Effects of maternal energetic efficiency on egg traits, chick traits, broiler growth, yield, and meat quality[1]

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ABSTRACT This study assessed egg traits, chick traits, growth, yield, and meat quality characteristics of the offspring from broiler breeders classified by 2 measurements of energetic efficiency: residual feed intake (RFI), defined as the difference between observed and expected ME intake, and residual maintenance requirement (RME_m), defined as the residual of the relationship between hen maintenance requirement and feed intake. A group of 72 pullets were placed in laying cages from 16 to 60 wk of age. Individual hen-based feed allocation was provided following a standard BW target. At 41wk, eggs from 8 d of production were collected and pedigree hatched. Chicks were assigned to 1 of 3 maternal RFI (RFI_{mat}) categories: low, average, and high. A total of 366 chicks were placed in 36 floor pens, 6 per sex × RFI_{mat} interaction, and raised to 38 d. At the end of the breeder experiment (60 wk), broilers were retrospectively assigned to a low or high maternal RME_m (RME_{mmat}) category. Low RFI_{mat} broilers had greater 38-d BW than average and high RFI_{mat} broilers. That was achieved through a greater BW gain and feed intake of low RFI_{mat} broilers from 21 to 28 d. It was found that RFI_{mat} had no effect on feed conversion, yield, or meat quality characteristics. Low RME_m hens produced heavier eggs (62.3 g) and chicks (42.5 g) than high RME_m hens (60.0 g; 41.0 g), but RME_{mmat} did not affect broiler 38-d BW. High RME_{mmat} broilers had greater breast yield (29.5%) and lower breast shear force (4.7 kg of force/g) than low RME_{mmat} broilers (28.5%; 5.6 kg of force/g). The low RFI_{mat} × high RME_{mmat} broilers had the greatest growth to 38 d. It was found that RFI_{mat} was inversely related to broiler growth, particularly when RME_{mmat} was high. Although low maintenance requirements may be desirable for egg and chick production, hens with a high maintenance requirement produced broilers with greater breast yield and tenderness. Minimizing maintenance requirements may not be compatible with maximizing broiler performance and meat yield.

Key words: energetic efficiency, residual maintenance requirement, residual feed intake, broiler growth, meat quality

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INTRODUCTION

Feed efficiency is enhanced by nutrient partitioning toward marketable outputs. Because of differences in production objectives, mechanisms affecting feed efficiency in parent stocks may differ from those controlling broiler efficiency, growth, and development. Understanding these relationships is important for continued improvements in broiler productivity without causing productivity losses in parent stocks.

Maintenance energy requirements are the most important factor affecting feed efficiency in laying hens (Luiting, 1990). It may be possible to separate variation in maintenance requirements of hens from other sources of variation in energetic efficiency. Residual feed intake (**RFI**), which is defined as the difference between the observed and expected ME intake after accounting for metabolic BW, BW gain, and egg mass production (**EM**; Bordas et al., 1992), has been used as a measure of energetic efficiency in hens (Flock, 1998). Recently, Romero et al. (2008) refined the RFI methodology to obtain a more specific estimate of hen maintenance. They described residual maintenance requirement (**RME_m**), which is the residual of the relationship between hen maintenance requirement and feed intake. Romero et al. (2008) also reported that low maintenance requirements in broiler breeders were related to high productivity. It is not clear whether high broiler breeder energetic efficiency has a positive effect on broiler production.

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Energetic efficiency of broiler breeders may affect growth and development of their progeny in 2 main ways: first, through heritable factors affecting efficiency and second, through egg size and composition. The size and metabolic activity of visceral organs and muscle mass are the main variables that affect breeder metabolic rate (Spratt et al., 1990) and broiler growth and development (Konarzewski et al., 2000). Variability in those traits may be captured in the calculation of breeder RME_m and may affect broiler growth and development. Variation in the composition of both eggs and BW gain can also be captured in the calculation of hen RFI (Luiting, 1990) and may affect broiler growth potential. Additional phenotypic effects affecting broiler growth are relationships between egg size and early muscle development (Sklan et al., 2003) and albumen proportion and embryonic growth (Enting et al., 2007).

The objective of this study was to assess egg traits, chick traits, growth, yield, and meat quality characteristics of high breast yield broilers produced from broiler breeder hens classified by 2 measures of energetic efficiency: RFI and RME_m. We hypothesize that, within a commercial high breast yield population, low RFI breeders will contribute efficiency-related traits that improve broiler performance, but breeders with low maintenance requirements will produce broilers with a lower proportion of high-energy demand tissues such as breast muscle. This was an exploratory study to relate maternal energetic efficiency with several egg and broiler variables.

MATERIALS AND METHODS

Stocks and Management

A total of 600 Ross 708 broiler breeder pullets (Aviagen Inc., Huntsville, AL) were raised in floor pens to 16 wk of age. Seventy-two pullets were randomly selected and placed in laying cages to 60 wk. A more detailed description of the broiler breeder experiment was described by Romero et al. (2008). Unique feed allocations were provided to individual hens, following the standard BW target for the strain. Artificial insemination was performed weekly from 30 wk of age. At 40 wk, eggs from 3 d of production were collected for analysis of egg traits. At 41 wk, eggs were collected for 8 d, identified by hen and date, stored at 16°C, and set into single-stage incubators with a randomized location. At 19 d of incubation, eggs were transferred to pedigree hatching trays with a newly randomized tray position in the hatcher. At hatch, chicks were feather-sexed and identified with bar-coded neck tags (Heartland Animal Health, Fair Play, MO). Chicks were placed in floor pens (1.7 × 2.1 m) at 32°C. Temperature was decreased by 1°C each 3 d to 22°C. Photoperiod was 23L:1D for the entire experiment. Pelleted wheat-soybean-based diets were provided ad libitum (Table 1). At 39 d, birds were processed in a federally inspected facility. Duplicate bar-coded wing bands identified birds during processing. The fasting and water withdrawal period before slaughter was 10 h.

