Pedigree and genomic analyses of feed consumption and residual feed intake in laying hens

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ABSTRACT Efficiency of production is increasingly important with the current escalation of feed costs and demands to minimize the environmental footprint. The objectives of this study were 1) to estimate heritabilities for daily feed consumption and residual feed intake and their genetic correlations with production and egg-quality traits; 2) to evaluate accuracies of estimated breeding values from pedigree- and marker-based prediction models; and 3) to localize genomic regions associated with feed efficiency in a brown egg layer line. Individual feed intake data collected over 2-wk trial periods were available for approximately 6,000 birds from 8 generations. Genetic parameters were estimated with a multitrait animal model; methods BayesB and BayesCπ were used to estimate marker effects and find genomic regions associated with feed efficiency. Using pedigree information, feed efficiency was found to be moderately heritable (h^2 = 0.46 for daily feed consumption and 0.47 for residual feed intake). Hens that consumed more feed and had greater residual feed intake (lower efficiency) had a genetic tendency to lay slightly more eggs with greater yolk weights and albumen heights. Regions on chromosomes 1, 2, 4, 7, 13, and Z were found to be associated with feed intake and efficiency. The accuracy from genomic prediction was higher and more persistent (better maintained across generations) than that from pedigree-based prediction. These results indicate that genomic selection can be used to improve feed efficiency in layers.

Key words: feed efficiency, layer, quantitative trait loci, genomic breeding value

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INTRODUCTION

The long-term challenge for animal breeders is to improve the productivity of the major livestock species to feed the growing human population while at the same time minimizing the environmental impact (Hume et al., 2011; Van Arendonk, 2011). Feed efficiency has for many years been included in selection objectives for layer chickens (see review by Flock, 1998), which has resulted in a substantial reduction in emission of greenhouse gases (Hume et al., 2011), as well as an improvement of economic efficiency by reducing feed required per unit of product. Development of high-density SNP genotyping has provided tools to obtain further insights into the genetic basis of variation in feed efficiency and to improve accuracy of selection.

The objectives of this study were 1) to estimate heritabilities for daily feed consumption (**DFC**) and residual feed intake (**RFI**) and their genetic correlations with production and egg-quality traits; 2) to evaluate accuracies of estimated breeding values (**EBV**) from pedigree- and marker-based prediction models; and 3) to localize genomic regions associated with feed efficiency in a brown egg layer line.

MATERIALS AND METHODS

Individual feed-intake data on approximately 6,000 hens from an experimental brown-egg pure line layer population were available for this study. Prior to and during the experiment, the line was selected on an index combining 16 production and egg-quality traits. In generation 5, full-sib families were split into 2 lines: a line that continued under conventional selection using phenotypic and pedigree information with a 13-mo generation interval; a line that was under genomic selection, with a shorter generation interval (around 6 mo). In the pedigree-selected subline, ~60 males were mated to 360 females, producing 4,000 selection candidates per generation; in the genomic subline, 50 males were mated to 50 females, producing only 600 selection candidates to reduce genotyping cost. In the conventional selection line, data were collected for one more

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Table 1. Number of records, means, SD, and ranges of the traits analyzed[1] for animals used in pedigree-based analyses (All) and in marker-based analysis, separated by animals with own genotypes and phenotypes (Own) and animals that were included into progeny means of genotyped individuals (Progeny)

	All					Own			Progeny		
Trait	N	Mean	SD	Minimum	Maximum	N	Mean	SD	N	Mean	SD
RFI	6,088	0.0	22.5	−170.5	109.7	1,555	1.0	16.3	2,449	−0.6	16.8
DFC	6,088	145.4	55.4	15.6	375.7	1,555	123.9	20.7	2,449	122.9	21.8
PD	4,817	80.4	10.6	27.5	106.1						
SM	6,072	149.4	9.7	121.0	199.0						
EW	6,034	62.4	4.7	47.5	82.0						
PS	6,037	1,461.4	55.4	1,228.9	1,640.5						
AH	6,040	7.4	1.1	3.6	11.5						
CO	6,040	73.2	9.1	35.4	101.6						
YW	6,007	17.7	1.4	11.8	23.3						

[1]Residual feed intake (RFI, g), average feed consumption (DFC, g), egg production rate (PD, %), age at sexual maturity (SM, d). Egg-quality traits recorded at 42 to 46 wk of life: egg weight (EW, g), shell quality (PS, N), albumen height (AH, mm), egg color (CO, index units), and yolk weight (YW, g).

generation (generation 6). In the genomic selection line, feed-intake data were collected in generations 7 and 8 but not in generations 5 and 6 because of technical issues arising from shortened generation interval. Data and genotypes from the 2 lines were combined for the analyses.

