Genetic analysis of survival and fitness in turkeys with multiple-trait animal models[1]

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ABSTRACT Genetic parameters for production, survival, and structural fitness traits recorded in pedigreed turkey sire and dam parental lines from a nucleus breeding program were estimated with multiple-trait animal models. Survival and conformation traits were scored in binary terms of health, where 0 = died or affected, and 1 = survived or healthy. Walking ability at 20 wk was subjectively scored from 1 (poor) to 6 (excellent). Body weights and egg production displayed moderate heritability ($h^2 = 0.18$ to 0.35). Early survival (to 3 wk) displayed low heritability ($h^2 = 0.02$ and 0.04 for the dam and sire lines, respectively). Late survival (3 to 23 wk) and longevity (age at death or cull) had low to moderate heritability ($h^2 = 0.12$ to 0.14). Walking ability had moderate heritability ($h^2 = 0.26$, 0.25). Leg structure health displayed low heritability ($h^2 = 0.08$), as did hip structure, foot, and skin health ($h^2 \leq 0.02$). Crop health displayed moderate heritability ($h^2 = 0.12$). Walking ability, hip and leg structures, footpad, and breast skin health had negative genetic correlations with BW ($r_G = -0.50$ to -0.23). Egg production had moderate positive genetic correlation with late survival ($r_G = 0.61$). Genetic correlations between early and late survival were close to zero ($r_G = 0.10$ and 0.03 for the dam and sire lines, respectively). Walking ability had high positive genetic correlations with late survival, longevity, hip structure, and leg structure in both lines ($r_G = 0.51$ to 0.91). These genetic parameters indicate that unchecked selection for growth could decrease survival, walking ability, and hip, leg, footpad, and skin health in turkeys. However, index selection should be effective at improving fitness, survival, and growth simultaneously in commercial turkey lines. Walking ability should be a good indicator trait for selection to improve overall late survival and hip and leg health in turkeys.

Key words: turkey, genetics, selection, mortality, health

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INTRODUCTION

Fitness traits are of considerable importance for turkey producers, not only because they are directly related to production and economic profitability, but increasingly because of societal concern about animal welfare (Wood, 2009a,b). In turkey breeding, the term fitness may encompass a range of defined traits, from general survival to specific health or reproductive traits that affect a bird's quality of life and commercial productivity. A variety of factors contribute to a bird's performance for fitness traits, including genetic predisposition, and environmental factors such as hatchery and barn management and pathogen exposure. Although poultry breeding programs have had great success in improving productivity through selecting for higher growth rate and meat yield, success in the selection for survival and health traits is inherently more difficult (Hunton, 1990).

Survival is a general measure of an animal's fitness. In commercial turkey production, mortality can result from a range of conditions, including disease, physiological stress, and aggressive behavior. In addition, it may be necessary for producers to slaughter sick or unfit birds. Consequently, bird survival recorded as a binary trait (either dead or alive at a given time) is a potential indicator for many underlying health traits that could be improved simultaneously. Selection for general survival has been applied widely in turkeys and broilers but with sporadic success (Flock et al., 2005; Havenstein et al., 2007). More precise understanding of fitness genetics has been investigated for specific health traits displaying lethal and sub-lethal phenotypes. Turkeys are susceptible to several structural disorders that

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have a demonstrated genetic basis, such as twisted leg, tibial dyschondroplasia, and deep pectoral myopathy (reviewed by Whitehead et al., 2003). These disorders are a major poultry welfare issue as they cause pain and affect the birds' ability to eat and drink, and furthermore cause economic losses for farmers in terms of culled or downgraded birds (Nääs et al., 2009). Selection and management that have increased growth rate in meat poultry strains have been associated with several such structural disorders (Buss, 1990; Whitehead et al., 2003).

Despite the importance of these fitness traits in turkey genetic improvement programs, genetic parameters for survival, skeletal and locomotion traits, and their associations with other economic production traits have been rarely estimated and published in turkeys. The objective of this study was to use multiple-trait linear animal models to calculate heritability and genetic correlations for survival and structural fitness traits recorded in pedigreed turkey sire and dam parental lines. These parameters will help determine optimal selection methods to improve survival and fitness in a commercial turkey breeding program.