Maternal Energetic Efficiency

Hen RFI was calculated from 35 to 41 wk using individual BW, average daily gain (**ADG**), and EM data as reported by Luiting and Urff (1991). Additional data from 216 broiler breeders from the experiment described by Romero et al. (our unpublished data) were included in the regression. Residual feed intake was calculated for each hen as the observed minus the predicted ME intake from equation [1]:

$$MEI_d = BW^{0.75}(147.44 - 0.85T) + 0.97ADG + 1.14EM \quad [1]$$

where MEI_d = the ME intake (kcal/d); $BW^{0.75}$ = the metabolic BW ($kg^{0.75}$); ADG and EM were expressed in grams per day; and T = temperature (°C).

Hen RME_m was calculated from 20 to 60 wk of age using the methodology reported by Romero et al. (2008). Briefly, a nonlinear mixed regression model included a random variable that described the deviation of each hen from the mean maintenance requirement. This enabled a unique maintenance requirement estimate for every hen. Residual maintenance requirement was defined as the residual of the linear regression of maintenance requirement and average ME intake. The following equations were calculated by Romero et al. (our unpublished data):

$$MEI_d = (a+u)BW^{0.54} + 1.18BW^{0.60}ADG_P^{1.10} - 0.46BWADG_N + 4.99BW^{-2.07}EM^{1.40} \quad [2]$$

$$E(a+u) = 21.5 + 0.34MEI \quad [3]$$

where ADG_P = a positive and ADG_N = a negative ADG (g/d); E(a + u) = the expected maintenance requirement per hen ($kcal/kg^{0.54}$); E(a) = the mean maintenance requirement and was estimated as 141 kcal/$kg^{0.54}$; and u~N(0,72) = a random variable that described the deviation of each hen from the mean maintenance requirement. The residual of equation [3] was the RME_m value.

Three maternal RFI (**RFI_{mat}**) categories were delimited by the 33.3 and 66.6 percentiles. Two maternal RME_m (**RME_{mmat}**) categories corresponded to values above or below the mean. Figure 1 shows the distribution of RFI and RME_m values for individual hens. Because RFI and RME_m values were residuals, lower values indicated greater efficiency. The number of hens in each RFI category was balanced, because RFI was known before the broiler experiment. Offspring from 3 hens were excluded, because they died before 60 wk. Hen number in each RME_m category was not balanced within RFI (Table 2). The number of broilers within each interaction is reported in Table 3.

Table 1. Composition and analysis of experimental diets

Item	Starter (0 to 11 d)	Grower (11 to 21 d)	Finisher (21 to 38 d)
Ingredient (%)			
Corn	18.00	18.00	15.00
Vegetable fat	3.77	3.36	4.13
Fish meal - menhaden	3.00	5.00	3.51
Soybean meal	26.87	16.21	15.10
Wheat	42.93	53.24	58.04
Calcium carbonate	1.50	1.05	1.07
Dicalcium phosphate	1.55	1.00	1.08
Salt	0.43	0.34	0.36
L-Lysine	0.23	0.15	0.15
DL-Methionine	0.23	0.10	0.09
L-Threonine	0.05	0.10	0.03
Broiler premix[1]	1.45	1.45	1.45
Total	100.00	100.00	100.00
Calculated nutrient composition			
CP (%)	23.0	20.2	19.0
ME (kcal/kg)	3,068.0	3,152.0	3,196.0
Calcium (%)	1.10	0.90	0.85
Available phosphorus (%)	0.50	0.45	0.42
Lysine (%)	1.35	1.10	1.01
Methionine (%)	0.60	0.46	0.42
Methionine + cysteine (%)	0.97	0.79	0.75

[1]Broiler premix provided the following per kilogram of diet: choline chloride premix, 3,000 mg; generic enzyme, 500 mg; coccidiostat, 500 mg; antibiotic growth promoter, 500 mg; vitamin A (retinyl acetate), 10,000 IU; cholecalciferol, 2,500 IU; vitamin E (DL-α-tocopheryl acetate), 50 IU; vitamin K, 2.0 mg; pantothenic acid, 14 mg; riboflavin, 5.0 mg; folacin, 0.8 mg; niacin, 65 mg; thiamine, 2.0 mg; pyridoxine, 4.0 mg; vitamin B_{12}, 0.015 mg; biotin, 0.18 mg; iodine, 0.5 mg; Mn, 70 mg; Cu, 8.5 mg; Zn, 80 mg; Se, 0.1 mg; Fe, 100 mg.