Two scenarios were considered to evaluate the accuracy of pedigree- (EBV) or genome-based estimates of breeding values (**GEBV**): scenario 1: train using data from generations 1 to 4 before the lines were split and from generations 5 and 6 of the conventional selection line, and validate in generations 7 and 8 of the genomic selection line to evaluate persistency of accuracy (decline of accuracy over generations), and scenario 2: train with generation 7 added to training and validate in generation 8 to evaluate accuracy in progeny. Validation generations 7 and 8 had 294 and 277 individuals, respectively.

Feed-intake data were typically collected late in the laying period, and because the genomic line had a short generation interval, to have the same breeding objective in both lines, neither line was directly selected for feed efficiency. Feed-intake data were captured during a 2-wk feeding test on adult birds (greater than 38 wk of age). Birds were housed in individual cages and feed was provided in individual containers during a 1-wk adaptation period. Feed consumption was measured over the entire feeding period and used to derive average DFC (g). Individual BW were taken just before the start of the feed test. Residual feed intake (RFI) data were calculated as residuals from a regression model of DFC on egg mass (egg weight × number of eggs laid during the testing period) and metabolic BW (BW raised to the power of 0.75). All measurements and calculations of RFI were done within line and generation.

Genetic parameters for feed-consumption traits were estimated using all data, with a multitrait animal model using ASReml (Gilmour et al., 2008), fitting the fixed effect of hatch-week-line (Table 1). Groups of 8 traits (7 production and egg-quality traits, plus 1 feed-related trait) were analyzed jointly, and the 2 feed-related traits were analyzed in a separate bivariate analysis because of slow convergence with more traits. Production traits analyzed were egg production (number of saleable eggs/number of days × 100 during 38–47 wk of age); age at sexual maturity (d); egg-quality traits collected at 42 to 46 wk of age, and recorded as the average of between 3 and 5 eggs per hen, including egg weight (g); shell color collected from same eggs by a chroma meter that measured lightness (L) and hue [as a function of a red-green (a) and a yellow-blue (b) scale]; shell quality measured as puncture score (N)—a nondestructive deformation test averaged over 2 points of the shell; albumen height (mm); and yolk weight (g). Information on available phenotypes is in Table 1. The last generation of the conventional selection line had not finished their production records when this study was initiated, accounting for the lower number of observations for egg production in that line.

All parents of phenotyped individuals from generations 1 to 5 and validation animals from generations 7 and 8 (genomic selection line) were genotyped with a custom Illumina 42K chip (Illumina Inc., San Diego, CA), with 24,383 segregating SNP selected after quality control (minor allele frequency >0.025; proportion of missing genotypes <0.05; parent-offspring mismatches <0.05). Marker effects and GEBV were estimated using the GenSel software (Fernando and Garrick, 2009). Method BayesCπ (Habier et al., 2011) was used to estimate the number of markers associated with the traits of interest, which was subsequently used to define the prior for the proportion of SNP with zero effects (π) in BayesB (Meuwissen et al., 2001). In the marker-based methods, only the phenotypes of genotyped individuals or their progeny (data included as full-sib family means) were used, whereas pedigree analysis included all available data (Table 1).

