to a 6-h dark period, meeting forthcoming European Government recommendations (Council of the European Union, 2007), though the reasons for this effect are unclear.

The effectiveness of selecting for a low prevalence of TD has been demonstrated in several selection experiments (e.g., Wong-Valle et al., 1993; Yalçin et al.,

Table 5. Heritabilities (marked with asterisk, diagonal), genetic correlations (above diagonal) and phenotypic correlations (below diagonal) for BW, long bone deformity (LD), crooked toes (CT), tibial dyschondroplasia (TD), and hock burn (HB)[1]

Trait	BW	LD	CT	TD	HB
Line A					
BW	0.360 (0.012)*	0.089 (0.051)	0.145 (0.060)	0.189 (0.055)	0.293 (0.037)
LD	−0.062	0.068 (0.006)*	0.120 (0.049)	0.110 (0.023)	−0.025 (0.030)
CT	0.010	−0.010	0.014 (0.002)*	−0.115 (0.057)	−0.058 (0.028)
TD	0.008	0.028	0.000	0.274 (0.025)*	0.079 (0.045)
HB	0.130	−0.013	−0.002	0.008	0.094 (0.006)*
Line B					
BW	0.399 (0.015)*	0.197 (0.046)	0.157 (0.033)	0.221 (0.039)	0.241 (0.029)
LD	−0.017	0.037 (0.004)*	0.432 (0.059)	0.099 (0.108)	0.032 (0.012)
CT	0.010	−0.043	0.104 (0.009)*	0.245 (0.102)	0.016 (0.026)
TD	0.008	0.192	0.232	0.103 (0.016)*	0.147 (0.056)
HB	0.082	0.000	−0.007	0.000	0.060 (0.004)*
Line C					
BW	0.326 (0.011)*	0.249 (0.041)	0.130 (0.022)	0.158 (0.027)	0.368 (0.022)
LD	−0.039	0.051 (0.004)*	0.124 (0.023)	−0.061 (0.027)	0.056 (0.020)
CT	0.007	−0.019	0.018 (0.002)*	−0.255 (0.053)	0.001 (0.012)
TD	−0.005	−0.021	0.020	0.147 (0.017)*	0.161 (0.041)
HB	0.129	−0.015	−0.010	0.013	0.084 (0.004)*

[1]SE in parentheses.

Table 6. Phenotypic SD (σ_{phen}) and proportion of variance attributed to the maternal permanent environmental effect (PEm) for BW (in dg), long bone deformity (LD), crooked toes (CT), tibial dyschondroplasia (TD), and hock burn (HB)

	Line A		Line B		Line C	
Trait	σ_{phen}	PEm	σ_{phen}	PEm	σ_{phen}	PEm
BW	19.9	0.030	15.1	0.043	15.2	0.041
LD	32.8	0.017	30.2	0.009	27.3	0.009
CT	7.9	0.007	15.9	0.021	7.9	0.005
TD	26.8	0.010	22.0	0.028	27.0	0.038
HB	13.1	0.010	8.8	0.013	13.4	0.007

2000). The prevalence of TD in this study is lower than reported by Sanotra et al. (2003) in a range of commercial crosses and environments (45 to 57%). In this study, only subclinical forms of TD were measured on birds that were already free from LD, CT, or both—the prevalence of TD in the birds that were not selected may be higher. The increase in TD in 2007, particularly noticeable in lines A and C, coincides with the introduction of a new lixiscope. Following this peak, all lines showed a steady decline.

The total prevalence of HB in this study is within the wide range (1 to 89%) found in Europe (Kjaer et al., 2006; Haslam et al., 2007; Ask, 2010), but the scoring systems differed considerably, with scales comprising 3 to 6 categories. The recent increase in HB coincides with a change in litter management policy from April 2010 onward. The prevalence of both HB and FPD in the pedigree lines became very low, but for effective and accurate selection, both traits need to be expressed sufficiently in selection candidates through a higher prevalence and variation (Kapell et al., 2012). To increase the expression, litter is now supplemented with fewer fresh shavings on a routine basis, leading to a reduction in litter quality through an increase in moisture.