MATERIALS AND METHODS

Populations

Data were obtained for a parental dam (**DL**) and sire line (**SL**) from a nucleus breeding program. The SL was selected for superior growth, feed conversion, and meat traits. The DL was selected for both commercial and reproductive traits. The lines were reared under conditions that resembled commercial production practices, including commercial ventilation, litter treatment, and housing densities. The analysis used the complete pedigree data going back 23 and 18 generations in DL and SL, respectively.

Data Collection and Traits

Production and fitness data were compiled from birds hatched in 2000 to 2008. On average, there were 24 hatch groups (contemporary groups of birds that hatched on the same day and reared together) per line per year. Within each hatch group, individual birds were weighed and assessed for fitness at 15 wk and 20 to 21 wk. Ages at which individual birds died or were removed from the population were recorded, as well as the removal reason. To maintain consistent pen densities, birds exhibiting poor conformational phenotypes (poor BW or structural fitness disorders; see Structural Fitness Traits description below) were culled from the population at the 2 observation times. Up to 30% of birds were removed, even though most of these would survive to slaughter age under normal rearing circumstances. Three main types of traits were defined for genetic analysis: production traits (BW and egg production), survival traits (if a bird survived to specific ages, or longevity, defined as age at death or culling in units of weeks), and structural fitness traits (walking ability and the occurrence of defects).

Production Traits. Body weights were recorded at 15 ($\mathbf{BW_{15}}$) and 20 to 21 wk ($\mathbf{BW_{20}}$). Total egg production (**EP**) was only recorded for hens that were selected as parents. Because EP was only recorded on hens that survived to maturity (i.e., all had same survival phenotypes), phenotypic correlations between EP and survival traits could not be estimated. Production trait data had continuous, approximately normal distributions.

Survival Traits. Survival to specific ages were defined as binary traits, with 0 = died or removed due to poor BW or poor conformation, and 1 = survived. Two main stages were identified. Early survival (**SURVE**) was survival to 3 wk and was recorded for all birds. Late survival (**SURVL**) was survival from 3 to 23 wk and was only recorded for birds that survived the first 3 wk. Birds that did not have a mortality/removal date or age were assumed to have survived the recording period. A trait of total survival (all birds' survival from hatch to 23 wk) could also be defined, but due to very high SURVE, this trait does not differ greatly from SURVL. If different characteristics contribute to SURVE and SURVL, total survival would confound these differences. Economic analyses indicate that later mortality is more economically important than early mortality due to the larger investment in the bird in feed, labor, and housing (Wood, 2009a).

Longevity (**LONG**) was defined as the number of weeks from hatch to death or removal. Birds with no mortality/removal date were assigned LONG = 66 wk. Birds that were removed for reasons unrelated to health had LONG observations set to missing unless a mortality age was recorded. Longevity data was continuous but highly left (negatively) skewed because most (61% in DL; 56% in SL) birds had LONG = 66 wk.

Structural Fitness Traits. Turkeys were individually observed and subjectively scored for walking ability (**WA**) at 20 wk according to a system developed for commercial breeder evaluation by Hybrid Turkeys (Table 1; J. McCurdy, Hybrid Turkeys, Kitchener, ON, Canada, personal communication). Expert personnel scored WA from 1 (poor motion, pitch, and balance; severe inward leg angulation, weak hip or hock; bow/twisted leg) to 6 (fluid motion; excellent pitch and balance; low outward leg angulation; strong hip and hock; no leg defects). Although walking score data were discretely distributed (i.e., scores were observed only as 1, 2, 3, 4, 5, or 6), the set approximated a continuous normal distribution.