Marker estimates obtained from generations 1 to 7 of the combined data from both lines were used to identify regions of 1 Mb (based on Build WUGSC 2.1/galGal3; http://genome.wustl.edu/genomes/view/gallus_gallus/#sequences_maps) that explained the larg-

Table 2. Estimates of pedigree-based and marker-based heritabilities, proportions of markers with zero effects, and genetic and phenotypic correlations between the feed-efficiency traits, and estimates of genetic correlations of feed-efficiency traits with production and egg-quality traits[1]

Item	DFC	RFI
Pedigree-based heritability	0.46 ± 0.03	0.47 ± 0.03
Marker-based heritability	0.37 ± 0.02[2]	0.14 ± 0.02[2]
Proportion of zero-effect markers	0.95	0.98
Genetic correlation	0.94 ± 0.01	
Phenotypic correlation with	0.94 ± 0.00	
PD	0.09 ± 0.08	0.13 ± 0.08
SM	0.07 ± 0.06	0.03 ± 0.06
EW	0.13 ± 0.05	−0.05 ± 0.05
PS	−0.11 ± 0.08	−0.04 ± 0.08
AH	0.19 ± 0.06	0.12 ± 0.06
CO	−0.09 ± 0.05	−0.08 ± 0.05
YW	0.16 ± 0.06	0.04 ± 0.06

[1]Estimates are based on data from both lines and all generations. DFC = daily feed consumption; RFI = residual feed intake; PD = egg production; SM = age at sexual maturity; EW = egg weight; PS = shell quality; AH = albumen height; CO = egg color; and YW = yolk weight.

[2]Standard error of marker-based heritability was calculated as a SD of its posterior distribution.

est proportion of genetic variance. These regions were considered to be associated with the traits and were further investigated by choosing the individual SNP in each region with the highest posterior probability of inclusion. The significance of each chosen SNP was then independently tested in validation generation 8 by fitting a mixed model in ASReml with hatch week and SNP genotype as fixed effects and a random polygenic effect with relationships to correct for family structure. Regions within 1 Mb from the most significant SNP were searched for previously reported QTL (http://animalgenome.org) and known candidate genes (http://www.ncbi.nlm.nih.gov/).

RESULTS AND DISCUSSION

Pedigree-Based Analysis

Estimates of heritabilities were 0.46 and 0.47 for DFC and RFI. Several studies, including selection experiments, have shown that feed intake and efficiency have a sizeable heritable component and respond to selection (see review by Flock, 1998). Genetic and phenotypic correlations between the feed-consumption traits and estimates of genetic correlations of DFC and RFI with egg production and egg-quality traits are in Table 2. Hens that consumed more feed and had greater RFI had a genetic tendency to lay slightly more eggs with greater yolk weights and albumen heights.

Accuracy of Pedigree- and Marker-Based EBV

The marker-based heritability estimate was similar to the pedigree-based estimate for DFC, but it was lower than the pedigree-based estimate for RFI (Table 2). The estimates of the proportion of markers with zero effects on traits were 0.95 for DFC and 0.98 for RFI, which is within the range of values estimated for production and quality traits in this population (Wolc et al., 2011b). Correlations between EBV and phenotypes of validation individuals are in Table 3. In scenario 1, selection candidates were more distantly related to the training individuals (2 and 3 generations apart) than in scenario 2 (1 generation apart). This lower degree of relatedness is reflected in a very-low accuracy of pedigree-based EBV (Table 3). Genomic EBV had substantially higher accuracies than did EBV. In scenario 2, generations 1 to 7 were used for training, and prediction was in generations 7 (included in training) and 8 (progeny of

Table 3. Estimates of the accuracy of estimated breeding values (EBV) for residual feed intake (RFI) and daily feed consumption (DFC) based on pedigree- (EBV) and marker-based methods BayesB and BayesCπ for 2 validation scenarios,[1] based on correlations of phenotypes in generations 7 and 8 divided by the square root of heritability

		Scenario 1		Scenario 2	
Method	Generation	RFI	DFC	RFI	DFC
EBV	7	−0.04	−0.03	1.28	1.33
	8	−0.13	−0.13	0.31	0.31
BayesB[2]	7	0.09	0.21	1.01	1.14
	8	0.13	0.31	0.38	0.46
BayesCπ	7	0.09	0.18	1.04	1.15
	8	0.13	0.28	0.38	0.47

[1]Generation 7 is the last generation of training in scenario 2, so the correlations in generation 7 are with fitted data.

[2]For RFI and DFC, proportion of markers with nonzero effect was estimated with BayesCπ.

