Asian-Aust. J. Anim. Sci.
Vol. 22, No. 5 : 747 - 755
May 2009

www.ajas.info

Genetics of Residual Feed Intake in Cattle and Pigs: A Review

M. A. Hoque* and K. Suzuki[1]

Department of Animal Breeding and Genetics, Bangladesh Agricultural University, Mymensingh 2202, Bangladesh

ABSTRACT : The feed resource for animals is a major cost determinant for profitability in livestock production enterprises, and thus any effort at improving the efficiency of feed use will help to reduce feed cost. Feed conversion ratio, expressed as feed inputs per unit output, is a traditional measure of efficiency that has significant phenotypic and genetic correlations with feed intake and growth traits. The use of ratio traits for genetic selection may cause problems associated with prediction of change in the component traits in future generations. Residual feed intake, a linear index, is a trait derived from the difference between actual feed intake and that predicted on the basis of the requirements for maintenance of body weight and production. Considerable genetic variation exists in residual feed intake for cattle and pigs, which should respond to selection. Phenotypic independence of phenotypic residual feed intake with body weight and weight gain can be obligatory. Genetic residual feed intake is genetically independent of its component traits (body weight and weight gain). Genetic correlations of residual feed intake with daily feed intake and feed conversion efficiency have been strong and positive in both cattle and pigs. Residual feed intake is favorably genetically correlated with eye muscle area and carcass weight in cattle and with eye muscle area and backfat in pigs. Selection to reduce residual feed intake (excessive intake of feed) will improve the efficiency of feed and most of the economically important carcass traits in cattle and pigs. Therefore, residual feed intake can be used to replace traditional feed conversion ratio as a selection criterion of feed efficiency in breeding programs. However, further studies are required on the variation of residual feed intake during different developmental stage of production. (**Key Words :** Consequences of Selection, Genetic Variation, Residual Feed Intake)

INTRODUCTION

Profitability of livestock production depends on keeping costs to a minimum without sacrificing production or quality. Feed represent a large proportion of the variable cost of livestock production and genetic improvement programs for reducing input costs should include traits related to feed utilization. This has long been recognized by the poultry and porcine industries, where the cost of feed is readily quantified. These industries have made significant improvements in feed efficiency through both genetic and non-genetic means (Luiting, 1991). Generally, selection programs have focused on production traits, with little attention given to production costs. Recently, this view has begun to change, and the efficiency of conversion of feed (i.e., ratio of feed intake to product or the reverse) has been recognized as more important. However, the statistical properties of ratio traits (e.g. feed conversion ratio) are poor and selection responses to traits measured as ratios can be erratic (Gunsett, 1986). In addition, selection against feed intake reduces appetite, which might be undesirable (Ollivier et al., 1990). As with growth traits, the expression of any feed efficiency trait is dependent on the stage of maturity at which the trait was measured on the animals. For residual feed intake, there is a high genetic correlation between the trait measured in the young animal and that measured in the adult, while for the other feed efficiency traits, such as feed conversion ratio, this correlation is low (Archer et al., 2002).

Residual feed intake is a linear index and derived from the combination of feed consumption and production traits. The residual feed intake was first proposed as an alternate measure of feed efficiency by Koch et al. (1963). It can be defined as the difference between actual feed intake and the expected feed requirements for maintenance of body metabolic processes and production. A low residual feed intake implies a reduced energy requirement for maintenance, although other sources of variation include digestibility and metabolizability of the diet, net availability of metabolizable energy for gain or protein turnover.

* Corresponding Author: M. A. Hoque. Tel: +88-091-55695/2618, Fax: +88-091-55810, E-mail: azharhoque@yahoo.com

[1] Laboratory of Animal Breeding and Genetics, Graduate School of Agricultural Science, Tohoku University, Aoba-ku, Sendai, 981-8555, Japan.

Received August 22, 2008; Accepted December 14, 2008

Research has shown that there is considerable individual animal variation in feed intake above and below that expected or predicted on the basis of body size and growth rate. That statement, along with the fact that individuals of the same body weight require rather widely different amounts of feed for the same level of production, establishes the scientific base for measuring residual feed intake in animals. The objective of this study is to review some of the evidence on genetic variation in residual feed intake and its consequences for selection on feed utilization, growth and carcass traits in cattle and pigs.

TRADITIONAL MEASURES OF FEED EFFICIENCY

The efficiency of feed utilization is more difficult to quantify than that of growth; consequently, different measures of feed efficiency have been developed over the years. These include feed conversion ratio (Brody, 1945), partial efficiency of growth (Kellner, 1909), relative growth rate (Fitzhugh and Taylor, 1971), Kleiber ratio (Kleiber, 1947), etc. Among these measures, the feed conversion ratio has been used extensively in the past. However, the use of ratio traits has some problems. Feed conversion ratio is closely correlated to the feed intake and rate of gain of the animal (Gunsett, 1986). So, two animals might have similar gain:feed and still be very different in their feed intakes and rates of gain. Conversely, the same animal at different intakes would certainly have different gain:feed ratios, even though the genetics of the animal had not changed. Studies have shown that direct selection for feed efficiency has not been very effective (e.g. Webb and King, 1983) and selection programs which give emphasis to efficiency rather than lean growth rate on *ad libitum* feeding have led to a reduction of feed intake (Webb, 1989; Smith et al., 1991) which may be detrimental in the long term.