Experimental Design

A total of 138 eggs were analyzed for composition and quality traits with a 3 × 2 factorial design with 3 categories of RFI (low, average, and high) and 2 categories of RME_m (low and high), where hen was a random term. In the broiler experiment, chicks were assigned to 1 of 3 RFI_{mat} categories at hatch (low, average, and high). A total of 366 chicks were placed in 36 floor pens, 6 per each sex × RFI_{mat} interaction. At 60 wk of age, RME_{mmat} was calculated and broilers were retrospectively assigned to a low or high RME_{mmat} category. To analyze set eggs and newly hatched chick characteristics, the design was a 3 × 2 factorial with 3 categories of RFI_{mat} and 2 categories of RME_{mmat}, where each egg or chick was an independent experimental unit. For growth analysis, the design was a split plot with sex as the main plot and RFI_{mat} category, pen, and RME_{mmat} category as subplots. Pen nested within sex × RFI_{mat} and pen × RME_{mmat} nested within sex × RFI_{mat} were declared as random effects. Analysis of feed intake and feed conversion was only possible for RFI_{mat} and sex using a 3 × 2 factorial design with pen as the experimental unit. A 2 × 3 × 2 factorial with 2 sex, 3 RFI_{mat}, and 2 RME_{mmat} categories was used for yield and meat quality, where each carcass was an independent experimental unit. A total of 338 carcasses were analyzed. Breast sample weight was included as a covariate in cooking loss analysis.

To ensure random fertilization, hens were inseminated using 0.5 mL of pooled semen from 60 Ross roosters (Aviagen Inc.). This approach allowed study of variation due to female efficiency categories and vertical analysis of maternal factors like egg composition. Therefore, sire efficiency was assumed to be randomly distributed and independent from dam efficiency.

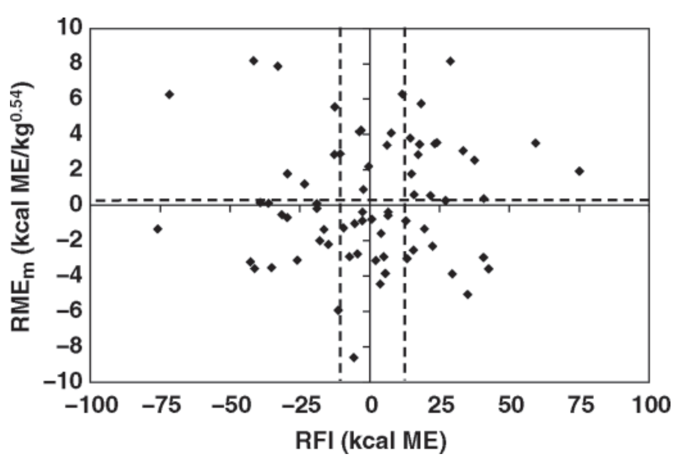

Figure 1. Residual feed intake (RFI) and residual maintenance requirement (RME_m) values of 69 Ross 708 dams, source of the broilers used in the current study. The RFI was defined as the difference between expected and observed ME intake and was measured from 35 to 41 wk of age. The RME_m was defined as the residual of the relationship between the hen maintenance requirement and feed intake and was calculated from 20 to 60 wk of age. Broken lines indicate the borders of maternal RFI and RME_m categories.

Table 2. Mean hen energetic efficiency measurements[1]

RFI[2] category	Hens (n)	RME_m[3] category	Hens (n)	Hen RFI (kcal/d)	Hen RME_m (kcal/$kg^{0.54}$)
Low	22	Low	15	−30.4	−1.8
		High	7	−32.0	4.8
Average	24	Low	16	0.6	−2.3
		High	8	4.0	3.5
High	23	Low	9	27.4	−2.7
		High	14	29.9	3.2

[1]Broiler offspring from these broiler breeders were assigned to experimental treatments based on these measures.

[2]Residual feed intake. Observed minus predicted ME intake calculated from 35 to 41 wk of age. Lower values indicated greater energetic efficiency, because feed intake was lower than predicted.

[3]Residual maintenance requirement. Residual of the relationship between hen maintenance requirement and feed intake calculated from 20 to 60 wk of age. Lower values indicated greater energetic efficiency, because maintenance requirement was lower than predicted.

Data Collection

Yolk weight, dried shell weight, and albumen height were measured as described by Wolanski et al. (2007). Equatorial shell thickness was recorded. Albumen weight was estimated as the egg weight minus yolk and shell weights. To assess albumen quality, Haugh units (HU; Kemps et al., 2006) were calculated using equation [4]:

$$HU = 100 \log_{10} (h - 1.7\, w^{0.37} + 7.6) \qquad [4]$$

where h = albumen height (mm) and w = egg weight (g).

Incubated eggs were weighed at collection and transfer. At hatch, chicks were weighed, and the length from the beak to the toe, excluding the nail, was measured. Chick yield was the chick weight as a proportion of the fresh egg weight. Individual weights were recorded at 11, 21, 28, and 38 d, and the daily weight gains were calculated between weighing periods. Breast pH was measured approximately 15 min after slaughter using a 10-mm incision in the ventral side of the right pectoralis major. Distilled water was added before inserting a pH probe (HI 98240, Hanna Instruments, Woonsocket, RI). Breast temperature was immediately recorded by inserting a temperature probe at the cranial end of the breast to the greatest temperature point. Carcasses were cut up by trained personnel approximately 5 h postmortem, after reaching an internal breast temperature of 4°C (maximum). Weights of the whole carcass, pectoralis major, pectoralis minor, thighs, drums, and wings were recorded.