A variety of conformation disorders were observed in the populations. Recording changed over the 9 yr, so similar observations were grouped together. Conformation disorders were breast structure (**BST**): crooked breast and knobby keel; humped back structure (**HBS**); weak hip structure (**HS**); leg structure (**LS**): poor hocks or angulation, short leg; foot structure (**FS**): crooked

Table 1. Scoring system to evaluate walking ability in commercial breeder turkeys, characterizing individual birds' walking motion, pitch, balance, leg angulation, hock and hip strength, and leg structure[1]

Score	Motion	Pitch	Balance	Leg angulation	Hock strength	Hip strength	Leg structure
1	Poor	Poor to good	Poor to good	Severe to some inward	Very weak to weak	Very weak to low weakness	Slight to severe bow / twisted leg
2	Poor to fair	Poor to good	Poor to good	Severe inward to none	Very weak to weak	Some to low weakness	Slight to severe bow / twisted leg
3	Fair to good	Fair to good	Fair to good	Some inward or some outward	Some weakness	Some to no weakness	Slight bow / twisted leg
4	Good to very good	Good to very good	Good to very good	Some outward, low inward, or absolute straightness	Low to no weakness	No weakness	Slight to no twisted leg
5	Good to fluid	Good to excellent	Good to excellent	Some outward	Very low to no weakness	No weakness	No leg defect
6	Fluid	Very good to excellent	Very good to excellent	Low outward	No weakness	No weakness	No leg defect

[1]J. McCurdy, Hybrid Turkeys, Kitchener, ON, Canada, personal communication.

toe and twisted foot; footpad dermatitis (**FTPAD**); breast skin (**BSK**): breast blister or button; head and eye (**HE**) defects; pendulous crop (**PC**); and wing structure (**WS**): broken wings. Most of these disorders occurred at very low frequency (less than 2% of the population), but leg defects were more common, affecting approximately 18% of birds (Table 2). For analysis, these traits were defined in binary terms of health, with 0 = affected and 1 = healthy.

Descriptive Statistics

Trait descriptive statistics for each population are shown in Table 2. Binary traits that are better for analysis (i.e., have sufficient variance as indicated by higher incidence observed) are apparent. Several defects had very low incidence (less than 1,000 observations since 2000): skeletal defects in breast, back, and foot; BSK in the dam line; and broken wings in the sire line.

Genetic Analysis

Genetic parameters were estimated within each population with multiple-trait animal models using ASReml 3.0 (Gilmour et al., 2009). The DL and SL were analyzed separately because there was no genetic connection between them. Results from preliminary univariate analyses were applied as starting values in subsequent multivariate analyses. Several structural fitness traits had very low variance (i.e., low frequency of defects)

Table 2. Trait, numbers of observations, population means, SD, minima, and maxima

	Dam line					Sire line				
Trait[1]	n	Mean	SD	Minimum	Maximum	n	Mean	SD	Minimum	Maximum
Production										
BW_{15}	111,594	8,128	1,262	3,684	13,880	204,510	9,901	1,821	3,850	17,150
BW_{20}	143,694	12,068	3,183	4,520	25,880	149,811	17,050	4,590	7,900	31,400
EP	5,008	104.2	19.4	0	152	9,555	60.5	18.3	0	112
Survival										
SURVE	256,545	0.989	0.104	0	1	292,713	0.975	0.156	0	1
SURVL	175,983	0.515	0.500	0	1	202,326	0.496	0.500	0	1
LONG	155,833	37.12	25.01	0	66	193,584	36.68	25.35	0	66
Structural fitness										
WA	164,202	2.53	0.91	1	6	167,808	2.48	0.94	1	6
BST	250,316	0.999	0.028	0	1	280,370	1.000	0.010	0	1
HBS	250,316	0.995	0.068	0	1	280,370	0.999	0.035	0	1
HS	250,316	0.979	0.144	0	1	280,370	0.970	0.170	0	1
LS	250,336	0.833	0.373	0	1	280,371	0.831	0.375	0	1
FS	250,316	0.997	0.052	0	1	280,370	0.996	0.060	0	1
FTPAD	250,316	0.990	0.100	0	1	280,370	0.986	0.118	0	1
BSK	250,316	0.998	0.047	0	1	280,370	0.992	0.087	0	1
HE	250,316	0.972	0.166	0	1	280,370	0.976	0.153	0	1
PC	253,736	0.991	0.094	0	1	285,415	0.981	0.137	0	1
WS	250,316	0.992	0.090	0	1	280,374	0.997	0.059	0	1

[1]BW_{15} = BW at 15 wk, BW_{20} = BW at 20 wk (g); EP = egg production (no. of eggs); SURVE = early survival, SURVL = late survival (score 0 = died/culled, 1 = survived); LONG = longevity (wk); WA = walking ability (scored from 1 = poor to 6 = excellent); BST = breast structure, HBS = humped back structure, HS = hip structure, LS = leg structure, FS = foot structure, FTPAD = footpad dermatitis, BSK = breast skin, HE = head and eye, PC = pendulous crop, WS = wing structure (score 0 = affected, 1 = healthy).