It is well noted that feed conversion efficiency is both phenotypically and genetically correlated with aspects of production. Buttazzoni and Mao (1989) cited a number of studies showing high positive phenotypic correlations and very high genetic correlations between milk yield and feed conversion efficiency of milk production of dairy cows. Veerkamp and Emmans (1995) reviewed the literature on gross efficiency of dairy production and concluded that feed conversion ratio largely reflects the increased proportion of energy being utilized for production compared with maintenance in high producing cows. The strong genetic correlations between feed conversion efficiency and production traits suggest that selection for production (growth rate, milk yield, etc.) will produce a correlated improvement in feed conversion efficiency, and hence there is little justification for measuring feed intake in order to improve feed conversion efficiency.

Most of the traditional measures of feed efficiency are expressed as ratio of feed intake to product (or the reciprocal). The use of a ratio trait, such as feed conversion ratio, for genetic selection presents problems associated with prediction of the change in the component traits in future generations (Arthur et al., 2001a). This is due to the fact that feed conversion ratio is genetically correlated to growth, body size, body composition, and appetite. A linear index (residual feed intake), however, places a predetermined amount of selection pressure on the traits and thus, in principle, results in a more predictable genetic change in each trait. Gunsett (1984) compared the efficiency of direct selection for a two-component trait with a linear index trait derived from the same two components and concluded that the use of linear index increases selection responses as compared with direct selection on the ratio trait.

PHENOTYPIC RESIDUAL FEED INTAKE

Koch et al. (1963) suggested that feed intake could be adjusted for body weight and weight gain (or any other production trait) by effectively partitioning into the feed intake expected for the given level of production and a residual portion. The residual portion of feed intake can be used to identify animals which deviate from their expected level of feed intake, with efficient animals having lower residual feed intake. Calculation of residual feed intake in a phenotypic approach, as reported in several studies (Archer et al., 1997; Arthur et al., 2001a,b; Hoque et al., 2005; Hoque et al., 2007a), can be generally summarized as:

$$RFI_{Phe} = FI-\beta_{w(phe)}\times MWT-\beta_{g(phe)}\times DG$$

where RFI_{phe} = phenotypic residual feed intake, FI = daily feed intake, MWT = metabolic body weight at mid test, DG = average daily gain, and $\beta_{w(phe)}$ and $\beta_{g(phe)}$ = partial regression coefficients of animal's FI on MWT and DG, respectively.

This equation is usually used in cattle. However, residual feed intake can be calculated without correction for carcass composition for growing bulls. The reason might be that these animals have a low fat content (Jensen et al., 1991). On the other hand, in the case of pigs, variation in maintenance requirements as predicted from metabolic body weight is not significantly related to variation in feed consumption, because pigs are usually tested over a relatively fixed weight range (e.g. 30 to 90 kg). This view has been supported by Haer (1992) who found little variation in metabolic body weight and no significant effect of metabolic body weight on feed intake, when weight gain and lean are included in the model to estimate residual feed

Table 1. Some literature estimates of heritability for residual feed intake in cattle

Breed[1]	Type[2]	n	Heritability[3]			Source
			RFI_{phe}	RFI_{gen}	RFI_{nut}	
A	B	1,180	0.39±0.03	-	-	Arthur et al. (2001a)
Ch	B	792	0.39±0.02	-	0.43±0.04	Arthur et al. (2001b)
British	B	966	0.44±0.07	-	-	Arthur et al. (1997)
British	B and H	760	0.34±0.12 to 0.64±0.15	-	-	Archer et al. (1997)
CrB	B	650	0.28±0.11	-	-	Jensen et al. (1992)
British	B	1,324	0.28±0.11	-	-	Koch et al. (1963)
A	B	263	-	-	0.23±0.12	Fan et al. (1995)
R and W	H	417	0.22±0.11	-	-	Korver et al. (1991)
TT	S and H	1,481	0.18±0.06	-	0.13±0.05	Robinson & Oddy (2004)
JB	B	740	0.24±0.11	0.25±0.10	-	Hoque and Oikawa (2004)
CrB	S	464	0.21±0.12	0.42±0.15	-	Nkrumah et al. (2007)

[1] A = Angus; Ch = Charolais; Breed listed as British if it includes 2 or more of Angus, Hereford or Shorthorn; CrB = Crossbreds; R and W = Swedish Red and White; TT = Tropical and temperate adapted breeds; JB = Japanese Black.
[2] B = Bulls; H = Heifers; S = Steers.
[3] RFI_{phe} = Phenotypic residual feed intake; RFI_{gen} = Genetic residual feed intake; RFI_{nut} = Nutritional residual feed intake.

intake. Thus, different measures of residual feed intake can be estimated in pigs as the difference between actual feed intake and that predicted from analyses with various combinations of production traits. It can be summarized from published studies that residual feed intake of pigs can be calculated by including i) daily gain (RFI_1), ii) daily gain and backfat (RFI_2), or iii) daily gain, backfat and eye muscle area (RFI_3) in the regression model as described above.