The right pectoralis major was stored to measure pH and color 24 h after processing. Breast color was measured in 3 different points at the dorsal side of the pectoralis major, using a Chroma-meter CR-400 (Konica Minolta, Mississauga, Ontario, Canada). Color measurement was based on the L*a*b* 3-dimensional color space, with 1 dimension for lightness (L*) and 2 for color (a* = green to red; b* = blue to yellow; Zhang and Barbut, 2005). A 25 × 50 mm core, cut in the same direction as the muscle fibers, was taken at the thickest part of the left pectoralis major from 1 male and 1 female per broiler breeder for cooking loss and shear force measurements. Samples were weighed and stored at 2°C in trays with absorbent pads within plastic bags until 24 h after slaughter. After weighing, samples were placed in parchment paper-lined trays and cooked at 200°C to an internal temperature of 80°C using an electric convection oven and individual temperature probes (92000, Digi-Sense, Vernon Hills, IL). Cooking loss was calculated as the weight difference after cooling down the sample at room temperature. An Instron 411 (In-

Table 3. Experimental design[1]

Sex	n	RFI_{mat}[2]	n	RME_{mmat}[3]	n
Female	173	Low	47	Low	33
				High	14
		Average	64	Low	44
				High	20
		High	62	Low	24
				High	38
Male	193	Low	61	Low	46
				High	15
		Average	66	Low	40
				High	26
		High	66	Low	21
				High	45

[1]Numbers of broilers placed from each sex, $RFI_{mat,}$ and RME_{mmat} category. A split-plot design with sex as main plot and RFI_{mat}, pen, and RME_{mmat} as subplots was used for the broiler growth trial.

[2]Maternal residual feed intake. Observed minus predicted ME intake calculated from 35 to 41 wk of age.

[3]Maternal residual maintenance requirement. Residual of the relationship between hen maintenance requirement and feed intake calculated from 20 to 60 wk of age.

Table 4. Characteristics of eggs collected for 3 d before collection of eggs incubated for the broiler experiment[1]

RFI	RME_m	Albumen	Yolk	Shell	Albumen quality (HU[2])	Shell thickness (μm)
		% of egg weight				
Low		61.1	30.3	8.55	78.8	281.5
Average		60.0	31.4	8.63	77.1	284.6
High		60.5	31.2	8.24	76.5	274.3
SEM		0.4	0.4	0.17	0.8	6.9
	Low	61.0[a]	30.6	8.31	76.4	276.6
	High	60.0[b]	31.3	8.63	78.5	283.7
	SEM	0.4	0.4	0.14	1.4	5.6
Source of variation		Probability				
RFI		0.14	0.13	0.14	0.60	0.43
RME_m		0.031	0.13	0.08	0.25	0.32
RFI × RME_m		0.84	0.73	0.12	0.47	0.35

[a,b]Least squares means within a column within effect with no common superscript differ ($P < 0.05$).

[1]Breeders were classified in 3 RFI and 2 RME_m categories. RFI = hen residual feed intake calculated from 35 to 41 wk of age; RME_m = hen residual maintenance requirement calculated from 20 to 60 wk of age.

[2]Haugh units. $HU = 100 \log_{10} (h - 1.7 w^{0.37} + 7.6)$; h = albumen height; w = egg weight.

stron, Norwood, MA) with an Allo-Kramer blade set (10 blades; Cavitt et al., 2005) was employed to assess shear force. Shear force was defined as the peak force in kilograms of force (**kgf**) per gram of sample.

Statistical Analysis

Analyses of variance were performed using the MIXED procedure of SAS (SAS Institute, Cary, NC). Data are presented as least squares mean ± SEM. Significant differences between least squares means were determined using a Tukey-Kramer adjustment for unbalanced data. Unless specified otherwise, statements of significance are based on testing at $P \leq 0.05$.

Animal Use

This research project was carried out in compliance with the Guide to the Care and Use of Experimental Animals (Canadian Council on Animal Care, 1984). It was approved by a Faculty Animal Policy and Welfare Committee.

RESULTS AND DISCUSSION

Egg and Chick Characteristics

The proportion of albumen was greater in the low RME_m (61.0%) than in the high RME_m category (60.0%; Table 4). This was the only evident effect of efficiency categories on egg composition and quality. Consistent with the hypothesis that hens with a lower requirement for maintenance had more nutrients available for reproduction, low RME_m hens had greater egg weights (62.3 g) than high RME_m hens (60.0 g; Table 5). However, that difference was not found in low RFI hens where feed intake was lower (Romero et al., 2008). Enting et al. (2007) stated that a greater egg weight and a greater proportion of albumen gave broilers advantages for embryonic growth. In contrast, the greater albumen proportion and egg weight of low RME_m hens neither affected chick yield nor chick length, considered an indicator of development at hatch (Wolanski et al., 2004).

Chick yield was greater for high RFI_{mat} than low and average RFI_{mat} broilers. This difference may have been caused by differences in embryo metabolism among RFI categories, because chick yield was neither a reflection of egg weights (Table 5) nor shell quality (Table 4). Tona et al. (2004) found a lower weight loss and heat production for an experimental broiler strain with a lower egg weight compared with a commercial broiler strain, and Lourens et al. (2006) reported greater heat production during incubation for large eggs compared with small eggs. Although differences in transfer and chick BW were detected among RFI_{mat} categories, no differences in chick length were found.