Table 3. Summary of traits analyzed (X) in each of 15 multitrait animal models[1]

	Both dam and sire lines										Dam line only				
Trait[2]	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
BW_{15}	X	X	X	X	X	X	X	X	X	X					
BW_{20}	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
EP											X	X	X	X	X
SURVE	X	X									X				
SURVL	X		X									X			
LONG				X									X		
WA		X	X	X	X	X	X	X	X	X	X	X	X	X	X
HS					X									X	
LS						X									X
FS							X								
FTPAD								X							
PC									X						
BSK										X					

[1]Model numbers 1 to 10 were fit for both lines. Model numbers 11 to 15 were fit for the dam line only.

[2]BW_{15} = BW at 15 wk, BW_{20} = BW at 20 wk (g); EP = egg production (no. of eggs); SURVE = early survival, SURVL = late survival (score 0 = died/culled, 1 = survived); LONG = longevity (wk); WA = walking ability (scored from 1 = poor to 6 = excellent); HS = hip structure, LS = leg structure, FS = foot structure, FTPAD = footpad dermatitis, PC = pendulous crop, BSK = breast skin (score 0 = affected, 1 = healthy).

and heritability ($h^2 < 0.02$) in univariate analysis; consequently, multivariate analyses were not conducted for these.

A series of 4-trait animal models were used to calculate correlations among traits within each line (Table 3). For both lines, BW_{15} and BW_{20} were incorporated into multitrait analyses numbers 1 to 10 because growth is a major selection trait. Additionally, for the DL, analyses that included BW_{20} and EP were run because selection is based on growth and reproductive performance in this line.

In both lines, the models for each trait, except EP, were

$$y_{ijkl} = \mu_i + sex_{ij} + group_{ik} + A_{il} + e_{ijkl},$$

where y_{ijkl} is the observation of trait i for individual l, μ_i is the population mean of trait i, sex_{ij} is the fixed effect of sex j on trait i, $group_{ik}$ is the random effect of hatch group k on trait i, A_{il} is the random animal genetic effect of trait i for individual l, and e_{ijkl} is the random residual error of trait i for individual l. The model for EP was similar to that above, but with the sex effect removed.

Traits could only be measured on birds that survived the early phase (i.e., SURVE = 1). Therefore, residual covariances between SURVE and all other traits were set to 0 and corresponding phenotypic correlations were not estimable. Similarly, EP was only measured on females that survived the investigated period; thus, all individuals with EP observations had SURVE = SURVL = 1. Therefore, residual covariances between EP and SURVE or SURVL were set to 0 in analyses.

Heritability (h^2) and common environment (c^2) were ratios of genetic variance and hatch group variance, respectively, to total phenotypic variance. For survival to specific ages and structural fitness traits in this study, it was likely that although the phenotypes were dichotomous on an observed scale, there was an underlying continuous scale.

RESULTS

Several models were used to estimate all parameters; therefore, multiple estimates were generated for most traits. In Tables 4, 5, and 6, only 1 representative estimate is shown for each trait combination. Estimates for given traits were similar across different models.

Heritability and Variances

Production Traits. Body weights displayed expected moderate heritability ($h^2 = 0.18$ to 0.35; Table 4) in both lines. Body weights at 15 wk displayed higher heritability than weights at 20 wk and estimates were slightly higher in the DL than in the SL. Egg production in the DL also displayed moderate heritability ($h^2 = 0.25$).

Survival Traits. Early survival (to 3 wk) displayed low heritability in both lines ($h^2 = 0.02$ and 0.04 for the DL and SL, respectively; Table 4). Late survival (3 to 23 wk) showed slightly higher heritability than SURVE ($h^2 = 0.14$), and LONG heritability estimates in both lines were similar to those for SURVL.