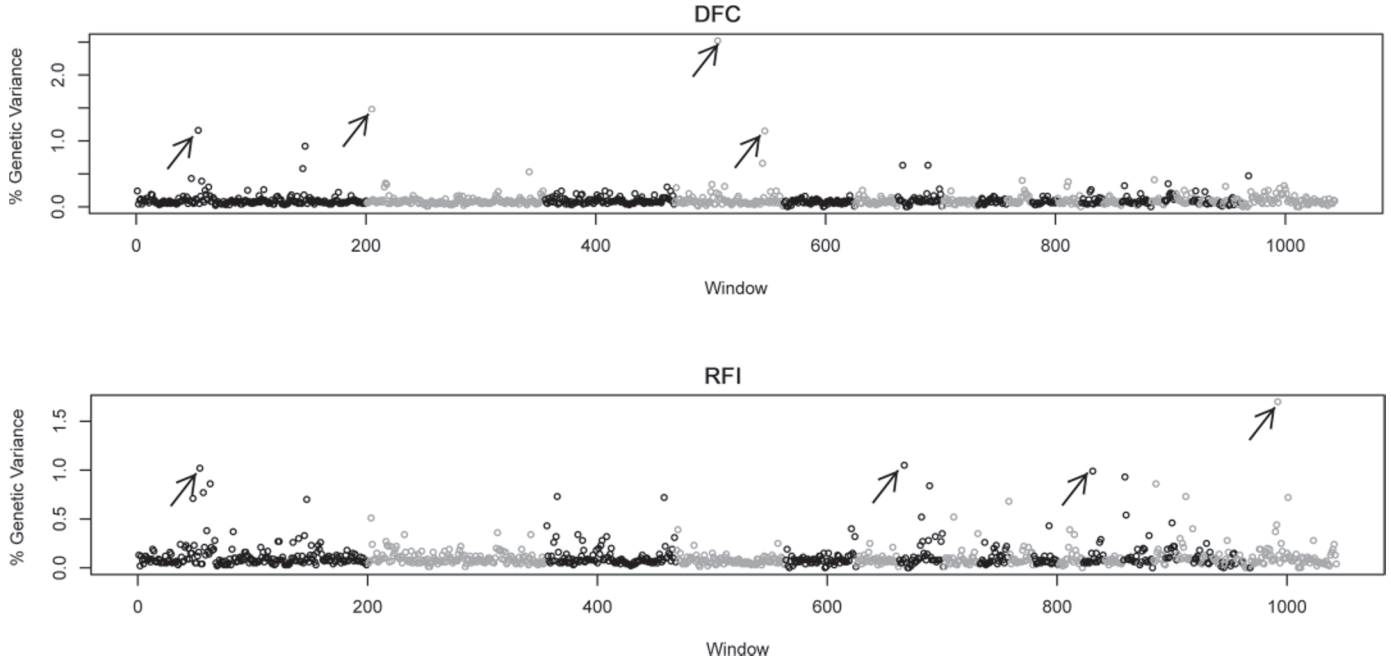

Figure 1. Percentage of genetic variance explained by 1-Mb regions across the genome for average feed consumption (DFC) and residual feed intake (RFI). Arrows point to the regions that explain the largest amount of variation, and alternating colors code the consecutive chromosomes. The last chromosome is Z.

training). Pedigree-based EBV had higher correlations with the last generation of training (generation 7) than did GEBV, but their predictive ability in the progeny (generation 8) was poorer than for GEBV (Table 3). The accuracies for more distantly related animals were lower than for progeny. However, the decline for GEBV was much less rapid than for EBV, and some accuracy was maintained even in the third generation after training (Table 3). This tendency for greater persistency of the accuracy of GEBV compared with EBV has also been observed in other studies (Habier et al., 2010; Saatchi et al., 2011; Wolc et al., 2011a).