Broiler Growth, Yield, and Feed Conversion

Differences in chick weight were no longer evident by 11 d (Table 6). From 21 to 28 d, the low RFI_{mat} broilers exhibited a greater BW gain (77.7 g/d) than high (73.6 g/d) RFI_{mat} broilers. Additionally, low RFI_{mat} broilers had a greater feed intake (128.0 g/d) compared with the average RFI_{mat} category (118.7 g/d; Table 7) during that period. These 2 factors contributed to the greater BW at 28 and 38 d of low RFI_{mat} broilers (1,297 and 2,255 g, respectively) compared with high RFI_{mat} broilers (1,234 and 2,144 g, respectively) and compared with average RFI_{mat} broilers (2,151 g) at 38 d. Notably, the effect of RFI_{mat} on BW gain occurred at a BW before the rate of energy retention as fat and protein are maximum (Lopez et al., 2007); therefore, RFI_{mat} may have affected the shape of the energy retention pattern. Interbreeder variation in BW gain composition was expected to be captured by RFI_{mat} and may be involved in determining differences in broiler growth.

The high RME_{mmat} broilers gained more weight (94.1 g/d) than the low RME_{mmat} broilers (90.7 g/d) from 28

Table 5. Egg weight, transfer egg weight, chick weight, chick yield, and chick length at hatch of eggs and chicks classified in 3 RFI_{mat}[1] and 2 RME_{mmat}[2] categories

RFI_{mat}	RME_{mmat}	Egg weight (g)	Transfer egg weight (g)	Chick BW (g)	Chick yield[3] (%)	Chick length[4] (mm)
Low		61.6	52.3^{ab}	41.7^{ab}	67.4^{b}	181.7
Average		60.2	51.2^{b}	40.9^{b}	67.8^{b}	182.8
High		61.7	53.0^{a}	42.7^{a}	68.9^{a}	181.9
SEM		0.6	0.4	0.3	0.3	0.6
	Low	62.3^{a}	52.9^{a}	42.5^{a}	68.2	182.5
	High	60.0^{b}	51.4^{b}	41.0^{b}	67.8	181.8
	SEM	0.5	0.3	0.3	0.3	0.5
Low	Low	61.2^{ab}	52.0^{a}	41.6^{b}	67.9	181.5
Low	High	62.0^{ab}	52.5^{a}	41.8^{ab}	67.0	181.9
Average	Low	62.5^{ab}	52.7^{a}	42.5^{ab}	67.9	183.5
Average	High	57.9^{c}	49.6^{b}	39.2^{c}	67.6	182.0
High	Low	63.2^{a}	53.9^{a}	43.5^{a}	69.0	182.3
High	High	60.2^{bc}	52.1^{a}	41.9^{ab}	68.8	181.5
SEM		1.0	0.7	0.6	0.5	1.0
Source of variation				Probability		
RFI_{mat}		0.039	0.0005	<0.0001	0.0002	0.33
RME_{mmat}		0.0001	0.0006	<0.0001	0.18	0.29
$RFI_{mat} \times RME_{mmat}$		0.001	0.003	0.0005	0.64	0.45

[a–c]Least squares means within a column within effect with no common superscript differ ($P < 0.05$).

[1]Maternal residual feed intake calculated from 35 to 41 wk of age. Broilers were assigned to 1 of 3 RFI_{mat} categories before hatching.

[2]Maternal residual maintenance requirement. Calculated from 20 to 60 wk of age. Broilers were retrospectively assigned to 1 of 2 RME_{mmat} categories.

[3]Chick weight as a percentage of fresh egg weight.

[4]Measured from the beak to the toe, excluding the nail.

to 38 d. Hens with greater maintenance requirements produced broilers with a greater growth rate during the last part of the experimental growth period. Interestingly, the interaction between RFI_{mat} and RME_{mmat} indicated that only low RFI_{mat} × high RME_{mmat} broilers had a greater 38-d BW (2,335 g) than the other subgroups. We therefore hypothesize that RFI_{mat} captured feed efficiency characteristics in breeders that affected

Table 6. Body weight at 11, 21, 28, and 38 d and BW gains between weighing periods from broilers classified in 3 RFI_{mat}[1] and 2 RME_{mmat}[2] categories

			BW (g)				BW gain (g/d)			
RFI_{mat}	RME_{mmat}	Sex	11 d	21 d	28 d	38 d	0 to 11 d	11 to 21 d	21 to 28 d	28 to 38 d
Low			252.7	749.5	$1,297.2^{a}$	$2,255.4^{a}$	19.2	48.9	77.7^{a}	95.1
Average			240.4	726.2	$1,242.7^{ab}$	$2,151.0^{b}$	18.1	49.2	74.0^{ab}	91.0
High			241.7	720.4	$1,234.1^{b}$	$2,144.4^{b}$	18.1	48.3	73.6^{b}	91.2
SEM			5.8	16.4	20.2	31.2	0.5	2.6	1.3	1.6
	Low		242.2	727.2	1,253.7	2,159.8	18.2	48.7	75.0	90.7^{b}
	High		247.7	736.9	1,262.3	2,207.5	18.5	48.9	75.2	94.1^{a}
	SEM		4.5	12.9	16.0	24.7	0.4	1.6	1.0	1.3
Low	Low		239.5	722.6	1,258.4	$2,175.9^{b}$	18.0	47.5	75.6	91.7
Low	High		266.0	776.4	1,336.1	$2,335.0^{a}$	20.4	50.3	79.8	98.4
Average	Low		242.8	730.9	1,249.9	$2,139.9^{b}$	18.2	49.5	74.6	89.5
Average	High		238.1	721.5	1,235.5	$2,162.1^{b}$	18.1	49.0	73.4	92.6
High	Low		244.4	728.1	1,252.8	$2,163.5^{b}$	18.3	49.0	74.7	91.1
High	High		239.1	712.7	1,215.4	$2,125.3^{b}$	17.9	47.6	72.5	91.3
SEM			9.2	25.9	34.1	53.0	0.8	3.0	2.2	2.8
		Female	250.6	722.9	$1,214.3^{b}$	$2,068.6^{b}$	19.0	47.5	70.3^{b}	85.0^{b}
		Male	239.3	741.2	$1,301.8^{a}$	$2,298.7^{a}$	17.9	50.2	79.9^{a}	99.9^{a}
		SEM	4.3	12.5	14.8	22.7	0.4	2.2	1.0	1.2
Source of variation						Probability				
RFI_{mat}			0.33	0.46	0.041	0.012	0.31	0.96	0.041	0.12
RME_{mmat}			0.42	0.61	0.68	0.14	0.30	0.82	0.84	0.045
$RFI_{mat} \times RME_{mmat}$			0.19	0.33	0.08	0.049	0.20	0.42	0.14	0.31
Sex			0.16	0.37	<0.0001	<0.0001	0.14	0.51	<0.0001	<0.0001