Structural Fitness Traits. Walking ability had moderate heritability in both lines similar to production traits ($h^2 = 0.26$ and 0.25 for the DL and SL, respectively; Table 4). Leg structure had the highest heritability of the skeletal structural traits, likely due to higher incidence of defined defects. Leg structure displayed quite low heritability ($h^2 = 0.08$), and HS and FS displayed very low heritability ($h^2 = 0.02$). Pendulous crop displayed moderate heritability ($h^2 = 0.12$) in both lines. These estimates should be interpreted with caution, because although estimates changed by only 1% or less between iterations, ASReml log-likelihood

Table 4. Representative estimates of production and fitness traits: additive genetic $\left(\sigma^2_G\right)$, contemporary group $\left(\sigma^2_C\right)$, and phenotypic $\left(\sigma^2_P\right)$ variances; heritability (h^2); and common environmental effects (c^2) in dam and sire parent lines

Trait[1]	Model[2]	σ^2_G	σ^2_C	σ^2_P	$h^2 \pm$ SE	$c^2 \pm$ SE
Dam line						
BW_{15}	1	222,612	250,902	637,385	0.35 ± 0.015	0.39 ± 0.024
BW_{20}	1	463,963	901,603	2,090,295	0.22 ± 0.011	0.43 ± 0.025
EP	11	98.4	62.2	390.2	0.25 ± 0.028	0.16 ± 0.019
SURVE	1	0.0002	0.0006	0.0109	0.02 ± 0.002	0.05 ± 0.005
SURVL	1	0.0526	0.1589	0.3759	0.14 ± 0.007	0.42 ± 0.025
LONG	4	107.4	434.3	897.4	0.12 ± 0.007	0.48 ± 0.025
WA	2	0.228	0.041	0.8650	0.26 ± 0.007	0.05 ± 0.005
HS	5	0.0003	0.0003	0.0209	0.02 ± 0.001	0.02 ± 0.002
LS	6	0.0115	0.0056	0.1409	0.08 ± 0.003	0.04 ± 0.004
FS	7	0.0000	0.0000	0.0027	0.02 ± 0.002	0.01 ± 0.001
FTPAD	8	0.0001	0.0002	0.0100	0.01 ± 0.001	0.02 ± 0.002
PC	9	0.0011	0.0001	0.0091	0.12 ± 0.004	0.01 ± 0.001
BSK	10	0.0000	0.0000	0.0000	0.00 ± 0.001	0.00 ± 0.001
Sire line						
BW_{15}	1	341,054	426,179	1,283,217	0.27 ± 0.010	0.33 ± 0.022
BW_{20}	1	696,159	1,613,600	3,962,119	0.18 ± 0.009	0.41 ± 0.024
SURVE	1	0.0011	0.0002	0.0246	0.04 ± 0.002	0.01 ± 0.001
SURVL	1	0.0527	0.1420	0.3793	0.14 ± 0.006	0.37 ± 0.024
LONG	4	110	266	848	0.13 ± 0.005	0.31 ± 0.022
WA	2	0.2301	0.0478	0.9214	0.25 ± 0.007	0.05 ± 0.006
HS	5	0.0007	0.0005	0.0289	0.02 ± 0.002	0.02 ± 0.002
LS	6	0.0121	0.0048	0.1433	0.08 ± 0.003	0.03 ± 0.003
FS	7	0.0001	0.0000	0.0035	0.02 ± 0.002	0.00 ± 0.000
FTPAD	8	0.0002	0.0003	0.0140	0.02 ± 0.001	0.02 ± 0.002
PC	9	0.0022	0.0003	0.0192	0.12 ± 0.004	0.02 ± 0.002
BSK	10	0.0001	0.0001	0.0076	0.02 ± 0.001	0.01 ± 0.001

[1]BW_{15} = BW at 15 wk, BW_{20} = BW at 20 wk (g); EP = egg production (no. of eggs); SURVE = early survival, SURVL = late survival (score 0 = died/culled, 1 = survived); LONG = longevity (wk); WA = walking ability (scored from 1 = poor to 6 = excellent); HS = hip structure, LS = leg structure, FS = foot structure, FTPAD = footpad dermatitis, PC = pendulous crop, BSK = breast skin (score 0 = affected, 1 = healthy).