Localization of Genomic Regions Associated with Feed Intake and Efficiency

The proportion of genetic variance explained by each 1-Mb region across the genome for DFC and RFI is plotted in Figure 1. The 4 regions explaining the largest proportion of genetic variance for each trait are in Table 4, together with the estimate of the effect of the most significant SNP within each region. Each of the identified regions on chromosomes 1, 2, and 4 explained more than 1% of genetic variance for DFC. For RFI, regions located on chromosomes 1, 7, 13, and Z had the

Table 4. Regions (1 Mb) of the genome that explained the largest proportion of genetic variation for daily feed consumption (DFC) and residual feed intake (RFI), and results for the most significant SNP within these regions, including the *P*-values for the effect of these SNP in validation[1]

	1-Mb region									
		%Var			Most significant SNP within region					
Chromosome_Mb	Loci	DFC	RFI	$P > 0$	SNP	PIP	MAF	GenVar	α	*P*-value
4_037	15	2.52		0.960	rs14739643	0.933	0.405	3.527	−2.705	0.133
2_004	33	1.48		0.978	rs13534867	0.823	0.248	1.773	−2.182	0.542
1_053	30	1.16		0.978	rs13866006	0.290	0.082	0.111	−0.860	0.822
4_078	19	1.15		0.857	rs14491030	0.561	0.186	0.981	1.800	0.0003
Z_023	24		1.70	0.712	rs14758816	0.154	0.278	0.012	−0.170	0.354
7_004	28		1.05	0.667	rs14602043	0.295	0.500	0.073	0.382	0.268
1_053	30		1.02	0.733	rs13866115	0.129	0.164	0.010	0.192	0.643
13_008	25		0.99	0.628	chr13–8359861	0.262	0.465	0.060	−0.348	0.179

[1]Loci = number of SNP in the 1-Mb region, %Var = percentage of genetic variance explained by the region, $P > 0$ = frequency of samples for which the region had a nonzero effect, SNP = marker with the highest posterior probability of inclusion (PIP) in the region and its position, minor allele frequency (MAF), genetic variance explained (GenVar = $2pq\alpha^2$), allele frequencies p and q and substitution effect (α), *P*-value for the SNP effect in the validation data.

Table 5. Known genes and previously reported QTL in the neighborhood of the regions associated with feed intake and efficiency

Chromosome	SNP	Genes located within 1 Mb from the most significant SNP[1]	Previously identified trait QTL within 1 Mb from the most significant SNP[2]
Daily feed consumption			
4	rs14739643	*MMRN1*, *GRID2*	TW, WINGWT, SFWT, LIVWT, GROWTH, BW, DSWT, BTEMP, ABFP, CREAT, FEAR, MD
2	rs13534867	*TBRG4*, *CTDSPL*, *ACAA1*, *PLCD1*	SGRAV, BW, EW, FEAR, HU, MD, ABR, DSWT, IGF, FI
1	rs13866006	*LGALS2*, *CYTH4*, *SSTR3*	IGF, INTES, CW, BW, AF, SPLWT, SHKLN, IF, BL, ABFP, ABR, FBMD, EP, EW, BCo, HU, LIVWT
4	rs14491030	*LCORL*, *NCAPG*, *LAP3*	SFWT, LIVWT, GROWTH, BW, BTEMP, ABFP, EW, FI, TW, WINGWT, DSWT, BPh, SHKLN, BDPHT, BMWT, HBMC, AW, ESP, FEAR, SLE, PECMAJW, CW
Residual feed intake			
Z	rs14758816	*GFM2*, *HEXB*, *ENC1*	EST, BW, ABR, LIVWT, MD, FBMD, CORT
7	rs14602043	*ABCA12*	AF, DSWT, FATDIST, SFWT, BW, INTES, ABFP
1	rs13866115	*LGALS1*, *LGALS2*, *TMPRSS6*	IGF, INTES, CW, BW, AF, SPLWT, SHKLN, IF, BL, ABFP, ABR, FBMD, EP, EW, BCo, HU, LIVWT
13	chr13–8359861	*ADRB2*, *FABP6*	SFWT, GROWTH, DSWT, BMWT, BW, AF, GL, BROOD, TL, SHKLN

[1]The expansions of gene symbols can be obtained from http://www.ncbi.nlm.nih.gov/gene/.