[a,b]Least squares means within a column within effect with no common superscript differ ($P < 0.05$).

[1]Maternal residual feed intake calculated from 35 to 41 wk of age. Broilers were assigned to 1 of 3 RFI_{mat} categories before hatching.

[2]Maternal residual maintenance requirement calculated from 20 to 60 wk of age. Broilers were retrospectively assigned to 1 of 2 RME_{mmat} categories.

Table 7. Partial and total feed intakes and feed conversion ratios from male and female broilers classified in 3 RFI_{mat}[1] categories

		Feed intake[2] (g/d)					Feed conversion ratio[2] (g of feed/g of BW)				
RFI_{mat}	Sex	0 to 11 d	11 to 21 d	21 to 28 d	28 to 38 d	Total (g)	0 to 11 d	11 to 21 d	21 to 28 d	28 to 38 d	Total
Low		27.7	77.2	128.0[a]	172.9	3,701.7	1.46	1.56	1.67	1.86	1.70
Average		26.5	74.1	118.7[b]	161.7	3,480.5	1.47	1.53	1.60	1.81	1.66
High		26.3	73.3	122.1[ab]	170.6	3,583.4	1.48	1.54	1.67	1.88	1.71
SEM		0.5	1.5	2.6	4.5	67.9	0.04	0.03	0.03	0.06	0.03
	Female	27.9	75.7	120.7	167.0	3,578.3	1.47	1.60[a]	1.71[a]	1.99[a]	1.77[a]
	Male	25.7	74.1	125.2	169.8	3,598.8	1.47	1.49[b]	1.59[b]	1.71[b]	1.61[b]
	SEM	0.4	1.2	2.1	3.6	54.6	0.03	0.02	0.02	0.05	0.03
Source of variation		Probability									
RFI_{mat}		0.10	0.15	0.05	0.17	0.08	0.93	0.68	0.13	0.66	0.39
Sex		0.001	0.33	0.13	0.58	0.79	0.99	0.001	0.001	0.0003	0.0001
RFI_{mat} × sex		0.016	0.07	0.79	0.80	0.74	0.011	0.08	0.41	0.97	0.83

[a,b]Least squares means within a column within effect with no common superscript differ ($P < 0.05$).

[1]Maternal residual feed intake calculated from 35 to 41 wk of age. Broilers were assigned to 1 of 3 RFI_{mat} categories before hatching.

[2]Least squares mean values were calculated for 36 pens used in the experiment.

broiler growth, especially in birds with a greater metabolic rate (high RME_{mmat}). Tona et al. (2004), based on a calorimetric study, suggested that faster-growing broiler strains have greater metabolic rates beginning during the final stage of incubation. In contrast, Malan et al. (2003) compared the total heat production (measured by comparative slaughter) of chicken genotypes differing in growth rate and reported that fast-growing strains had a lower heat production per kilogram$^{0.75}$ than slow-growing strains. It is possible that differences in development among strains at the time of the trial as well as the assumption of $BW^{0.75}$ as scaling metabolic BW (Lopez and Leeson, 2005) may have affected their conclusions.

Interspecies work (Ricklefs et al., 1996) has shown that the relationship between basal metabolism and total energy expenditure is very weak in birds compared with mammals, which suggests that in birds, independent mechanisms may affect nutrient partitioning at periods of high metabolic demand, as is the case in fast-growing broilers. Konarzewski et al. (2000) reported that a fast-growing line of chickens had a lower or equal resting metabolic rate than a slow-growing line. However, the fast-growing line had a greater peak metabolic rate when subjected to a cold stress, which was explained by a larger relative muscle mass. In the current study, we observed differences between low RME_{mmat} and high RME_{mmat} broilers in breast weight (386.6 g vs. 406.5 g, respectively) and breast yield (28.5 vs. 29.5%, respectively; Table 8). This difference was not the result of differences in BW, because the interaction was not significant, which supported our hypothesis that low maintenance breeders produce less muscular broilers. A high metabolic rate is required to support rapid growth because of energetic demands for maintenance of muscle and supply organs (Konarzewski et al., 2000).

No differences in carcass yield or abdominal fat pad percentage were evident among RME_{mmat} categories (Table 8). Abdominal fat pad weight was greater for low RFI_{mat} (1.84%) than average RFI_{mat} broilers (1.63%), even though carcass yield and breast proportion did not differ. Evidently, the nutrient partitioning of these 2 subgroups was different, but the mechanisms are unknown. Early differences in egg and chick weight between high and average RFI_{mat} categories suggest that phenotypic maternal effects may be involved. Additionally, voluntary intake (Table 7) may have played a role, because the low RFI_{mat} broilers had a greater intake than average and high RFI_{mat} broilers ($P = 0.08$).