To be a candidate for selection, the economically relevant trait must exhibit genetic variability, which is to say that variability in phenotypic expression must be to some extent dependent on additive genetic variance. The variation in residual feed intake, however, shows that there is variation in efficiency among animals beyond the variation that is related to daily gain and body weight. An overview of some recent studies presenting heritability estimates for residual feed intake in cattle and pigs is given in Table 1 and Table 2, respectively. The published estimates of heritability indicate that genetic variation exists in residual feed intake. All studies that have estimated genetic variance for residual feed intake in cattle reported that the heritability estimates for this parameter were moderate to high (ranged from 0.21 to 0.60), except for the estimate by Robinson and Oddy (2004), which was low (0.18). Published studies also indicated that residual feed intake calculated by different combinations of growth traits are moderately heritable in pigs (ranged from 0.22 to 0.41), except the for estimate by von Flede (1996), which was low (0.18) (Table 2). Selection for residual feed intake, therefore, would be expected to result in genetic change relatively comparable to that obtained with other moderately to highly heritable traits.

GENETIC RESIDUAL FEED INTAKE

Kennedy et al. (1993) showed that genetic regression may provide additional insight into the true relationship in cases where phenotypic measurements such as weight gain are subjected to considerable measurement errors. They suggested that although phenotypic residual feed intake is phenotypically independent of production, it may be genetically correlated to production. The residual feed intake can be, therefore, calculated as a genetic regression

Table 2. Some literature estimates of heritability for residual feed intake in pigs

Breed[1]	Type[2]	n	Heritability[3]				Source
			RFI_1	RFI_2	RFI_3	RFI_{nut}	
LW	B and S	169	-	-	0.24±0.03	-	Gilbert et al. (2007)
L	B	341	0.47±0.11	0.29±0.11	-	-	Hoque and Suzuki (2008)
D	B	514	0.41±0.14	-	-	0.34±0.15	Hoque et al. (2007a)
LW	B	26,706	0.26±NE	0.26±NE	0.26±NE	-	Johnson et al. (1999)
Y, L and D	B	7,562	0.33±0.05	0.30±0.06	-	-	Mrode and Kennedy (1993)
LW	B and S	1,584	0.24±0.08	0.22±0.08	-	-	Nguyen et al. (2005)
LW and L	B	3,188	-	0.18±0.03	-	-	von Flede et al. (1996)

[1] LW = Large White; L = Landrace; D = Duroc; Y = Yorkshire. [2] B = Boars; S = Sows.
[3] RFI_1, RFI_2, and RFI_3 = Residual feed intake calculated from model included daily gain, included daily gain and backfat, and included daily gain, backfat and eye muscle area, respectively; RFI_{nut} = Nutritional residual feed intake; NE = Not estimated.

Table 3. Genetic correlations of residual feed intake with daily feed intake and growth traits in cattle

Traits[1]	FI	DG	MWT	YWT	Breed[2]	Source
RFI_{phe}	0.79±0.04	-0.10±0.13	-	0.32±0.10	Ch	Arthur et al. (2001b)
	0.64±0.16	0.09±0.29	0.22±0.29	0.15±0.28	H	Herd and Bishop (2000)
	-	-0.07±0.14	-	-0.43±0.26	JB**	Hoque et al. (2005)
	0.78±0.06	0.25±0.16	0.16±0.03	0.19±0.15	JB*	Hoque et al. (2006a)
	0.89±0.07	0.23±0.33	-	-	CrB	Jensen et al. (1992)
	0.73±0.18	0.46±0.45	0.27±0.33	-	CrB	Nkrumah et al (2007)
	0.43±0.15	0.09±0.20	-0.20±0.16	-	TT	Robinson and Oddy (2004)
RFI_{gen}	0.61±0.10	0.18±0.20	-0.07±0.14	-0.04±0.15	JB	Hoque et al. (2006a)
	0.65±0.16	-0.04±0.25	0.12±0.30	-	CrB	Nkrumah et al. (2007)
RFI_{nut}	0.50±0.07	-0.54±0.09	-	-0.02±0.10	Ch	Arthur et al (2001b)
	-	0.31±NE	-	-0.05±NE	H	Fan et al. (1995)
	-	-0.71±NE	-	-0.64±NE	A	Fan et al. (1995)
	0.32±0.20	-0.14±0.24	-0.26±0.18	-	TT	Robinson and Oddy (2004)

[1] FI = Daily feed intake; DG = Average daily gain; MWT = Metabolic body weight; YWT = Yearling weight; RFI_{phe} = Phenotypic residual feed intake; RFI_{gen} = Genetic residual feed intake; RFI_{nut} = Nutritional residual feed intake.

[2] Ch = Charolais; H = Hereford; JB = Japanese Black; CrB = Crossbreds; TT = Tropical and temperate adapted breeds; A = Angus.

* Residual feed intake and growth traits were measured on performance tested bulls; ** Residual feed intake and growth traits were measured on performance tested bulls and their station progeny, respectively.

from feed intake on metabolic body weight and daily gain. The genetic regression approach requires information of the genetic covariances of feed intake on metabolic body weight and production traits. As reported in recent studies (Hoque et al., 2005; Nkrumah et al., 2007), genetic residual feed intake (RFI_{gen}) can be expressed as:

$$RFI_{gen} = FI-\beta_{w(gen)}\times MWT-\beta_{g(gen)}\times DG$$

where FI = daily feed intake; MWT = metabolic body weight at mid test; DG = average daily gain; genetic regression coefficient, $\begin{bmatrix}\beta_{w(gen)}\\ \beta_{g(gen)}\end{bmatrix}$ = $G^{-1}c$; G = genetic covariance matrix of two production traits (MWT and DG); and c = vector of the genetic covariance of FI with production traits.