Heritabilities

The estimates of heritabilities for LD are comparable with those of Chen et al. (2011), but slightly lower than those of Le Bihan-Duval et al. (1996, 1997), who analyzed valgus and varus deformities as unordered categorical traits using a multinomial logit model, rather than the ordinal categories in our analysis. When transformed to a normal underlying scale (Dempster and Lerner, 1950), our heritability estimates for LD (0.10 to 0.17) are lower than those for splay and bow estimated by Mercer and Hill (1984) on the observed scale and subsequently transformed (0.27 to 0.62). For CT, heritability estimates transformed to the underlying scale (0.29 to 0.72) showed a larger range than those estimated (0.35 to 0.50) by Mercer and Hill (1984). Heritability estimates for TD in the present study on birds selected for low TD for almost 20 yr are lower than those of Wong-Valle et al. (1993) on birds selected for a high prevalence of TD for 4 generations. Heritability estimates of HB are in line with those found by Kjaer et al. (2006) and Ask (2010).

A PEm effect has not been included in all of the aforementioned analyses, which may have inflated their estimates. Studies comparing models with and without maternal effects show that the direct heritability may be overestimated if significant maternal environmental effects are not fitted (e.g., Koerhuis and Thompson, 1997; Clément et al., 2001; Grosso et al., 2010). To evaluate the effect of not fitting this effect, line B was analyzed using a model without PEm. As expected, the estimated heritabilities where higher at 0.57, 0.08, 0.24, 0.18, and 0.11 for BW, LD, CT, TD, and HB, respectively (cf. Table 5).

Because severe HB affected less than 1% of the birds across all lines, it was analyzed in a further analysis as a binary trait, whereby all affected birds were combined into score 100. There were no changes in the heritability estimates for HB and nonsignificant changes for its correlations with the other traits (results not shown). Whereas Ask (2010), who analyzed both HB and FPD, attributed the difference in heritability for FPD between lines in part to the difference in prevalence, we found no clear relation between prevalence and heritability estimate for HB. As we noted previously in an analysis of FPD in the same 3 lines and data as presented in this study (Kapell et al., 2012), 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). Although more categories would allow increased discrimination, for practical implementation in a breeding program traits need to be easy to distinguish and the scoring must be repeatable. Whereas transformation of the estimated heritabilities to the underlying continuous scale resulted in higher estimates, or an analysis using, say, a threshold model, is expected to give similar higher values (e.g., Gianola, 1982; Sorensen et al., 1995), from a practical point of view, genetic parameters and breeding value estimates on the observed scale are preferred.

Differences Between Sexes

Males generally showed higher prevalences of leg defects than females, in line with previous results for a range of leg defects (Mercer and Hill, 1984; Le Bihan-Duval et al., 1996; Yalçin et al., 2000). When the data were analyzed with males and females as separate traits, the estimated genetic correlation between CT in males and females was very high (0.94 to 0.98). For LD, the genetic correlation between males and females was high in lines B and C (0.85 to 0.87), but lower in line A (0.70). Reported estimates of the effect of sex on HB and FPD are inconsistent, ranging from higher to lower prevalences in males than females (e.g., Shepherd and Fairchild, 2010; Hepworth et al., 2011). The sex difference in prevalence of HB was also inconsistent in this study, but the estimate of the genetic correlation between sexes was high (0.87 to 0.89), so improvement in both can be achieved by selection in either one or both.

Correlations Between Leg Health Traits

Genetic parameters for leg health traits have been estimated in few studies. Estimates of genetic correlations between valgus and varus deformities ranged from −0.43 to 0.23 (Le Bihan-Duval et al., 1996) and between bowed leg and splay leg from −0.11 to 0.03 (Mercer and Hill, 1984). Preliminary analyses of 2 separate traits which are both included in LD (bow and valgus/varus deformity) showed positive genetic correlations between them (0.20 to 0.58). The estimated genetic correlations between CT and LD are in the same range as those of Mercer and Hill (1984) between CT and either splay leg or bowed leg. For the present study, a further analysis was performed in which the traits LD and CT were combined into a single trait called combined leg disorders (**CLD**). In lines A and C, the estimated heritabilities of CLD (0.07 and 0.05, respectively) did not differ from those for LD and that for CLD in line B (0.07) was intermediate between LD and CT. Genetic correlations of CLD with BW, TD, and HB did not differ significantly from those of LD with these 3 traits in any of the lines. Hence, combining LD and CT into a single trait is a reasonable approach, allowing greater selection pressure on a single skeletal leg health trait in a selection index. The traits TD and HB are best considered separately, however, in view of the inconsistent correlations between them and CT or LD.