[2]Models as described in Table 3.

Table 5. Representative estimates of genetic (r_G) and phenotypic (r_P) correlations between BW (g) and fitness traits in dam and sire parental lines

		BW at 15 wk		BW at 20 wk	
Trait[1]	Model[2]	$r_G \pm$ SE	$r_P \pm$ SE	$r_G \pm$ SE	$r_P \pm$ SE
Dam line					
SURVE	1	0.09 ± 0.032	NE[3]	0.03 ± 0.034	NE
SURVL	1	−0.22 ± 0.020	−0.06 ± 0.030	−0.24 ± 0.021	−0.17 ± 0.031
LONG	4	−0.15 ± 0.021	−0.05 ± 0.032	−0.18 ± 0.022	−0.28 ± 0.030
WA	2	−0.31 ± 0.019	−0.13 ± 0.011	−0.37 ± 0.019	−0.18 ± 0.009
HS	5	−0.26 ± 0.035	−0.05 ± 0.006	−0.28 ± 0.036	−0.05 ± 0.006
LS	6	−0.31 ± 0.022	−0.04 ± 0.010	−0.35 ± 0.023	−0.08 ± 0.009
FS	7	−0.08 ± 0.038	0.00 ± 0.004	−0.08 ± 0.039	−0.01 ± 0.005
FTPAD	8	−0.24 ± 0.041	−0.03 ± 0.006	−0.23 ± 0.042	−0.04 ± 0.006
PC	9	−0.09 ± 0.024	−0.04 ± 0.005	−0.08 ± 0.024	−0.06 ± 0.005
BSK	10	−0.35 ± 0.060	−0.01 ± 0.004	−0.39 ± 0.060	0.00 ± 0.004
Sire line					
SURVE	1	0.20 ± 0.023	NE	0.10 ± 0.025	NE
SURVL	1	−0.11 ± 0.019	−0.01 ± 0.026	−0.09 ± 0.021	−0.18 ± 0.028
LONG	4	−0.09 ± 0.020	0.00 ± 0.024	−0.10 ± 0.021	−0.21 ± 0.025
WA	2	−0.43 ± 0.016	−0.16 ± 0.010	−0.50 ± 0.016	−0.24 ± 0.009
HS	5	−0.36 ± 0.028	−0.06 ± 0.005	−0.41 ± 0.029	−0.08 ± 0.006
LS	6	−0.46 ± 0.018	−0.07 ± 0.008	−0.49 ± 0.019	−0.13 ± 0.008
FS	7	0.10 ± 0.035	0.01 ± 0.003	0.11 ± 0.036	0.01 ± 0.003
FTPAD	8	−0.24 ± 0.041	−0.03 ± 0.006	−0.23 ± 0.042	−0.04 ± 0.006
PC	9	−0.17 ± 0.021	−0.04 ± 0.006	−0.14 ± 0.022	−0.05 ± 0.007
BSK	10	−0.23 ± 0.034	−0.03 ± 0.005	−0.23 ± 0.035	0.01 ± 0.005

[1]SURVE = early survival, SURVL = late survival (score 0 = died/culled, 1 = survived); LONG = longevity (wk); WA = walking ability (scored from 1 = poor to 6 = excellent); HS = hip structure, LS = leg structure, FS = foot structure, FTPAD = footpad dermatitis, PC = pendulous crop, BSK = breast skin (score 0 = affected, 1 = healthy).

[2]Models as described in Table 3.

[3]NE = not estimable.