Large numbers of data are required to estimate the genetic covariances of feed intake on production traits. Few studies have been found on residual feed intake calculated by a genetic regression approach in cattle. Published heritability estimates indicate that genetic residual feed intake is moderately heritable (Table 1). These moderate heritability estimates indicate that sufficient genetic variation exists in this trait which should respond to selection. However, Hoque and Oikawa (2004) compared different measures of residual feed intake and concluded that RFI_{phe} and RFI_{gen} are regarded as the same trait and selection for RFI_{gen} would give results similar to selection for RFI_{phe}.

NUTRITIONAL RESIDUAL FEED INTAKE

The definitions and computational formulae for residual feed intake have been summarized by Arthur et al. (2001) and Hoque et al. (2006a). Differences in the formulae used to compute a particular residual feed intake could lead to differences in selection outcomes. For example, the calculation of residual feed intake requires the estimation of expected feed intake, which can be obtained through phenotypic or genetic regression (Kennedy et al., 1993) or can be obtained from the nutritional requirement of an animal through the use of a feeding standards formula (Fan et al., 1995; Arthur et al., 2001; Hoque et al., 2006a). Phenotypic and genetic correlations among these measures of residual feed intake were high. However, there are differences between these measures of residual feed intake in their relationships with other traits, such as growth traits (Table 3). Feeding standards for a specific breed are necessary to estimate nutritional residual feed intake. It is possible to estimate the nutritional residual feed intake for a few animals if the feeding standards for those specific animals are known. Relatively fewer heritability estimates are available in the literature for nutritional residual feed intake. Available heritability estimates for this trait in cattle and pigs ranged from low to moderate, with most of the values falling in the moderate range (Tables 1 and 2). However, the variation among estimates of heritability for residual feed intake is due in part to the different approaches by which traits were defined, calculated, or predicted, and also different breeds were used in studies. Furthermore, variation in residual feed intake is due to numerous intrinsic factors such as variation in feed digestibility, in energy efficiency partitioning between maintenance and production or energy requirement for physical activity, body thermo-regulation, maintenance of body tissues and basal metabolic rate (Haer et al., 1993).

Table 4. Genetic correlations of residual feed intake with feed intake and growth traits in pigs

Traits[1]	FI	DG	MWT	Breed[2]	Source
RFI_1	0.78±0.03	0.22±0.05	-	D	Hoque et al. (2008b)
	-	0.03±0.09	-0.16±0.15	L	Hoque and Suzuki (2008)
	0.81±0.09	0.23±0.12	0.02±0.11	D	Hoque et al. (2007a)
	-	0.11±NE	-	LW	Johnson et al. (1999)
	-	0.18±0.10	-	Y, L and D	Mrode and Kennedy (1993)
RFI_2	0.58±0.04	0.17±0.07	-	D	Hoque et al. (2008b)
	-	0.02±0.09	-0.13±0.08	L	Hoque and Suzuki (2008)
	-	0.17±NE	-	LW	Johnson et al. (1999)
	-	0.21±0.11	-	Y, L and D	Mrode and Kennedy (1993)
	0.97±0.01	0.41±0.10	-	LW and L	von Flede et al. (1996)
RFI_3	0.56±0.05	0.17±0.07	-	D	Hoque et al. (2008b)
	-	0.18±NE	-	LW	Johnson et al. (1999)
RFI_{nut}	0.24±0.03	0.01±0.07	0.25±0.02	D	Hoque et al. (2007a)

[1] FI = Daily feed intake; DG = Average daily gain; MWT = Metabolic body weight; RFI_1, RFI_2, and RFI_3, = Residual feed intake calculated from model included daily gain, included daily gain and backfat, and included daily gain, backfat and eye muscle area, respectively; RFI_{nut} = Nutritional residual feed intake.

[2] D = Duroc; L = Landrace; LW = Large White; Y = Yorkshire.

IMPACT ON FEED INTAKE, EFFICIENCY AND GROWTH TRAITS

Some published results on genetic correlations between measures of residual feed intake with daily feed intake and growth traits in cattle and pigs are presented in Table 3 and Table 4, respectively. Genetic correlations of residual feed intake calculated by phenotypic and genetic approaches with daily feed intake are strong and positive. However, the residual feed intake calculated by feeding standards formulae is moderately correlated with daily feed intake. Selection for low residual feed intake is expected to favor animals with lower maintenance energy expenditure. At both phenotypic and genetic levels, correlations between residual feed intake and maintenance energy expenditure per metabolic body weight were highly positive for British Hereford cattle selected for lean growth rate and lean feed conversion over 10 years (Herd and Bishop, 2000). Residual feed intake has the potential to improve feed conversion efficiency in the young growing animal, to improve the efficiency of maintenance energy expenditure, and to avoid increasing the size of the cow (Herd and Bishop, 2000). Published studies have also reported strong positive correlations for RFI_{phe} with feed conversion ratio in cattle (0.70, Herd and Bishop, 2000; 0.85, Arthur et al., 2001b; 0.66, Arthur et al., 2001a; 0.64, Hoque et al., 2006a; 0.62, Nkrumah et al., 2007; 0.78, Hoque et al., 2008a) and in pigs (0.63, Von Felde et al., 1996; 0.86, Hoque et al., 2007a). Similarly, positive genetic correlations of 0.62 (Hoque et al., 2006a) and 0.78 (Nkrumah et al., 2004) in cattle and of 0.84 (Hoque et al., 2007a) in pigs have been reported for RFI_{gen} with feed conversion ratio. Thus selection for improved residual feed intake (i.e. decreased excessive intake of feed) will be associated with better feed efficiency and a corresponding declining genetic change for feed intake.