Correlations Between Leg Health and BW

The low to moderately unfavorable estimates of genetic correlations between BW and the leg health traits are in line with estimates of Mercer and Hill (1984). Low estimates, −0.06 to 0.09, between BW and valgus or varus deformities were also obtained by Le Bihan-Duval et al. (1997). However, their estimates increased slightly to 0.01 to 0.12 when the weights of severely affected and probably thereby lighter birds were excluded. In a recent trial study in broilers, the mean lesion scores for TD or valgus deformities were higher in the fastest than the slowest growing quarters of a population (Shim et al., 2012). A continuous screening approach is followed in the breeding program to ensure that severely affected birds are detected and culled for welfare reasons well before their weight reduces drastically, but leg health may have influenced the weight of the moderately affected birds. Mercer and Hill (1984) observed higher genetic than phenotypic correlations between BW and skeletal health traits. Although the scoring system may have played a role in this, it is likely also due to a negative environmental correlation between the traits, with affected birds being less vigorous (Mercer and Hill, 1984). A similar contrast between the genetic and phenotypic correlations was found in the present study, with negative estimates for the correlations between both PEm effects (−0.08 to −0.36) and residual effects (−0.10 to 0.00) between BW and LD, CT, or TD.

Previous estimates of the genetic and phenotypic correlations between BW and HB were unfavorable, but few differed significantly from zero (Sørensen et al., 2000; Kjaer et al., 2006; Ask, 2010). The present study confirms this, with moderately positive genetic but weaker phenotypic correlations between BW and HB. Kjaer et al. (2006) hypothesized that a positive correlation between these 2 traits may be due to a tendency for heavier birds to sit more on their hocks, whereas lighter birds stand more.

Mercer and Hill (1984) predicted that selection programs for BW would at best maintain the current levels of incidence. Nevertheless, despite relatively low heritabilities for leg defects and unfavorable correlations with BW, a balanced approach has led to a significant improvement in both BW (34 to 39 g/yr between 1985 and 2010) and leg health (Figures 4 to 7) in all 3 lines.

Trials and industry statistics have shown that improvements in production trends at the industry level have been accompanied by improvements of livability, in part due to improved leg health. McKay et al. (2000) reported that the percentage of growth plate lesions in pedigree lines and of leg culls in trials had declined steadily. Meanwhile, these pedigree lines showed an annual improvement of live weight of 2.4% and a reduction of the feed conversion ratio (**FCR**) by 1.2%. In 2007, a comparison of 3 modern broiler lines with their 1972 unselected control lines showed that modern lines were significantly heavier and had better FCR, but did not differ significantly in mortality and generally had a higher percentage of birds with good leg health (Fleming et al., 2007a,b).

More recently, industry statistics from the United States showed an annual reduction in FCR of 0.025 and improvement in livability of 0.2% over a 5-yr period (McKay, 2009). Similarly, Dutch industry statistics show an improvement in live weight from 1.9 kg in 1986 to 2.2 kg in 2009, whereas the FCR improved from 1.83 to 1.75 and livability from 94.8 to 96.3% (Landbouw Economisch Instituut/Centraal Bureau voor de Statistiek, 2002, 2011). In Canada, publicly available industry statistics on the number of condemnations per 10,000 broilers slaughtered showed a decrease of valgus and varus deformities from 4.8 in 1999 to 0.2 in 2007 and a decrease in leg conditions from 0.8 in 2008 to 0.5 in 2011. Between 1999 and 2011, the average weight of these broilers at slaughter increased from 1.59 to 1.65 kg (Agriculture and Agri-Food Canada, 2011).

In conclusion, we have shown that both broiler leg health and weight have been improved in a selection program. Considerable decreases in the prevalence of leg disorders have been achieved by a strong focus on accurately scoring selection candidates and a stringent culling policy of discarding any selection candidate with clinical leg defects. In addition, predicted breeding values for candidates with nonclinical leg defects allowed the identification of families that were prone to develop leg issues. Although the heritabilities of all 4 leg health traits were low and their genetic correlations with BW unfavorable but low to moderate, breeding strategies for simultaneous selection for live performance and leg health have been, and continue to be, effective. Broad breeding goals including traits related to production, welfare, adaptability, livability, and reproductive fitness are essential to achieve a balanced progress in pedigree broiler lines. This approach has had and will continue to have benefits for the broiler industry globally.

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