Table 6. Representative estimates of genetic (r_G) and phenotypic (r_P) correlations between walking ability (WA) and other fitness traits in dam and sire parental lines[1]

		Dam line WA		Sire line WA	
Trait[2]	Model[3]	$r_G \pm$ SE	$r_P \pm$ SE	$r_G \pm$ SE	$r_P \pm$ SE
SURVE	2	0.02 ± 0.036	NE[4]	−0.12 ± 0.026	NE
SURVL	3	0.65 ± 0.014	0.59 ± 0.007	0.69 ± 0.012	0.62 ± 0.006
LONG	4	0.51 ± 0.017	0.52 ± 0.009	0.58 ± 0.015	0.57 ± 0.007
HS	5	0.85 ± 0.023	0.26 ± 0.003	0.86 ± 0.018	0.29 ± 0.003
LS	6	0.91 ± 0.007	0.65 ± 0.002	0.91 ± 0.007	0.63 ± 0.002
FS	7	0.08 ± 0.040	0.03 ± 0.003	0.06 ± 0.037	0.02 ± 0.003
FTPAD	8	0.08 ± 0.044	0.07 ± 0.003	0.08 ± 0.044	0.07 ± 0.003
PC	9	0.02 ± 0.026	0.00 ± 0.004	0.04 ± 0.023	0.06 ± 0.004
BSK	10	0.05 ± 0.063	0.02 ± 0.003	0.03 ± 0.037	0.04 ± 0.003

[1]WA is scored from 1 = poor to 6 = excellent.

[2]SURVE = early survival, SURVL = late survival (score 0 = died/culled, 1 = survived); LONG = longevity (wk); HS = hip structure, LS = leg structure, FS = foot structure, FTPAD = footpad dermatitis, PC = pendulous crop, BSK = breast skin (score 0 = affected, 1 = healthy).

[3]Models as described in Table 3.

[4]NE = not estimable.

for these models did not converge within 300 iterations. Footpad dermatitis and BSK defects had very low incidence (>98% healthy) and heritability ($h^2 \leq 0.02$) in both lines.

Correlations

SURVE and SURVL. Genetic correlations between SURVE and SURVL were close to zero in both lines (r_G = 0.10 ± 0.036 in DL, r_G = 0.03 ± 0.026 in SL). Corresponding phenotypic correlations were not estimable because all birds with SURVL records had SURVE = 1 observations.

Growth and Fitness Traits. Genetic correlations of fitness traits with BW were mostly negative in both lines (Table 5). The exceptions were SURVE, which had zero or very mild positive genetic correlation with BW in both lines, and FTPAD, which had very mild positive genetic correlation with BW in SL. Walking ability, HS, LS, FTPAD, and BSK had the strongest genetic correlations with BW (r_G = −0.39 to −0.23 in DL; r_G = −0.50 to −0.23 in SL). Late survival had stronger genetic correlations with BW in DL than in SL. Longevity tended to be less correlated with BW than survival score. Correlations tended to be stronger in SL. Phenotypic correlations were generally weaker than genetic correlations, except for SURVL in SL and LONG.

EP and Fitness Traits. In the DL, EP had positive genetic correlation with SURVL (r_G = 0.61 ± 0.037). Early survival (r_G = −0.01 ± 0.075), LONG (r_G = 0.00 ± 0.000), and WA (r_G = 0.07 ± 0.046; phenotypic correlation, r_P, = 0.02 ± 0.017) were not significantly correlated with EP. Corresponding phenotypic correlations with survival traits were not estimable because all birds with EP records survived the observation period. Correlations with defect traits could not be estimated, likely because there were too few observations.

WA and Fitness Traits. Walking ability had high positive genetic correlations with SURVL, LONG, HS, and LS in both lines (Table 6). Early survival, FS, PC, and BSK had near-zero correlations with WA.

DISCUSSION

Early survival and SURVL displayed low heritability, as did LONG. Survival and the other structural fitness traits presented some challenges in analysis. Survival to specific ages and occurrence of defects were defined as dichotomous phenotypes and did not conform to the continuous normal distribution assumed by linear analysis. Longevity was also not normally distributed because most birds survived to the end of the rearing period (i.e., the data was right censored). Additionally, the data set was truncated such that once an animal was culled, it had no further records. Therefore, survival from 3 to 23 wk could respond well to selection.