Kennedy et al. (1993) theoretically showed that when expected feed intake is obtained by phenotypic regression, the RFI_{phe} is expected to be phenotypically independent of the component traits and in the other case, when expected feed intake is obtained by genetic regression, the RFI_{gen} is expected to be genetically independent of its component traits. They also mentioned that even with residual feed intake calculated by regression, there is no guarantee that its genetic correlations with these component traits will be close to zero. Published studies showed that both metabolic body weight and daily gain are phenotypically independent of RFI_{phe}, and genetically independent of RFI_{gen}. However, when residual feed intake is estimated with expected feed intake calculated from feeding standards formulae, it is not automatically independent of production traits and is usually correlated with these traits, as observed by Fan et al. (1995), Arthur et al. (2001a), and Hoque et al. (2007b). Genetic selection to reduce residual feed intake can result in progeny that eat less without sacrificing growth performance (Richardson et al., 1998). In contrast to feed conversion ratio, residual feed intake is independent of growth and maturity patterns (Herd et al., 1997). Selection for low residual feed intake by either phenotypic or genetic approaches might be helpful for improving feed efficiency while causing no correlated change in production traits. Therefore, residual feed intake should be a more sensitive and precise measurement of feed utilization, since it is based on energy intake and energy requirements.

IMPACT ON CARCASS TRAITS

Selection against either RFI_{phe} or RFI_{gen} would give

Table 5. Genetic correlations between residual feed intake and carcass traits in cattle

Traits[1]	CWT	EMA	MSR	SFT	Breed[2]	Source
RFI_{phe}	-	-	-0.31±0.47	-0.66±0.47	JB*	Hoque et al. (2005)
	-0.60±0.32	-0.42±0.33	-0.62±0.29	-0.30±0.27	JB**	Hoque et al. (2006b)
	-	-	-0.37±0.30	-	CrB	Jensen et al. (1992)
	0.05±0.38	-0.64±0.26	0.28±0.38	0.33±0.29	CrB	Nkrumah et al. (2007)
	-	-0.24±0.26	0.22±0.17	0.72±0.17	TT	Robinson and Oddy (2004)
RFI_{gen}	-	-	-0.41±0.23	-0.74±0.41	JB*	Hoque et al. (2005)
	-0.53±0.23	-0.45±0.29	-0.50±0.31	-0.27±0.20	JB**	Hoque et al. (2006b)
	-0.03±0.30	-0.69±0.32	0.18±0.26	0.27±0.24	CrB	Nkrumah et al. (2007)
RFI_{nut}	-	-0.15±0.22	0.31±0.20	0.87±0.21	TT	Robinson and Oddy (2004)

[1] CWT = Carcass weight; EMA = Eye muscle area; MSR = Marbling score; SFT = Subcutaneous fat thickness; RFI_{phe} = Phenotypic residual feed intake; RFI_{gen} = Genetic residual feed intake; RFI_{nut} = Nutritional residual feed intake.

[2] JB = Japanese Black; CrB = Crossbreds; TT = Tropical and temperate adapted breeds.

* Residual feed intake and growth traits were measured on performance tested bulls; ** Residual feed intake and growth traits were measured on performance tested bulls and their station progeny, respectively.

similar correlated responses in carcass traits. Recent published estimates of genetic correlation between measures of residual feed intake and carcass traits in cattle and pigs are presented in Table 5 and Table 6, respectively. Few published reports describe the relationship between residual feed intake and carcass weight in cattle, and there are wide ranges of genetic correlations between these two traits. The difference between studies in the estimates of genetic correlation is not conclusive because of their large standard errors. However, Jensen et al. (1991) noted that increases in dressing percentage are associated with lower residual feed intake. Baker et al. (2006) reported that no differences existed in hot carcass weight and eye muscle area among 3 (high, medium and low) residual feed intake groups. The genetic correlation between eye muscle area and residual feed intake is favorably negative.

It appears that the relationships among residual feed intake and carcass quality traits may not be same in purebred or crossbred groups of cattle, as there are some inconsistencies in the results reported to date. Baker et al. (2006) reported that no differences existed in backfat thickness and marbling score among 3 residual feed intake groups. Arthur et al. (2001a) reported a genetic correlation of 0.17±0.05 between residual feed intake and ultrasound rib fat thickness in Angus bulls and heifers. That report is further substantiated by the genetic correlation of -0.43±0.23 between residual feed intake and carcass lean content in Hereford bulls reported by Herd and Bishop (2000). In the studies by Robinson and Oddy (2004) and Nkrumah et al. (2007), positive but smaller genetic correlation coefficients for residual feed intake and beef marbling were reported. A small observed reduction in subcutaneous fat deposition in response to a single generation of selection against residual feed intake has been reported (Richardson et al., 1998). The reason for the discrepancy between studies is not apparent, but it is worth noting that different breeds were used, the method for measuring the beef marbling fat was different, and also the standard errors on the reported coefficients were large. Hoque et al. (2006) and Richardson et al. (1998) noted that the steer progeny of low residual feed intake parents grew faster than steers of high residual feed intake parents. Hoque et al. (2006) also noted that downward selection of residual feed intake (lowering excessive intake of feed) of sires would also lead to increase in MSR, REA and SFT of the carcass of their progeny. The genetic correlations of