No significant differences were found on feed conversion ratio among RFI_{mat} categories. Phenotypic selection for low RFI decreased feed conversion (Katle, 1991; Bordas et al., 1992) and voluntary ME intake (Swennen et al., 2007) in Leghorns. In restricted broiler breeders, feed intake strongly influences RFI, probably because of differences in dietary thermogenesis (Romero et al., 2008). In the current breeder experiment, feed intake was experimentally controlled to obtain a common BW. Feed intake may have affected reproductive performance. Therefore, RFI was confounded by an interaction between feed intake and reproductive performance. Selection for RFI may not consistently improve broiler feed conversion because of these confounding effects.

The split-plot design of the current broiler experiment did not allow calculation of feed conversion for RME_{mmat}, because pens contained both RME_{mmat} categories. However, maintenance requirements may affect feed conversion in older broilers when maintenance accounts for a greater proportion of total energetic costs. Repeated attempts to relate basal metabolic rate to feed conversion have not yielded consistent results in broilers (Skinner-Noble et al., 2003b). This is likely due to the multifactorial nature of the maintenance requirement (Emmerson, 1997). Even though a low maintenance requirement would be expected to improve feed efficiency, some factors may increase both maintenance requirements and feed efficiency. For instance, Skinner-

Table 8. Carcass weight, carcass yield, abdominal fat pad weight as proportion of the live BW, and breast, thigh, drum, and wing weights as a proportion of the carcass weight from broilers classified in 3 RFI_{mat}[1] and 2 RME_{mmat}[2] categories

RFI_{mat}	RME_{mmat}	Sex	Carcass weight (g)	Carcass yield	Fat pad	Breast	Thighs	Drums	Wings
				% BW		% carcass			
Low			1,397.6	62.5	1.84^{a}	29.2	17.1	14.9	11.9
Average			1,340.7	62.0	1.63^{b}	28.9	17.1	14.6	12.1
High			1,352.6	62.3	1.74^{ab}	28.9	17.0	14.8	12.1
SEM			22.0	0.2	0.05	0.5	0.2	0.1	0.1
	Low		1,352.9	62.1	1.72	28.5^{b}	17.2	14.8	12.1
	High		1,374.3	62.4	1.75	29.5^{a}	17.0	14.7	12.0
	SEM		17.2	0.2	0.04	0.4	0.1	0.1	0.1
Low	Low		1,357.7	62.1	1.76^{ab}	28.8	17.4	14.9	11.9
Low	High		1,437.5	62.8	1.92^{a}	29.7	16.9	14.8	11.9
Average	Low		1,329.7	62.0	1.60^{b}	28.6	17.2	14.7	12.2
Average	High		1,351.7	62.0	1.67^{ab}	29.3	17.0	14.6	12.0
High	Low		1,371.3	62.3	1.80^{ab}	28.1	16.9	14.8	12.0
High	High		1,333.9	62.2	1.68^{ab}	29.6	17.1	14.7	12.1
SEM			37.0	0.4	0.08	0.8	0.3	0.2	0.2
		Female	1,283.8^{b}	62.3	1.87^{a}	29.6^{a}	17.0	14.4^{a}	12.1
		Male	1,443.5^{a}	62.2	1.60^{b}	28.4^{b}	17.2	15.1^{b}	11.9
		SEM	15.8	0.2	0.03	0.3	0.1	0.1	0.1
Source of variation			Probability						
RFI_{mat}			0.12	0.31	0.003	0.84	0.80	0.35	0.49
RME_{mmat}			0.35	0.38	0.44	0.028	0.32	0.50	0.62
$RFI_{mat} \times RME_{mmat}$			0.12	0.29	0.045	0.79	0.23	0.90	0.68
Sex			<0.0001	0.52	<0.0001	0.008	0.40	<0.0001	0.16

[a,b]Least squares means within a column within effect with no common superscript differ ($P < 0.05$).

[1]Maternal residual feed intake calculated from 35 to 41 wk of age. Broilers were assigned to 1 of 3 RFI_{mat} categories before hatching.

[2]Maternal residual maintenance requirement. Calculated from 20 to 60 wk of age. Broilers were retrospectively assigned to 1 of 2 RME_{mmat} categories.

Noble et al. (2003a) found that more active broilers had greater feed efficiency than less active birds.

Meat Quality

A greater breast weight of high RME_{mmat} broilers resulted in a greater internal breast temperature at 15 min postmortem (37.6°C; Table 9) than low RME_{mmat} broilers (36.9°C; $P = 0.07$), but ultimate pH was not affected (5.93 vs. 5.96; $P = 0.32$). High RME_{mmat} broilers had breast meat with lower shear force (4.7 kgf/g) than low RME_{mmat} broilers (5.6 kgf/g). Based on the regression equations between sensory evaluation and shear force developed by Cavitt et al. (2005), this shear force difference is undetectable by consumers. Increased breast weight and yield has been associated with decreased muscle glycolytic potential and decreased lactate content at 15 min postmortem (Berri et al., 2007). If high RME_{mmat} broilers indeed had a lower glycolytic potential, development of rigor mortis may have been faster, which could have affected shear force at this postslaughter cooling period as reported by Alvarado and Sams (2000).