General survival can display a range of heritability for several reasons, including differential genotype expression with different environmental stressors, selection, non-additive genetic and environmental factors, antagonistic relationships among underlying health traits, and social interactions (Merilä and Sheldon, 1999; Ellen et al., 2008, 2010). Furthermore, heritability of binary traits such as survival on the observed scale is a function of the population frequencies of each phenotype; higher heritability is estimated when there are equal proportions of each phenotype (Lynch and Walsh, 1998). Studies in laying hens have found survival and robustness to be heritable (Pakdel et al., 2005; Ellen et al., 2008, 2010), but comparable literature estimates of survival genetic parameters are sparse for meat poultry. Early survival and late survival were not genetically correlated, indicating these are independent traits. Although these estimates are subject to the same limitations discussed above, this result indicates that selection to improve survival will only affect the life stage under selection.

Genetic correlations of survival and LONG with BW were mostly negative in both lines. Consequently, SURVL or a correlated trait, such as WA, should be included in a selection index to prevent correlated decreased survival in response to selection for growth. In the DL, EP had a moderate positive genetic correlation with SURVL, but no significant genetic correlation with SURVE or LONG. As a result, the selection for increased egg production should not negatively affect survival.

Walking ability displayed moderate heritability. This result agrees with some strain comparisons that have indicated a genetic basis for WA in turkeys and broilers (e.g., Ye et al., 1997; Kestin et al., 2001), but contrasts with the much lower heritability (0.06) found by Havenstein et al. (1988). The results of the current study may reflect differences in the commercial WA scoring used versus scoring systems used in other studies (e.g., Nestor, 1984; Kestin et al., 1992), but also likely derive from a greater amount of information in multi-generation data as well as high-quality observations from experienced phenotypic scorers. Noble et al. (1996) found WA can be influenced by genotype by environment interactions. The commercial rearing environment of the birds in this study likely allowed greater genotypic expression of WA, leading to higher heritability. Walking ability had high positive genetic correlations with SURVL, LONG, and hip and leg health in both lines. Therefore, WA should be a good indicator trait for selection to improve both overall survival and hip and leg health.

Leg health had the highest heritability of the skeletal structural traits, likely due to higher incidence of a recorded defect. Leg health, as defined in this study, was a composite trait and thus, unsurprisingly, displayed lower heritability than has been calculated for some specific defects in broilers (e.g., bowed and splayed legs, Mercer and Hill, 1984; tibial dyschondroplasia, Kuhlers and McDaniel, 1996; valgus and varus angulations, Le Bihan-Duval et al., 1997).

Hip structure, FS, FTPAD, and BSK health displayed very low heritability. Footpad dermatitis is of particular interest because this trait is an important poultry welfare criterion in the European Union (Hocking et al., 2008). The low heritability of footpad health found in this study indicates that this trait is mainly environmentally caused, and likely best controlled through improved management.

Pendulous crop, a condition in which the bird's crop becomes distended and filled with fluid, is another welfare concern, and affected birds may grow poorly and be culled from flocks (Butterworth and Weeks, 2010). Pendulous crop displayed moderate heritability in both lines, indicating that genetic selection should be effective to decrease incidence of this condition. Although PC is commonly considered to have some genetic basis (Asmundson and Hinshaw, 1938; Butterworth and Weeks, 2010), no comparable heritability estimates have been found in the scientific literature.

Most fitness traits had negative genetic correlations with BW, indicating unchecked selection for growth could decrease survival, WA, and HS, LS, footpad, and BSK health. This result agrees with Nestor et al. (2008) who found that long-term selection for growth negatively affected turkey WA. Similarly, Kestin et al. (2001) concluded that selection for increased weight and rapid growth resulted in lameness in broiler chickens. Genetic correlations between growth and skeletal defects have varied in studies and specific traits can relate to growth differently (Le Bihan-Duval et al., 1997). As genetic correlations between the general fitness traits in this study and BW were not overly strong, individuals with superior genotypes for both BW and fitness traits should exist in the populations. In addition, DL EP had no significant genetic correlation with walk score and, therefore, selection to improve WA should not affect EP. In conclusion, genetic parameters in this study indicate that index selection should be effective at improving fitness, survival, and growth simultaneously in commercial turkey lines. Walking ability was found to be a good indicator trait for selection to improve overall SURVL and HS and LS health in turkeys.

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