Table 6. Genetic correlations between residual feed intake and carcass traits in pigs

Traits[1]	EMA	IMF	BF	Breed[2]	Source
RFI_1	-	-	0.46±0.15	L	Hoque and Suzuki (2008)
	-0.61±0.09	0.17±0.09	0.76±0.08	D	Hoque et al. (2007b)
	-0.51±NE	-	0.67±NE	LW	Johnson et al. (1999)
	-	-	0.34±0.07	Y, L and D	Mrode and Kennedy (1993)
RFI_2	-	-	0.06±0.14	L	Hoque and Suzuki (2008)
	-0.31±NE	-	0.22±NE	LW	Johnson et al. (1999)
	-	-	0.15±0.09	Y, L and D	Mrode and Kennedy (1993)
RFI_3	-	-	0.44±0.16	LW	Gilbert et al. (2007)
	-0.31±NE	-	0.20±NE	LW	Johnson et al. (1999)
RFI_{nut}	-0.64±0.09	0.16±0.04	0.73±0.08	D	Hoque et al. (2007b)

[1] EMA = Eye muscle area; IMF = Intramuscular fat; BF = Backfat thickness; RFI_1, RFI_2, and RFI_3 = Residual feed intake calculated from model included daily gain, included daily gain and backfat, and included daily gain, backfat and eye muscle area, respectively; RFI_{nut} = Nutritional residual feed intake.

[2] L = Landrace; D = Duroc; LW = Large White; Y = Yorkshire.

residual feed intake of bulls with beef marbling and subcutaneous fat of their progeny were negative (Hoque et al., 2005; Hoque et al., 2006b), which suggests that selection against residual feed intake of bulls may have contributed to the increase in marbling and subcutaneous fat of progeny carcasses. That is, selection for decreased residual feed intake would tend to increase carcass fatness (genetically fat animals tend to be more efficient). This is because residual feed intake is independent of the time needed to raise the animal to slaughter weight.

In pigs, the eye muscle area is favorably negatively correlated with residual feed intake. Genetic correlations between residual feed intake and intramuscular fat in pigs are low, implying a small positive association between residual feed intake and pork fatness. There is evidence of a positive genetic relationship between residual feed intake and backfat (Mrode and Kennedy, 1993; Johnson et al., 1999; Hoque et al., 2007b; Hoque and Suzuki, 2008) in Landrace, Yorkshire and Duroc pigs. The genetic correlation between residual feed intake and lean content is strong and negative in Large White pigs (Gilbert et al., 2007). These results indicate that lowering of residual feed intake (higher efficiency) with increasing leaner pork seems to be possible.

FUTURE DIRECTIONS

Residual feed intake is an alternative measure to traditional ratio-type efficiency traits. Relatively small numbers of heritability estimates are available in the literature for residual feed intake. These estimations were made in growth stages of both beef cattle and pigs and also in mature cows. However, there is a lack of knowledge to determine whether or not genetic variation in residual feed intake over an entire production system exists within these animals. The residual feed intake results reported in studies were calculated on records of individual feeding. Nevertheless, group feeding with automatic feeder or other means needs to be studied, because there is a competition effect in animals during group feeding. In published studies, the weights of the component traits in the residual feed intake (linear index) were determined by only biological (co)variances. However, profitability will be maximized when index weights on feed intake (or residual feed intake), growth and other traits are determined by both biological and economic parameters, which need to be investigated. Also, comparative studies on genetic gain using ratio and linear index traits are required.

The association between residual feed intake of bulls and carcass traits of their progeny have been studied by few researchers. Validation studies need to be conducted to verify that selection based on expected progeny difference for residual feed intake will result in realized phenotypic improvement. Whether the biological properties of residual feed intake are equivalent across gender and management schemes is unknown. The usefulness of measuring residual feed intake of growing animals at performance test is dependent on the genetic correlations with total merit of the animals in the production system. Total merit includes energy utilization of other groups of animals in the production system, such as their female relatives used to replace candidate females. This is an area where much further research is needed.

Given the present lack of understanding of the biological basis of residual feed intake and its effect on various traits, any selection for residual feed intake in animal production systems should be accompanied by monitoring for correlated responses; clearly, more research is needed to fully understand possible effects of residual feed intake on end-product quality. Prospects also exist for identification of major genes which account for significant proportions of variation in residual feed intake. Interest in application of marker-assisted evaluation to residual feed intake is prevalent, because feed intake is difficult and costly to measure and has relatively low effective indicators. There is also a lack of understanding of the mechanisms responsible for the observed variation in feed efficiency.

CONCLUSION

Residual feed intake has been proposed as a measure of feed efficiency, and reported heritability estimates for residual feed intake indicate that sufficient additive genetic variance exists in this trait, which should lead to response from selection. Phenotypic residual feed intake is phenotypically independent of measures of growth and body size, while genetically these relationships are either low or near zero. The residual feed intake calculated by genetic regression equation is genetically independent of production traits. The genetic correlations of residual feed intake with daily feed intake and feed conversion efficiency are strong and positive. Selection for lowering residual feed intake makes it possible to improve feed efficiency and most of the important carcass traits without compromising growth rate, in spite of the reduction in voluntary feed consumption.