[2]The QTL information was obtained from ChickenQTLdb at http://www.genome.iastate.edu/cgi-bin/QTLdb/GG/index. ABFP = abdominal fat percentage; ABR = antibody response; ADG = average daily gain; AF = abdominal fat weight; AW = albumen weight; BCo = breast color; BDPHT = body depth; BL = bacterial load; BMWT = breast muscle weight; BpH = breast pH; BTEMP = body temperature; BW = body weight; CORT = corticosterone response; CREAT = creatinine kinase level; CW = carcass weight; DRUMBWT = drumstick bone weight; DSWT = drumstick weight; EP = egg production; ESP = eggshell percentage; EST = eggshell thickness; FBMD = femur bone mineral density; FEAR = fear-related behavior; GL = glucose level; HBMC = humeral bone mineral content; IF = intramuscular fat; INTES = intestine length; LIVWT = liver weight; MD = Marek's disease; PECMAJW = pectoralis major weight; RFI = residual feed intake; SFWT = skin fat weight; SGRAV = specific gravity; SHKLN = shank length; SLE = short length of egg; SLL = serum lipid level H; SPLWT = spleen weight; TL = tibia length; TW = tibia width; WINGWT = wing weight.

highest contribution to genetic variance. On chromosome 1, one associated region was common to both RFI and DFC. The region on chromosome 4 was also found to be significant for egg weight in this population (Wolc et al., 2012).

In validation, only the region on chromosome 4 for DFC was confirmed to be significant, but power to detect the effect with only 277 validation individuals may have been limited, especially for SNP with a low minor allele frequency. Some independent confirmation of the identified regions can, however, be found in the literature. For feed conversion and feed intake, De Koning et al. (2004) and Nones et al. (2006) mapped a QTL close to the same region on chromosome 1. On chromosome 2, a feed-intake QTL was reported by van Kaam et al. (1999). The distal part of chromosome 3 was reported to carry a QTL for RFI (De Koning et al., 2004; Parsanejad et al., 2004). Both regions on chromosome 4 were previously reported as carrying feed-intake QTL, at 37 Mb by van Kaam et al. (1999) and at 78 Mb by Tuiskula-Haavisto et al. (2002). Moura et al. (2006) and De Koning et al. (2004) reported a feed-intake QTL on chromosome 7 but in a more distant location than the one found in this study; however, for a similar location, QTL were found for fat deposition (Ikeobi et al., 2002; Zhou et al., 2006), which may contribute to feed efficiency. A region reported on chromosome 13 for RFI by De Koning et al. (2004) does not colocalize to the region found in this study. No previously reported QTL for feed intake or efficiency were found for the region at 23 Mb on chromosome Z, thus it can be considered a novel region potentially associated with RFI.

In addition to the few studies reporting QTL for feed intake and efficiency, several reports on other traits that are related to feed efficiency, such as growth and fat deposition, have been published. A summary of known genes and reported QTL within 1 Mb from the most significant SNP is in Table 5. Based on their annotation and studies in other species, several of these genes can be considered functional candidates for feed intake and efficiency. The *LCORL* (ligand dependent nuclear receptor corepressor-like) and *NCAPG* (non-SMC condensin I complex, subunit G) genes were shown to be significantly associated with feed intake in beef cattle (Lindholm-Perry et al., 2011), although the underlying mechanisms are not yet understood. The *ACAA1* (acetyl-CoA acyltransferase 1) gene showed differential expression in a feed-to-fasting experiment in chickens (Désert et al., 2008). Genes *ADRB2* (adrenergic, β-2-, receptor) and *TFAP2B* (transcription factor AP-2 β) were previously suggested as candidate genes for obesity-related adiposity and fat distribution traits in humans (Lindgren et al., 2009; Speliotes et al., 2010; Angeli et al., 2011). The *FABP6* (fatty acid binding protein 6) gene regulates fatty acid intake and transportation and metabolism (Chmurzyńska, 2006). The *PLCD1* (phospholipase C, delta 1) gene belongs to a group of enzymes that hydrolyze phospholipids into fatty acids and other lipophilic molecules (http://www.

genecards.org/cgi-bin/carddisp.pl?gene=PLCD1). The *MUT* (methylmalonyl CoA mutase) gene is involved in the degradation of several amino acids, odd-chain fatty acids, and cholesterol (http://www.genecards.org/cgi-bin/carddisp.pl?gene=MUT).

Conclusions

Feed intake and feed efficiency were found to be moderately heritable, and genomic breeding values for DFC and RFI were found to be more accurate and more persistent than pedigree-based estimates. Regions on chromosomes 1, 2, 4, 7, 13, and Z were found to be associated with feed intake and efficiency.

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