Despite growth differences, no differences in meat functional properties were detected among RFI_{mat} categories. Nonetheless, in high RME_{mmat} broilers, a greater a* value was observed in high RFI_{mat} broilers (8.94) than in average RFI_{mat} (8.12) broilers. Such a* difference may not be noticeable for consumers, because Fletcher (1999) reported that fillets selected as darker than normal by visual assessment had an a* value that was 1.6 units greater than normal fillets. Hens that were inefficient based on both measures of efficiency may have produced broilers with unique muscle characteristics, such as greater myoglobin (Boulianne and King, 1998) or lower fat content (Jaturasitha et al., 2008). Breast muscle lightness (L*) was greater in low RFI_{mat} birds (61.2, 60.7, and 60.5 for low, average, and high RFI_{mat} broilers, respectively; $P = 0.08$). Light breast muscles have been associated with lower pH and poorer water-holding capacity in chickens (Zhang and Barbut, 2005) as an unintended effect of selection for growth and muscle mass (Dransfield and Sosnicki, 1999). Cooking loss did not differ among RFI_{mat} ($P = 0.19$) nor RME_{mmat} ($P = 0.36$) categories. Although a negative correlation between ultimate pH and lightness was present ($r = -0.21$; $P < 0.0001$), our results do not support the idea that broilers from breeders of any efficiency category were more susceptible to pale, soft, and exudative-type problems.

Overall, low RFI_{mat} values were related with increased broiler growth to 38 d, although no substantial effects of RFI_{mat} on feed conversion, parts yield, or meat quality characteristics were detected. Low maintenance requirements are advantageous for egg and chick production; however, high maintenance hens produced broilers with desirable traits such as greater breast yield and tenderness. Maximizing economic efficiency in the chicken meat supply chain depends on strategic decisions of energy partitioning; minimizing maintenance

Table 9. Meat quality characteristics of broilers classified in 3 RFI_{mat}[1] and 2 RME_{mmat}[2] categories

RFI_{mat}	RME_{mmat}	Sex	Temperature 15 min[4] (°C)	pH		Color[3]			Cook loss[7] (%)	Shear force[8] (kgf/g)
				15 min[5]	24 h[6]	L*	a*	b*		
Low			37.7	6.91	5.93	61.2	8.44	5.54	17.8	5.30
Average			37.3	6.92	5.93	60.7	8.34	5.16	18.4	5.03
High			36.7	6.88	5.96	60.5	8.59	5.20	17.5	5.19
SEM			0.4	0.03	0.03	0.3	0.17	0.21	0.4	0.22
	Low		36.9	6.87	5.93	60.8	8.51	5.42	18.1	5.60[a]
	High		37.6	6.93	5.96	60.8	8.40	5.19	17.7	4.75[b]
	SEM		0.3	0.02	0.02	0.2	0.13	0.16	0.3	0.19
Low	Low		36.9	6.86	5.90	61.2	8.73[ab]	5.61	18.8	5.83
Low	High		38.5	6.96	5.96	61.3	8.15[ab]	5.48	16.9	4.77
Average	Low		37.1	6.93	5.91	60.6	8.57[ab]	5.22	18.1	5.48
Average	High		37.5	6.91	5.96	60.8	8.12[b]	5.10	18.8	4.59
High	Low		36.7	6.84	5.97	60.6	8.24[ab]	5.42	17.5	5.49
High	High		36.7	6.92	5.95	60.3	8.94[a]	4.99	17.4	4.89
SEM			0.6	0.05	0.04	0.4	0.28	0.34	0.8	0.36
		Female	37.0	6.88	5.97[a]	61.1[a]	8.56	5.46	18.0	5.02
		Male	37.5	6.93	5.92[b]	60.5[b]	8.36	5.14	17.9	5.32
		SEM	0.3	0.02	0.02	0.2	0.12	0.15	0.3	0.2
Source of variation			Probability							
RFI_{mat}			0.58	0.12	0.56	0.08	0.48	0.32	0.19	0.69
RME_{mmat}			0.07	0.07	0.32	0.97	0.53	0.29	0.36	0.001
$RFI_{mat} \times RME_{mmat}$			0.20	0.23	0.37	0.69	0.004	0.78	0.10	0.75
Sex			0.11	0.20	0.035	0.010	0.21	0.12	0.81	0.20

[a,b]Least squares means within a column within effect with no common superscript differ ($P < 0.05$).

[1]Maternal residual feed intake calculated from 35 to 41 wk of age. Broilers were assigned to 1 of 3 RFI_{mat} categories before hatching.

[2]Maternal residual maintenance requirement calculated from 20 to 60 wk of age. Broilers were retrospectively assigned to 1 of 2 RME_{mmat} categories.

[3]Mean of 3 measures at the dorsal side of the pectoralis major. Based on the L*a*b* 3-dimensional color space. A Chroma-meter CR-400 (Konica Minolta, Mississauga, Ontario, Canada) was used. L* = lightness; a* = green to red; b* = blue to yellow.

[4]A temperature probe was inserted 15 min postmortem at the greatest temperature point of the pectoralis major.

[5]Measured in an incision made 15 min postmortem at ventral side of the pectoralis major.

[6]Measured in an incision made 24 h postmortem at ventral side of the pectoralis major.

[7]Weight loss after cooking the samples at 200°C to an internal temperature of 80°C.

[8]Shear force from an Instron 411 (Instron, Norwood, MA) with an Allo-Kramer blade set (10 blades) measured as kilograms of force (kgf) corrected to kilograms of force per gram. Sample area was standardized to 25 mm × 55 mm.

requirements may not be compatible with maximizing broiler performance and meat yield.

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