REFERENCES

Archer, J. A., P. F. Arthur, R. M. Herd, P. F. Parnell and W. S. Pitchford. 1997. Optimum post-weaning test for measurement of growth rate, feed intake and efficiency in British breed cattle. J. Anim. Sci. 75:2024-2032.

Archer, J. A., A. Reverter, R. M. Herd, D. J. Johnston and P. F. Arthur. 2002. Genetic variation in feed intake and efficiency of mature beef cows and relationships with postweaning measurements. Proc. 7th Wld. Congr. Genet. Appl. Livest. Prod.

31:221-224.

Arthur, P. F., J. A. Archer, R. M. Herd, E. C. Richardson, S. C. Exton, J. H. Wright, K. C. P. Dibley and D. A. Burton. 1997. Genetic and phenotypic variation in feed intake, feed efficiency and growth in beef cattle. Proc. 12th Conf. Assoc. Advan. Anim. Breed. Genet. 12:234-237.

Arthur, P. F., J. A. Archer, D. J. Johnston, R. M. Herd, E. C. Richardson and P. F. Parnell. 2001a. Genetic and phenotypic variance and covariance components for feed intake, feed efficiency and other post weaning traits in Angus cattle. J. Anim. Sci. 79:2805-2811.

Arthur, P. F., G. Renand and D. Krauss. 2001b. Genetic and phenotypic relationships among different measures of growth and feed efficiency in young Charolais bulls. Livest. Prod. Sci. 68:131-139.

Baker, S. D., J. I. Szasz, T. A. Llein, P. S. Kuber, C. W. Hunt, J. B. Glaze, D. Falk, R. Richard, J. C. Millar, R. A. Battaglia and R. A. Hill. 2006. Residual feed intake of purebred Angus steers: effect on meat quality and palatability. J. Anim. Sci. 84:938-945.

Brody, S. 1945. Bioenergetics and growth, with special reference to the efficiency complex in domestic animals. Reinhold Publishing Corp., New York.

Buttazzoni, L. and I. L. Mao. 1989. Genetic parameters of estimated net energy efficiencies for milk production, maintenance and body weight change in dairy cows. J. Dairy Sci. 72:671-677.

Fan, L. Q., D. R. C. Bailey and N. H. Shannon. 1995. Genetic parameter estimation of postweaning gain, feed intake, and efficiency for Hereford and Angus bulls fed two different diets. J. Anim. Sci. 73:365-372.

Fitzhugh, H. A. and C. S. Taylor. 1971. Genetic analysis of degree of maturity. J. Anim. Sci. 33:717-725.

Gilbert, H., J. P. Bidanel, J. Gruand, J. C. Caritez, Y. Billon, P. Guillouet, H. Lagant, J. Noblet and P. Sellier. 2007. Genetic parameters for residual feed intake in growing pigs, with emphasis on genetic relationships with carcass and meat quality traits. J. Anim. Sci. 85:3182-3188.

Gunsett, F. C. 1986. Problems associated with selection for traits defined as a ratio of two component traits. Proc. 3rd World Cong. Gen. Appl. Livest. Prod. 11:437-442.

Gunsett, F. C. 1984. Linear index selection to improve traits defined as ratios. J. Anim. Sci. 59:1185-1193.

Haer, L. C. M. 1992. Relevance of eating pattern for selection of growing pigs. Ph.D. thesis. Research Institute for Animal Production (IVO-DLO) Schoonoord, Zeist, The Netherlands.

Haer, L. C. M., P. Luiting and H. L. M. Aarts. 1993. Relations among individual (residual) feed intake, growth performance and feed intake pattern of growing pigs in group housing. Livest. Prod. Sci. 36:233-253.

Herd, R. M., P. F. Arthur, J. A. Archer, E. C. Richardson, J. H. Wright and K. C. P. Dibley. 1997. Performance of progeny of high vs. low net feed conversion efficiency cattle. Proc. 12th Conf. Assoc. Advmt. Anim. Breed. Genet. Dubbo, Australia, pp. 142-745.

Herd, R. M. and S. C. Bishop. 2000. Genetic variation in residual feed intake and its association with other production traits in British Hereford cattle. Livest. Prod. Sci. 63:111-119.

Hoque, M. A., P. F. Arthur, K. Hiramoto, A. R. Gilmour and T. Oikawa. 2007a. Variance components due to direct genetic, maternal genetic and permanent environmental effect for growth and feed efficiency traits in young male Japanese Black cattle. J. Anim. Breed. Genet. 124:102-107.

Hoque, M. A., P. F. Arthur, K. Hiramoto and T. Oikawa. 2006a. Genetic relationship between different measures of feed efficiency and its component traits in Japanese Black (Wagyu) bulls. Livest. Sci. 99:111-118.

Hoque, M. A., P. F. Arthur, K. Hiramoto and T. Oikawa. 2006b. Genetic parameters for carcass traits of field progeny and their relationships with feed efficiency traits of their sire population for Japanese Black bulls. Livest. Sci. 100:251-260.

Hoque, M. A., K. Hiramoto and T. Oikawa. 2005. Genetic relationship of feed efficiency traits of bulls with growth and carcass traits of their progeny for Japanese Black (Wagyu) cattle. Anim. Sci. J. 76:107-114.

Hoque, M. A., M. Hosono and K. Suzuki. 2008a. Genetic parameters for dry matter, energy and protein intake, and their relationships with performance and carcass traits in Japanese Black cattle. J. Anim. Breed. Genet. 125:(in press).

Hoque, M. A., H. Kadowaki, T. Shibata, T. Oikawa and K. Suzuki. 2008b. Genetic parameters for measures of residual feed intake and growth traits in seven generations of Duroc pigs. Livest. Sci. (in press).

Hoque, M. A., H. Kadowaki, T. Shibata, T. Oikawa and K. Suzuki. 2007a. Genetic parameters for measures of the efficiency of gain of boars and the genetic relationships with its component traits in Duroc pigs. J. Anim. Sci. 85:1873-1879.

Hoque, M. A. and T. Oikawa. 2004. Comparison and relation among different estimates of residual feed intake for Japanese Black (Wagyu) bulls. Anim. Sci. J. 75:201-205.

Hoque, M. A. and K. Suzuki. 2008. Genetic parameters for production traits and measures of residual feed intake in Duroc and Landrace pigs. Anim. Sci. J. 79:543-549.

Hoque, M. A., K. Suzuki, H. Kadowaki, T. Shibata and T. Oikawa. 2007b. Genetic parameters for feed efficiency and their relationships with growth and carcass traits in Duroc pigs. J. Anim. Breed. Genet. 124:108-116.

Jensen, J., I. L. Mao and B. B. Andersen. 1992. Phenotypic and genetic relationships between residual energy intake and growth, feed intake, and carcass traits of young bulls. J. Anim. Sci. 70:386-395.

Johnson, Z. B., J. J. Chewning and R. A. Nugent. 1999. Genetic parameter for production traits and measures of residual feed intake in Large White swine. J. Anim. Sci. 77:1679-1685.

Kellner, O. 1909. The scientific feeding of animals. McMillan Co., New York.

Kennedy, B. W., J. H. J. Werf and T. H. E. Meuwissen. 1993. Genetic and statistical properties of residual feed intake. J. Anim. Sci. 71:3239-3250.

Kleiber, M. 1947. Body size and metabolic rate. Physiol. Rev. 27:511-541.

Koch, R. M., L. A. Seiger, D. Chambers and K. E. Gregory. 1963. Efficiency of feed use in beef cattle. J. Anim. Sci. 22:486-494.

Korver, S., E. A. M. van Eekelen, H. Vos, G. J. Nieuwhof and J. A. M. van Arendonk. 1991. Genetic parameters for feed intake and feed efficiency in growing heifers. Livst. Prod. Sci. 29:49-59.

Luiting, P. 1991. The value of feed consumption data for breeding in laying hens. Ph.D. thesis, Wageningen Agricultural University, The Netherlands.

Mrode, R. A. and B. W. Kennedy. 1993. Genetic variation in measures of food efficiency in pigs and their genetic relationships with growth rate and backfat. Anim. Prod. 56:225-232.

Nguyen, N. H., C. P. Mc Phee and C. M. Wade. 2005. Responses in residual feed intake in lines of Large White pigs selected for growth rate on restricted feeding (measured on *ad libitum* individual feeding). J. Anim. Breed. Genet. 122:264-270.

Nkrumah, J. D., J. A. Basarab, M. A. Price, E. K. Okine, A. Ammoura, S. Guercio, C. Hansen., C. Li, B. Benkel, B. Murdoch and S. S. Moore. 2004. Different measures of energetic efficiency and their phenotypic relationships with growth, feed intake and ultrasound, and carcass merit in Hybrid cattle. J. Anim. Sci. 82:2451-2459.

Nkrumah, J. D., J. A. Basarab, Z. Wang, C. Li, M. A. Price, E. K. Okine, D. H. Crews and S. S. Moore. 2007. Genetic and phenotypic relationships of feed intake and measures of efficiency with growth and carcass merit of beef cattle. J. Anim. Sci. 85:2711-2720.

Ollivier, L., R. Gueblez, A. J. Webb, H. A. M. Van der Steen. 1990. Breeding goals for nationally and internationally operating pig breeding organizations. Proc. 4th World Cong. Genet. App. Livest. Prod. 15:383-394.

Richardson, E. C., R. M. Herd, J. A. Archer, R. T. Woodgate and P. F. Arthur. 1998. Steers bred for improved net feed efficiency eat less for the same feedlot performance. Anim. Prod. Aust. 22:213-216.

Robinson, D. L. and V. H. Oddy. 2004. Genetic parameters for feed efficiency, fatness, muscle area and feeding behavior of feedlot finished beef cattle. Livest. Prod. Sci. 90:255-270.

Smith, W. C., M. Ellis, J. P. Chadwick and R. Laird. 1991. The influence of index selection for improved growth and carcass characteristics on appetite in a population of Large White pigs. Anim. Prod. 52:193-199.

Veerkamp, R. F. and G. C. Emmans. 1995. Sources of genetic variation in energetic efficiency of dairy cows. Livest. Prod. Sci. 44:87-97.

Von Flede, A., R. Roehe, H. Looft and E. Kalm. 1996. Genetic association between feed intake and feed intake behaviour at different stages of growth of group-housed boars. Livest. Prod. Sci. 47:11-22.

Webb, A. J. 1989 Genetics of feed intake in the pig. In: The voluntary food intake of pigs, British Soc. Anim. Prod. (occasional publication). 13:41-50.

Webb, A. J. and J. W. B. King. 1983. Selection for improved feed conversion ratio on *ad libitum* group feeding in pigs. Anim. Prod. 37:375-385.